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THE BIOLOGY OF THE FROG

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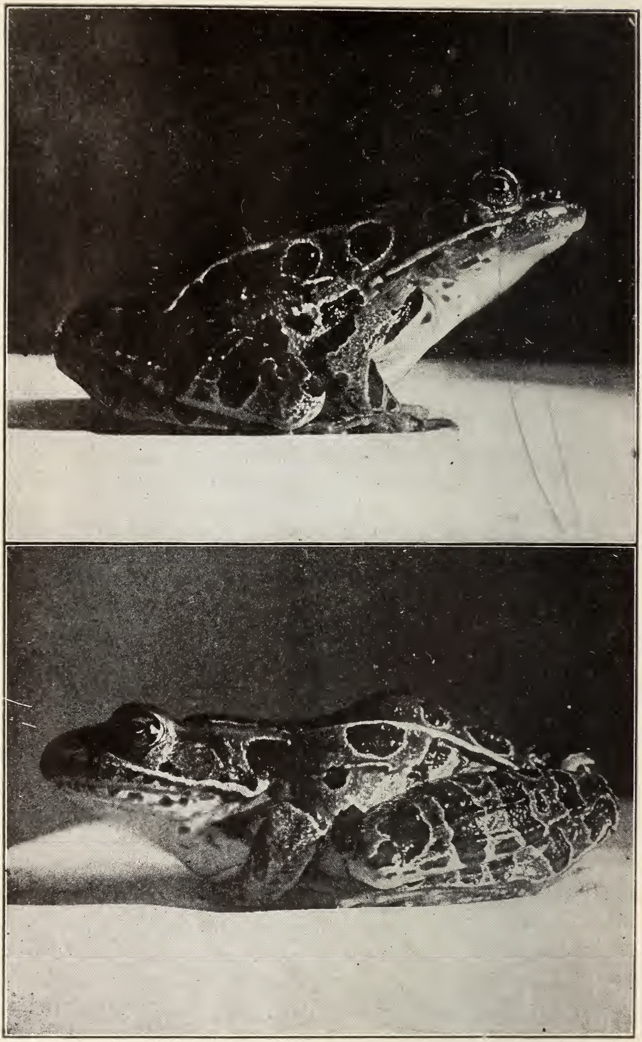

Rana pipiens. Upper figure, ordinary resting attitude; lower figure, crouching position. (From photographs by Mr. F. M. Abbott.)

THE
BIOLOGY OF THE FROG

BY

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OF CALIFORNIA

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PREFACE TO FIRST EDITION

The present book is the outgrowth of a course of lectures delivered during the past six years at the University of Michigan. This course with the accompanying laboratory work was based on the frog which was chosen as a convenient form with which to introduce students to a knowledge of the morphology, physiology, and life history of vertebrate animals. In writing this book I have had in mind the needs of students, such as most of those taking this course, who have had some preliminary work in general biology, but who have forgotten most of what little of the elements of physiology they may have learned in the schools. A certain amount of physiology of a more or less general nature has accordingly been introduced in addition to the descriptions of the special functions of the various organs of the body. The book is more suitable for use as a text in college or university classes than in high schools, although it is hoped that it will prove of service to teachers in high schools where the frog is studied in the course in zoölogy.

Considerable space has been devoted to describing the habits and natural history of the frog, and the endeavor has been made throughout the work to correlate the study of structure with that of the physiological functions of the body and the activities of the organism as a whole in relation to the environment. There is, I believe, a value in getting a fairly adequate idea of the whole life of any one organism which is not attained by the usual course of a study of types.

In preparing this work it has cost much deliberation in many cases to decide what material to include and what to reject, and probably several things have been omitted which it might have been desirable to have retained. The literature dealing with the frog is almost appalling in its extent. Perhaps no animal, except man, has been the subject of so many scientific investigations. One seldom picks up a volume of a physiological journal without finding that the frog comes in for a share of attention in one or more articles. It indeed seems, as is often remarked, that the frog is especially designed as a subject for biological research. In fact, most of what is known in certain departments of physiology is derived from a study of this animal.

The anatomy of the frog has been most exhaustively treated in Gaupp's excellent revision of Ecker and Wiedersheim's "Anatomie des Frosches," and I am naturally under great obligations to this work. Most of the statements made in the present book regarding the anatomy of the frog, however, I have verified by personal observation. Much of the material dealing with the physiology and natural history of the frog is here brought together for the first time. Where not otherwise mentioned, the statements in this book are made with reference to the common leopard frog of North America, *Rana pipiens*, except in cases where they may be understood to apply equally well to any species of the genus.

I am indebted to Professor Jacob Reighard for several suggestions and criticisms in connection with the preparation of this work; to Dr. W. P. Lombard for reading and criticising several of the chapters dealing with the physiology of the frog; and to Dr. J. E. Duerden for generously undertaking the labor of critically reading the whole of the manuscript before it went to press. To Dr. Ernst Gaupp and his publisher, Friedrich Vieweg, I wish to express my thanks for their permission to reproduce several of the figures in Gaupp's revision of Ecker and Wiedersheim's "Anatomie des Frosches."

PREFACE TO FOURTH REVISED EDITION

It is now twenty-one years since the issue of the first edition of *The Biology of the Frog.* After this lapse of time a book dealing with any of the rapidly advancing fields of biology begins to exhibit the infirmities of age. Since 1906 a good deal has been learned in several of the provinces of biological science to which the frog is accustomed to make contributions. Besides, a few of the things which it was thought were known when the first edition of this work was written are now found to be not quite as stated, if not positively erroneous. There have been, of course, changes in the scientific names of a number of the species. With the aid of my colleague, Dr. C. L. Camp, an attempt has been made to bring the generic and specific names into harmony with present usage among specialists in the systematic zoölogy of the Amphibia.

The continued use of *The Biology of the Frog,* despite the fact that parts of it were getting out of date, prompted me to undertake a thorough revision of the book. Although relatively little modification was necessitated in the sections on morphology, many changes have been made in the discussion of other topics, especially those dealing with physiology. The chapter on internal secretion has been made over twice its previous length on account of the remarkable discoveries of the past two decades in the field of endocrinology. Several new figures have been added and some of the old ones have been replaced by better substitutes. It is hoped that after these efforts to adjust the volume to its changing environment it will prove more useful than its predecessor to teachers and students of biology.

S. J. H.

University of California,
Berkeley, California, 1927.

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THE BIOLOGY OF THE FROG

CHAPTER I

THE AMPHIBIA IN GENERAL AND FROGS IN PARTICULAR

For a long time the frog has been a favorite object for the study of animal structure and function. Probably no species except man has been the subject of so many investigations. Whenever a physiologist plans to undertake a piece of research his first impulse is to pounce upon the poor frog. A mere list of the articles written about this well known animal would fill a volume larger than the present one. Doubtless the fact that frogs are usually easy to obtain is one reason why they have been so extensively studied. Then they are nice clean animals, easy to dissect and admirably adapted for physiological experimentation. The biological sciences owe much to the peculiar virtues of these humble creatures.

To the student of fundamental life processes it is a matter of secondary importance whether he devotes his attention to an Amœba, a bean plant, a frog or a man. If we had a profound and exhaustive knowledge of any one organism we should know most of the fundamental secrets of life in every form. Different species have their peculiar advantages for the investigation of this or that problem. But for a large part of the problems with which a biologist deals, the choice of a form for study is determined by such considerations as convenience and availability.

The circumstances which have made the frog a popular object of investigation have also caused it to be widely used in instruction. For anyone entering upon the study of biology there are several advantages in selecting an animal whose structure is more or less similar to that of the human body. No student can get very far in becoming acquainted with the anatomy of the frog without coming to realize that frogs and human beings exhibit numerous similarities of organization which the uninitiated observer would never have suspected.

THE FROG'S PLACE IN NATURE

Both frogs and human beings belong to that large subdivision of the animal kingdom known as the Vertebrata, a group characterized, as the name implies, by the possession of a vertebral column, or backbone. The term backbone, however, is sometimes a misnomer, since in the primitive fishes and their still simpler relatives the vertebral column is not bony, but cartilaginous. The vertebræ in all vertebrates are formed around a rod-like structure called the notochord. This organ is no longer found in the adult stage of the higher vertebrates, but it always appears in the embryo and forms the first rudiment of the spinal column.

In all vertebrate animals the brain and spinal cord lie dorsal to the digestive canal, whereas in such typical invertebrates as the insects and crustaceans the nerve cord extends along the ventral side of the body. In the vertebrates the heart is ventral in position while in the invertebrates we have mentioned it is dorsal. All vertebrates also have red blood which circulates in well defined blood vessels, and there is a well developed coelom, or body cavity between the digestive canal and the body wall. The orientation of several of the chief organ systems of the vertebrate body is just the reverse of that found in typical invertebrates. This is why the French naturalist Saint Hilaire was led to compare a vertebrate with an invertebrate walking on its back.

The lowest classes of vertebrates, the cyclostomes (hag fishes, lampreys) and the fishes, are aquatic animals and breathe by means of gills. The three highest classes, the reptiles, birds and mammals, are usually terrestrial in habitat and breathe by means of lungs. The frog belongs to a class called the Batrachia, or Amphibia which is partly aquatic and partly terrestrial, and which contains both gill breathers and lung breathers. In many respects the Amphibia are intermediate between aquatic and terrestrial vertebrates. Some of the more primitive species live permanently in the water, and even those forms which are best adapted to live on dry land usually repair to the water to lay their eggs which develop into gill-breathing tadpoles.

The Amphibia as a class are typically furnished with four legs fitted for locomotion on dry land or on the bottom of ponds and streams. Unlike the fins of fishes which are provided with many rays, the legs of the Amphibia are of the five-fingered, or pentadactyl type characteristic of the higher classes of vertebrates. One or more of the digits may be absent in some species, but the general plan of the feet and limb bones is essentially like that of the leg of a reptile or mammal.

The skin in the Amphibia lacks the scales characteristic of the fishes and the reptiles, and is usually smooth and moist in adaptation to its important function as an organ of respiration. The heart has three chambers, i.e., a ventricle and two auricles, and there are paired aortic arches. One of the peculiarities which distinguish the Amphibia from the reptiles is the characteristic covering of the eggs. Among the Amphibia the eggs are surrounded by a jelly-like substance secreted by the walls of the oviduct. The eggs of reptiles are enclosed by a calcareous shell, and the embryo during development is provided with an amnion and an allantois, while in the Amphibia such embryonic membranes are not formed.

Most amphibians differ from reptiles in undergoing a metamorphosis, the eggs hatching into aquatic gill-breathing tadpoles. There are a few amphibians which dispense with a metamorphosis, but in most cases gills are developed in the embryo, although they may not be retained after the young emerge from the coverings of the egg.

Amphibians are confined to the torrid and temperate zones. In the temperate zone they hibernate during the winter, crawling into the mud or other sheltered localities out of the reach of frost. In higher latitudes, where on account of the extreme cold the ground becomes frozen in the winter to a depth of several feet, the Amphibia are absent, since they could not easily get into situations where they could escape being frozen.

The Amphibia may be divided primarily into the **Stegocephali,** or **Labyrinthodonts,** and the **Lissamphibia.** The former group consists exclusively of fossil forms which first appear in the Carboniferous era and extend into the Upper Triassic. The bodies of the Stegocephali were usually covered with scales and bony plates, and the skull was provided with numerous dermal bones. Some of these extinct animals were of very large size, and in many species the dentine of the teeth was folded in a very complicated manner,—a feature which caused the name Labyrinthodont to be given to the group.

The **Lissamphibia** lack the extensive dermal skeleton of their extinct predecessors. Their tooth structure is simple and they never attain large proportions. They are commonly divided into three orders which may be determined by the following key:—

Legs absent	*Apoda.*
Legs present.	
Tailed amphibians	*Urodela.*
Tailless amphibians	*Anura.*

THE APODA

The **Apoda,** or **Cœcilians,** are creatures of wormlike form, entirely devoid of limbs and limb girdles. The skin is smooth and thrown into transverse rings. In some forms small scales are found embedded in the integument. The eyes are small functionless rudiments buried beneath the skin. The Apoda are generally found in moist ground, in which they burrow, and they are confined to tropical or subtropical regions. No species occur in North America north of Mexico.

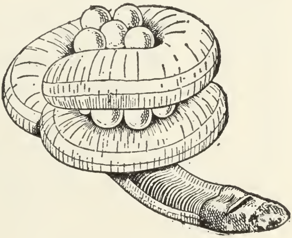

FIG. 1.—A legless amphibian, *Ichthyophis glutinosa,* female guarding her eggs. (From the Cambridge Natural History, after Sarasin.)

THE URODELA, OR TAILED AMPHIBIANS

The tailed amphibians occupy a more primitive position than the tailless forms. A large proportion of them live in the water, and some members of the group retain their gills in the adult state. The Urodela are divided by Gadow into four families as follows:—

Jaws without teeth. No hind limbs . . . . *Sirenidæ.*
Both jaws with teeth. Fore and hind limbs present.
  Gills persistent. No eyelids or maxillary bones *Proteidæ.*
  Gills usually absent in the adult. Maxillary bones present.
    Eyes with lids . . . . *Salamandridæ.*
    Eyes devoid of lids . . . . *Amphiumidæ.*

The **Proteidæ** constitute the most primitive of the Urodeles. At the sides of the neck there are three pairs of external gills. The species are aquatic in habit. There are only three genera, two of which, **Necturus** and **Typhlomolge,** are confined to North America. The remaining genus, **Proteus,** represented by a single species, *P. anguinus,* is found only in the caves of Austria. This species occurs in deep cool water in regions of complete darkness. Its eyes, like those of many cave animals, are rudimentary. Its color is nearly white, but if exposed to light its skin gradually turns dark and eventually may become nearly black.

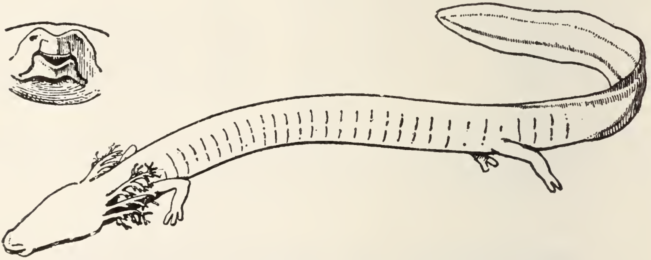

Fig. 2.—*Proteus anguinus.* Front view of the mouth in the upper left corner. (After Gadow, Cambridge Natural History.)

A cave salamander, *Typhlomolge rathbuni,* closely allied to Proteus, was found only a few years ago in Texas, where it was discovered in water thrown up from an artesian well.

The body of this species is slender and provided with a long, flattened tail. The legs are long and slender. The eyes, like those of Proteus, are rudimentary and buried beneath the skin. The most common representative of the Proteidæ are the "mud puppies" or "water dogs," which belong to the genus Necturus. *Necturus maculosus* is the most abundant species. It occurs in the northern and eastern part of the United States, west of the Alleghenies, and is especially abundant in the region of the Great Lakes. Its general color is brown above, marked with darker spots, and a dirty white or dusky color below. It has bushy red gills, which are kept moving back and forth at frequent intervals. Like most amphibians, it is most active at night; during the day it lies concealed out of the reach of light.

FIG. 3.—*Necturus maculosus.* (From Hegner.)

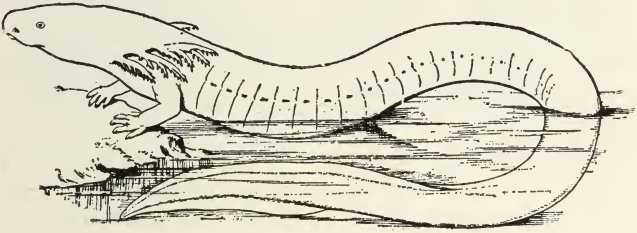

FIG. 4.—*Siren lacertina.* (From the Cambridge Natural History.)

The family **Sirenidæ** is represented by two genera, **Siren** and **Pseudobranchus,** both of which are confined to North America. Each genus contains but a single species. The larger of these, *Siren lacertina,* is found in the rivers and ponds of the Southern States, from Texas to North Carolina. The body is long and snakelike in appearance. The fore legs are very short and situated close behind the external gills; the feet are four-toed. There are three pairs of gill slits. The genus Pseudobranchus has only one pair of gill slits instead of three, and the feet possess but three toes. The single species, *P. striatus,* occurs in Georgia and Florida.

The **Amphiumidæ** include forms of quite diverse appearance, which are sometimes placed in distinct families. The genus Amphiuma is represented by a single species, *A. means* (Fig. 3), found in the Southern States of North America. The body is eel-like, with the very small legs situated far apart, near the two extremities. There is a single pair of gill slits behind the head, near the fore legs. The length of this species is often over two feet. The female lays her eggs in the latter part of the summer, and lies coiled about them in some protected spot, until they hatch.

The genera **Cryptobranchus** and **Megalobatrachus** are sometimes placed in a distinct family, the **Cryptobranchidæ.** The former is represented by the large "hellbender," *C. alleghaniensis,* of the eastern United States. This species may reach a length of twenty inches. Its body and head are much flattened, and the sides are bordered with curious fluted folds of skin. The eyes are relatively very small The hellbender is very sluggish in its habits, but it is, nevertheless, a very voracious eater. Its vitality, judging from an account by Mr. Frear,[1] is certainly remarkable. Mr. Frear tells of one specimen which had been picked up after it "had lain exposed to a summer sun for forty-eight hours." It was then brought into the museum and left a day before it was placed in alcohol. After it had been left in the alcohol "for at least twenty hours" it was taken out,

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[1] *Am. Nat.*, Vol. 16, 1882.

"when it began to open its big mouth, vigorously sway its tail to and fro, and give other undoubted signs of vitality." The giant salamander of Japan, *Megalobatrachus maximus*, is closely related to the preceding species. The largest specimens known exceed five feet in length.

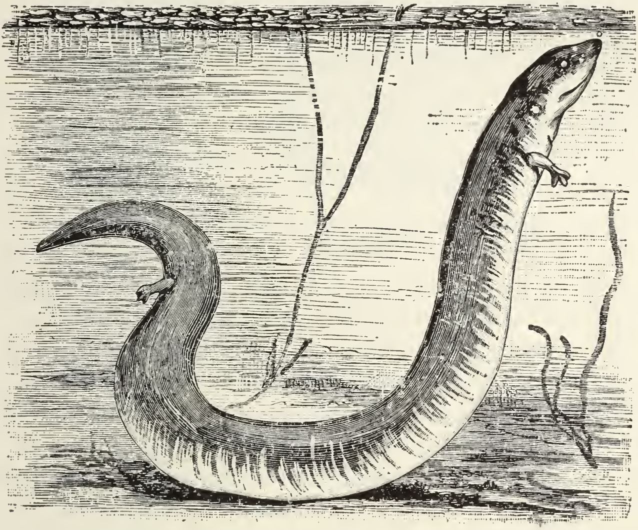

FIG. 5.—*Amphiuma means.* (From the Cambridge Natural History.)

The **Salamandridæ** form a large family, which is frequently divided into several different families by many writers. Only a few of the more noteworthy forms, therefore, will be described.

The group is divided by Gadow into four subfamilies as follows:—

A. Series of palatal teeth transverse or posteriorly converging.
  B. Parasphenoid without teeth. Vertebræ amphicœlous. Toes 4-5 . . . . . . *Amblystomatinæ.*

BB. Parasphenoid with teeth.
  C. Vertebræ opisthocœlous. Toes 5. Tongue largely free . . . . *Desmognathinæ.*
  CC. Vertebræ amphicœlous. Tongue small and largely free . . . . *Plethodontinæ.*
AA. Series of palatal teeth in two longitudinal series diverging behind. Parasphenoid toothless . . . . *Salamandrinæ.*

The subfamily **Amblystomatinæ** is represented in this country mainly by the two genera **Amblystoma** and **Chondrotus.** Amblystoma contains quite a large number of species. They are mostly of considerable size and frequently spotted in color. They are very retiring in their habits, and are not often seen except in the spring, when they go to the water to breed. Their eggs, which are surrounded by a very thick coat of jelly, are found in rounded or irregular masses attached to twigs or stems of grass.

The larvæ of *A. tigrinum* were formerly considered a separate species, the axolotl, which was placed in a distinct genus, Siredon, among the urodeles with permanent gills. Under certain conditions the external gills of this larva may be retained until after the breeding season, and this peculiarity led to its being mistaken for a normal adult form. It has been contended that the metamorphosis of the axolotls could be accelerated if they were forced to breathe air, but Professor Powers has shown that the factor of nutrition is probably the most important one, although others are influential, in producing this change, since it usually follows in sufficiently mature larvæ upon a sudden diminution of the food supply.

The **Desmognathinæ** include three genera, of which Desmognathus is the most common. It contains only three species, all of which are confined to the eastern part of the United States. The species live concealed in the daytime under stones or in sheltered nooks where the air is moist.

The female of *D. fuscus* lays her eggs in two long strings which she wraps around her body after having resorted to a suitable hiding place. Another representative of this subfamily is *Typhlotriton spelœus,* a blind species found in a cave in Missouri.

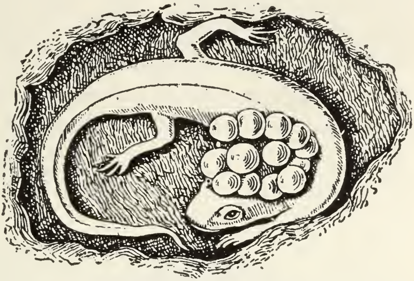

Fig. 6.—*Desmognathus fuscus.* Female with egg-mass. (After Wilder.)

The **Plethodontinæ** form a large group, which is mainly confined to America. The species of **Plethodon, Eurycea** and **Batrachoseps,** the more common genera, are mostly of small size. They are usually found in damp situations under rocks or decaying masses of wood. A California species, *Aneides lugubris,* has been found by Ritter [1] to have the peculiar habit of laying its eggs in holes high up in the branches of live-oak trees.

The **Salamandrinæ** are mainly found in the Old World. The well known fire salamander of Europe, *Salamandra maculosa,* reaches a length of from six to eight inches. The skin is smooth and shiny, and colored black except where marked with large irregular yellow spots. The conspicuous color of this species is frequently cited as an example of "warning coloration," since the glands of the skin secrete a substance which is very poisonous. By advertising its disagreeable qualities in this way the salamander is rendered free from the attacks of many animals which would otherwise unwittingly destroy it. Gadow tells of the dearly bought experience of two American bullfrogs that were kept in an inclosure with several salamanders. The next

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[1] Univ. of Calif. Publications. Zoölogy, Vol. 2, 1904.

morning after they were put in "the huge frogs were found dead, each having swallowed a salamander, which they were not acquainted with and had taken without suspicion." The poison of the salamander, which has been analyzed by Faust, is very different from that of the toad and has an especial affinity for the nervous system.

Salamandra atra is a shiny black species which lives high up in the Alps. The young are retained in the uterus until they attain an advanced stage of development. When they are born they have no external gills, as the young of the preceding species do, but these organs are nevertheless fully developed in the unborn larva, in which they attain a remarkable degree of development. The large size of the gills is doubtless dependent on the fact that they are worked in for the purpose of absorbing food.

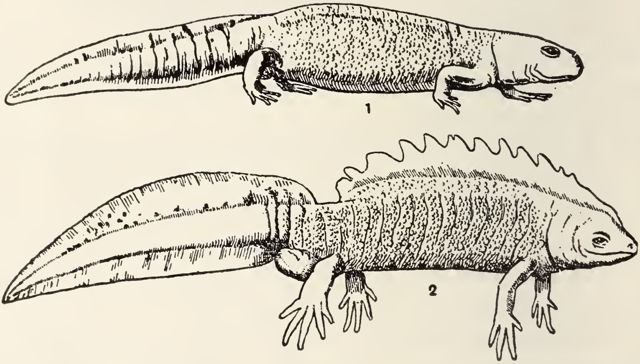

Fig. 7.—*Triton cristatus*. 1, female; 2, male as he appears during the breeding season. (After Gadow.)

The genus **Triton** is remarkable on account of the marked sexual dimorphism which occurs in several of the species, especially during the breeding season. The male of *T. cristatus* at this time possesses a high serrated crest above the head and body, and is marked with conspicuous colors. After the breeding season the dorsal crest becomes greatly reduced and the coloration becomes duller. The female has no crest and is not so conspicuously colored as the male, although she also becomes duller in color after the breeding period is past.

A close relative of the Tritons is the common newt (*Triturus viridescens*) of the northern and eastern parts of this country. It is a pretty species, being colored an olive-green, reddish or reddish brown above, orange or lemon-yellow below, and having a lateral row of scarlet spots, each surrounded by a black ring. A variety, *miniatus,* which has been described and which is characterized by possessing a vermilion red color, is said by Gage to be only an immature form of this species. Egg laying was found by Jordan to take place near Worcester, Massachusetts, from about April 10 to June. The eggs are laid in small nests attached to masses of vegetation, or wrapped within leaves of aquatic plants.

THE ANURA

The **Anura,** or **tailless Amphibia,** have a short, broad body, with well-developed hind legs fitted for jumping. They are divided by Gadow as follows:—

A. Tongue absent . . . . *Aglossa.*
AA. Tongue present (*Phaneroglossa*).
  B. Halves of the shoulder girdle overlapping in the middle line (*Arcifera*).
   C. Sacral diapophyses dilated.
    D. Terminal phalanges not claw shaped.
     Ribs present. Upper jaw with teeth . *Discoglossidæ.*
     No ribs. Upper jaw with teeth . . *Pelobatidæ.*
     No ribs. Both jaws without teeth . *Bufonidæ.*
    DD. Terminal phalanges claw shaped, usually supporting adhesive disks . . *Hylidæ.*

CC. Sacral diapophyses cylindrical . . .	*Cystignathidæ.*
BB. Halves of the shoulder girdle meeting in the middle line and forming a median bar (*Firmisternia*).	
C. Sacral diapophyses dilated	*Engystomatidæ.*
CC. Sacral diapophyses cylindrical . . .	*Ranidæ.*

The **Aglossa** include only a few aberrant forms characterized by the absence of a tongue and the fact that the Eustachian tubes open by a single median aperture in the posterior side of the palate. The most noteworthy member of this group is the peculiar Surinam toad, *Pipa americana,* from the northern part of South America. This creature has a most grotesque appearance. The back is broad and flattened, the head small, triangular, depressed, and furnished with irregular flaps near the lips; the eyes are small and have a round pupil. The most remarkable feature of the species is the mode in which the female carries the eggs and young. After the eggs are laid and fertilized, they be-

Fig. 8.—The Surinam toad, *Pipa americana.* (From Mivart.)

come pushed upon the back of the female, to which they adhere. The skin then grows up around the eggs, inclosing them in separate cavities which become entirely covered over. The tadpole stage is passed within these cavities. When the young Pipa is quite fully formed, it breaks out and makes its escape.

The **Discoglossidæ** are not represented by any American species. One of the most noteworthy of the European species of this family is the so-called obstetrical toad, *Alytes obstetricans.* In the breeding season the male clasps the female in the usual way, and when the egg strings are extruded, he tangles them around his hind legs and carries them about with him. When the young larvæ are about ready to escape, the male takes to the water and frees himself of the mass.

FIG. 9.—The obstetrical frog, *Alytes obstetricans;* male, with string of eggs. (From Sedgwick's Zoology, after Claus.)

The **Pelobatidæ** include but one American genus, **Scaphiopus.** These forms are commonly known as the spade-foot frogs, on account of the peculiar horny appendage which occurs on the inner side of the hind foot. This structure is employed in digging in the ground, where the animal is concealed during the day. *Scaphiopus holbrooki,* which is found in the southern and eastern parts of the United States, is very capricious in making its appearance. After rains in the spring or summer the spade-foot frogs come out in great numbers and lay their eggs, making a great clamor with their song. Then they disappear, and may not again show themselves for several years.[1]

[1] See Abbott, *Am. Nat.,* Vol. 16, and Hargitt, *Am. Nat.,* Vol. 22.

The **Bufonidæ,** or toads, comprise a large family which is found on all the continents of the globe. The principal genus is Bufo, which includes the best-known representatives of the family. The toads of this genus possess a very rough, warty skin, whose irregularities are caused by the large number of poison glands contained in it. These glands secrete a whitish, milky fluid of a very poisonous nature. Even a very small quantity of this substance when injected into the blood of a small animal soon produces fatal effects. The abundance of this secretion affords the toad very efficient protection, and not many animals have the hardihood to attack the creature. Faust[1] has isolated and analyzed two similar compounds from the poisonous secretion, bufonin and bufotalin. These are allied to digitalin and they produce similar effects. In weak doses they accelerate the action of the heart, but in larger quantities they act as a virulent heart poison. In addition to the poison, the skin secretes mucus, as in other amphibians, although not in great quantity.

Fig. 10.—*Bufo boreas.* (After Storer.)

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[1] Arch. exp. Pathol. Bd. 47, 49, 1902-3.

The color of toads, like that of frogs, may change under the influence of different external conditions. When exposed in a light-colored environment, the skin usually becomes lighter in color. In a dark environment it becomes darker, thus bringing about a certain adaptation of the color of the animal to that of its surroundings. This change is effected by means of changes in the pigment cells of the skin in the same manner as in the frog, which will be more fully described later.

Toads are nocturnal in habit. During the day they lie concealed under stones or in other damp, shady localities, venturing out only toward evening. They hop about like frogs, although with much less agility. On the other hand, they climb with considerable readiness. They feed upon earthworms, snails, and all sorts of insects. The latter are generally caught by suddenly throwing out the tongue and then withdrawing it along with the insect to which it adheres. Toads are very useful in destroying large numbers of injurious insects, and hence deserve all possible encouragement and protection. Kirkland[1] and Garman,[2] who have carefully examined the contents of the stomachs of a large number of toads, find that the variety of insects devoured is very great. Ants were the forms most commonly met with in the stomachs, and beetles, bugs, moths, and caterpillars were found by Garman to follow successively in order of frequency.

Toads keep within a certain locality for a long period. They have their particular holes or nooks, where they rest during the day and to which they return after their night's journey in search of food. Their sense of locality is apparently quite good, as is shown not only by the fact that they find their way home, but by their habitually visiting certain

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[1] Kirkland, Bull. No. 46, Mass. Agric. Exp. Sta.

[2] Garman, Bull. No. 91, Ky. Exp. Sta.

spots in the course of their nocturnal wanderings. The longevity of toads is somewhat uncertain. Boulenger kept one specimen for twelve years. There is a record of a specimen which lived to be thirty-six years old, and was then accidentally killed. Cases are recorded in which a toad has occupied a certain retreat for a longer period; but the identity of the individual is not assured. There are numerous stories of live toads found embedded in rocks or sealed up in trees; but usually they do not give evidence of sufficiently careful investigation to compel belief. Buckland[1] has shown that toads may live without food, when sealed up in blocks of limestone, for over a year; toads imprisoned in the limestone for two years were invariably found to be dead. We should be skeptical, therefore, about accepting stories about toads having been found alive in situations where they must have remained for a much longer time.

Toads hibernate under rocks, or in cavities in the ground, where they are protected from extreme cold. Often several toads may be found huddled together in one hiding place. Here they lie benumbed and almost stiff, although not actually frozen, until spring. Soon after their emergence from their winter sleep they usually betake themselves to water to deposit their eggs. The breeding period of *Bufo lentiginosus* in Massachusetts, according to Kirkland, is in April; in Ithaca, New York (Gage),[2] from the middle of April to May; in Ann Arbor, Michigan, I have found this species breeding in the latter part of April. The eggs are embedded in long strings of jelly which are usually found among vegetation near the shore. The males of *B. lentiginosus* are much smaller than the females. During the breeding season they frequently utter a peculiar shrill

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[1] Buckland, "Curiosities of Natural History."

[2] Gage, *Proc. Am. Ass. Adv. Sci.*, Vol. 47, 1898.

sound. After this period, according to Allen, the song changes to "a shorter, lower-toned note that, at night, has a peculiar weirdness, and reaches almost a wail. This note is heard mostly at evening and during the night, though I have occasionally heard it early in the morning and late in the afternoon." According to Courtis,[1] Miller,[2] and other observers the females are attracted by the sounds produced by the males.

When toads are handled, and often even when approached, they swell their bodies with air. Slonaker[3] tells of a toad which when approached by a snake would swell up and orient itself with its back toward the enemy. The inflation of the body makes it more difficult to retain hold of the creature, as any one may readily determine.

There are several species of toads in North America, but most of them are confined to the Western States.

The **Hylidæ,** or tree frogs, form an extensive and widely distributed family. The tips of the toes are furnished with small adhesive disks which enable the animal to climb up the trunks of trees. Many species are able to climb up a vertical surface of smooth glass. This is rendered possible not so much through the suction of the disks as by a sticky secretion which is produced by the glands of the skin at these points.

Male tree frogs are usually able to make a noise which is astonishingly loud for creatures of so small a size. In Hyla and its allies the vocal sac of the male is capable of great distension, and when fully inflated, becomes much larger than the head. The voice is heard most often in the breeding season, but it may also be heard during most of the summer, especially about dusk. The note of the tree frog

[1] *Am. Nat.*, Vol. 41, 677, 1907. [2] *Am. Nat.*, Vol. 43, 641, 1909.
[3] *Proc. Indiana Ac. Sci.*, 1900.

is often regarded as indicative of approaching rain. It is frequently heard immediately before a shower. The integument of the creature is easily affected by changes in moisture. Situations where the air is damp are always preferred, and it is not unnatural that their song should be heard when the atmosphere approaches the point of saturation.

A great many species of tree frogs have a remarkable power of changing their color under different external conditions. When among green leaves their color is usually green, but when on the bark of trees or on the ground their color may change to a brown or gray.

The North American species of this family north of Mexico and Texas fall into three genera. These are separated by Jordan by the following key:—

A. Disks small. Fingers not webbed. Palustrine.
  B. Toes broadly webbed. Tympanum indistinct . *Acris.*
  BB. Toes scarcely webbed. Tympanum distinct . *Pseudacris.*
AA. Disks round, conspicuous. Fingers somewhat webbed. Skin roughened. Arboreal . . *Hyla.*

Acris is represented by a single species, *A. gryllus*, the common "cricket frog," which is distributed over the greater part of the United States. Its typical color is brown or gray above. There is a dark triangular patch between the eyes, and the middle of back and head is bright green or reddish brown. Specimens from different regions show variations in color and there is a considerable power of color change in the individuals themselves. This species is usually found along the banks of ponds and swamps. Its note resembles that of a cricket.

Hyla is represented by over a hundred species, about twenty of which occur in North America. The species are mainly found in trees. *H. versicolor*, so-called on account of its remarkable change in color, is one of the most common and largest of the North American species, reaching a length of two inches. The eggs of this species are deposited singly or in small clusters on grass growing near the water's edge.

Many of the Hylidæ possess singular devices for carrying the eggs. In *Hyla goeldii* of Brazil the eggs are carried on the back of the female, the skin being produced into a fold which borders the egg mass. Nototrema, the "marsupial frog" of South America, has a large pouch opening near the posterior end of the back, in which the eggs are received, and where they undergo development as far as the tadpole stage.

Fig. 11.—*Hyla arenicolor.* (After Storer.)

The **Engystomatidæ** contain but one North American species, *Gastrophryne carolinense,* which is found in the Southern States, from South Carolina to Texas. The large family **Cystignathidæ** is represented on this continent by only three species, which are confined to Mexico and Florida.

The **Ranidæ,** or **true frogs,** comprise numerous genera, only one of which, the typical genus **Rana,** is found in North America. This genus contains over one hundred and fifty species, which occur in all of the continents of the globe, although they inhabit only the extreme northern parts of South America and Australia. There are seventeen North American species. Only a few of the better-known forms can be mentioned here. Full descriptions of the species may be found in Cope's "Batrachia of North America," and in Miss Dickerson's "Frog Book."

Rana catesbiana, the bullfrog.—This is by far the largest of North American species of Rana, and one of the largest of the genus. It attains a length of five to eight inches. It is widely distributed throughout the United States, east of the Rocky Mountains, from Mexico to Canada. The color of the upper surface varies from green to olive-brown, marked with small darker spots. The head is usually bright green, and the legs are marked with blotches of darker color. The tympanum or eardrum is very large, especially in the male. The toes of the hind feet are broadly webbed, the web extending to the tip of the fourth toe.

Fig. 12.—*Rana catesbiana*, the bullfrog.

This species rarely goes far from the water. It is usually found either partly immersed in the water or sitting on the bank of some pond or stream. It makes for the water very quickly when alarmed, and usually skims along the surface for several yards before diving below. According to Kalm, it may leap to a distance of three yards, but Abbot, who experimented with several specimens, found none that could jump quite seven feet. The males have a very loud, hoarse bass voice, which has been compared to the bellowing of a bull. When a number of them are croaking near by, the noise, as Kalm observes, is "so loud that two people talking by the side of a pond cannot understand each other. They croak all together; then stop a little, and begin again. It seems as if they had a captain among them; for when he begins to croak, all the others follow; and when he stops, the others are all silent. When this captain gives the signal for stopping, you hear a note like 'po-op!' coming from him. In daytime they seldom make any great noise, unless the sky is covered. But the night is their croaking time; and when all is calm, you may hear them, though you are near a mile and a half off."

Bullfrogs feed not only upon the creatures devoured by other species of frogs, but they frequently capture other animals which their smaller relatives are unable to swallow. They often devour full-grown specimens of other species of Rana, the young of ducks, and other water fowl, and even small chickens which venture too near their haunts.

The bullfrog requires two years to complete its metamorphosis. I have often captured its large tadpoles beneath the ice in midwinter.

A very closely allied species of bullfrog, *R. grylio,* has recently been described from Florida by Stejneger. It has somewhat longer toes and a darker color than *catesbiana,* and is said to have a quite different voice.

Rana clamitans.—This species has a nearly uniform green or brownish color above, marked only with small irregular black spots. The dermal plicæ are conspicuous. The hind legs are short and the web extends well out on the toes. The most conspicuous feature of this species is the very large tympanum, which in the male considerably exceeds the diameter of the eye. In the female the tympanum is considerably smaller, being about three fourths the diameter of the eye and "distant from the latter by nearly half its own diameter." This species is widely distributed from the Eastern States to Missouri and Minnesota and from Canada to Florida and Mississippi. It is closely confined to water like the bullfrog. It may reach a length of three inches.

Rana sylvatica, the wood frog.—Unlike the two preceding species, *R. sylvatica* is usually found in damp woods often far from water. It occasionally occurs at a considerable elevation, one specimen having been taken by Mr. Allen near the top of Mount Bartlett, New Hampshire, at an altitude of twenty-five hundred feet. This frog, says Mr. Allen, "is commonest in the damp beech woods and so closely resembles in color the dead beech leaves, that not infrequently, even after having seen one jump, it is with difficulty distinguished from the background. When frightened it takes prodigious leaps in an erratic course, and usually escapes into some hole or under a log. At night, while walking in a damp spot in the woods, I found numbers of them congregated in the path, where they had probably come to feed. . . . Rarely have I heard them utter a sound in the summer, though occasionally, when in the woods at night, I have detected their faint, rasping 'craw-aw-auk.'"

Rana pipiens, the leopard frog.—This is perhaps the most common of all the North American species of Rana. Its ground color is green marked with rather large black blotches edged with whitish. The legs are crossed above with black bars which may or may not be interrupted in the middle. There are usually two irregular rows of black spots on the back, between the prominent dermal plicæ; the lower side of the body is pale. The tympani are smaller than the eyes and there is no black ear patch. The vomerine teeth lie between the posterior nares. The legs are long, so that when the heel is brought forward it extends in front of the tip of the snout.

Cope distinguishes four varieties of this species, for a description of which the reader may be referred to this author's "Batrachia of North America."

Rana palustris, the pickerel frog.—This species resembles the preceding one. It is usually brownish in color, with two rows of large rectangular dark brown blotches between the dermal plicæ. There is a brown spot above each eye and a dark line between the eye and the nostril. The body is whitish below, but the lower side of the hind legs is yellow. External vocal sacs are absent.

This species is quite common in the eastern part of the United States. It is said by Cope to prefer "cold springs and streamlets, but is of all our frogs the most frequently seen in the grass."

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CHAPTER II

THE HABITS AND NATURAL HISTORY OF THE FROG

Habitat.—The habitat of *Rana pipiens,* like that of most species of frogs, is usually in or near the water. In damp or wet weather, however, this species frequently wanders for a considerable distance from its aquatic home. It is liable to be found almost anywhere near the shores of lakes, ponds, or streams in the wide territory over which it is distributed. Its range as given by Cope is from "Athabasca Lake, in the north, to Guatemala inclusive, in the south," and from the Atlantic coast to the Sierra Nevada Mountains. It has, therefore, the widest distribution of any of the North American species of Amphibia, although it is not known to occur on the Pacific slope.

That *Rana pipiens* is confined to the neighborhood of water depends in great measure on the fact that the skin must be kept moist in order that cutaneous respiration may take place. As soon as the integument becomes dry, as it quickly does if the frog is exposed to warm dry atmosphere, it is no longer capable of serving as an organ of respiration, and the animal soon perishes. The frog, unless it is among wet grass or weeds, or in a moist atmosphere, must remain where it can moisten the skin by an occasional plunge into the water. Another circumstance which serves to keep the frog in close proximity to water is the means thus afforded of escaping from enemies. Anyone who has walked along the margin of a pond or stream must have observed that when a frog is started up it almost invariably makes a jump for the water. In this way the creature has a ready mode of escaping, not only from man, but from a number of other enemies which might easily overtake it in a fair field. After its first plunge the frog usually swims some distance under the surface and then comes up, exposing only the tip of its snout above the water to get air. Frequently, if there is grass or weeds near the water's edge, the frog will swim a few strokes away from the shore and then turn back and quietly come to the surface among the vegetation, where its advent would usually not be suspected by the observer.

During the breeding season in the spring, frogs are more closely confined to the water than at other times of the year. In the summer they wander farther from the water in search of food. Different species vary greatly, however, in this respect. The wood frog, *Rana sylvatica,* is commonly found in woods miles away from any pond or stream. Most of the other North American species of Rana are more closely confined to an aquatic habitat. In Europe the water frog, *R. esculenta,* is decidedly aquatic in its habits, whereas other species, commonly spoken of as the grass frogs, scatter through the meadows and woodlands after the breeding season.

Food.—The food of frogs consists of earthworms, insects, spiders; in fact, of almost any kind of animal small enough to be seized and swallowed.[1] Large frogs have no sentimental scruples against devouring their smaller relatives. The large bullfrog is an especially dangerous enemy to other members of its genus. I have often found the stomach of this animal greatly distended from its having swallowed nearly full-grown specimens of *Rana pipiens.* Earthworms are a favorite article of diet; a hungry frog will devour several large worms one after the other, often

[1] Drake, C. J., The Food of *Rana pipiens. Ohio Nat.,* Vol. 41, 257, 1914.

seizing a new worm before having finished the one it is attempting to swallow. According to Fischer-Sigwart, *Rana fusca* will devour large May beetles, employing both fore limbs to push the rough legs of the insect into such a position that the prey can be forced down the throat, an operation which is accomplished only after considerable difficulty. The same observer found that *R. fusca* would devour large snails (*Helix hortensis* and *H. nemoralis*) after it had been accustomed to that form of diet by being fed with specimens from which the shell had been removed. After a short preliminary education the frog would catch the snails, of its own accord, and swallow them shells and all, one frog devouring six large specimens in succession. According to Fischer-Sigwart, this frog does not ordinarily devour snails although Dürigen reports *Rana muta* as swallowing specimens of Helix as well as species of mollusks devoid of shells. Bees and wasps are eaten with avidity notwithstanding their stings, which apparently affect the frog but little.

While the frog is a gourmand, he is nothing of an epicure. Almost any sort of living creature is acceptable to him, and even decayed meat when once seized is readily swallowed. Both taste and smell are apparently obtuse; if anything is taken into the mouth, it usually continues its course down the alimentary canal. Objects of a too objectionable nature may, however, be ejected.

In seizing food, the frog usually makes use of its extensile tongue, which can be thrown out of the mouth with surprising rapidity. The tongue is attached by its anterior end to the tip of the lower jaw, while the forked posterior end lies free. In the capture of prey the posterior end of the tongue is thrown forward until it comes in contact with the object, when it is quickly withdrawn. The sticky secretion with which the tongue is covered enables it to adhere to the objects it strikes against, so that they may be conveyed to the mouth.

The frog has an instinct to snap at small moving objects that come sufficiently near. This action is determined more by the motion and size of the objects than their form. Unless a thing is moving, the frog pays little attention to it. Frogs may often be caught by dangling small bits of red yarn before them on a hook. When the yarn is seized, the animal may be jerked out of the water. According to Knauer, frogs and toads have the power of ejecting indigestible bodies from the stomach by way of the mouth. Bits of grass or moss accidentally swallowed with the food are gotten rid of in this way.

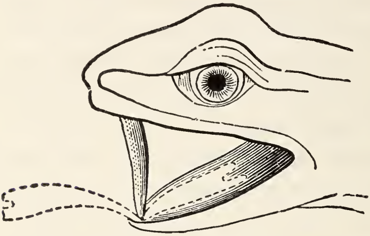
Fig. 13.—Figure showing the tongue of the frog in three different positions. (After Wiedersheim.)

Protrusion of the Tongue.—The frog is able to throw out its tongue with remarkable rapidity, but the method by which this feat is accomplished was, until recently, but inadequately understood. Hartog[1] and Gaupp[2] have found that the protrusion is brought about by the pressure of the lymph in the large sublingual lymph sac. This may be readily shown if we cut off the upper jaw of the frog and inject air or liquid through the mylohyoid muscle, which extends beneath the tongue. The lymph spaces become filled, and this causes the tongue to be raised up and thrown forward. "If," says Hartog, "we inject with melted cocoa butter colored with carmine or alkanet, and keep up the pressure until the mass sets, we find that it fills an enormous

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[1] Hartog, *Ann. Nat. Hist.*, May, (7), 7, 1901.
[2] Gaupp, *Anat. Anz.*, 19, 1901.

lymph sac between the muscle and the body of the hyoid, extending through the median intermuscular fissure into the tongue itself, sending branches between the fan-shaped ramification of the intrinsic muscles at the edges of the tongue and into its terminal dilatations." According to Hartog, the contraction of the mylohyoid muscle expels the lymph from the subhyoid space into the tongue and thus effects the protrusion of this organ.

Locomotion.—The locomotion of the frog is effected by leaping and swimming, and in both of these operations the long hind legs play the chief part. In the ordinary resting position the body is inclined upward in front, being supported on the fore legs, which are held in a peculiar twist so that the large thumb points nearly backward; the posterior part of the body rests upon the ground, and the hind limbs are folded up ready for a spring. No preliminary movements are required in order to get the animal in readiness for escape. By a sudden extension of the hind legs the body is propelled through the air. In leaping, the fore limbs are used more to hold up the anterior part of the body and to point the animal in the desired direction of movement than as actual organs for propulsion. If one causes a frog to leap in various directions, it will be observed that the body is adjusted before each leap in a new direction by the movements of the fore limbs. An ordinary specimen of *Rana pipiens* may leap from two to three feet. ✓

The movements of the hind legs in swimming are very much like those performed in jumping. In both operations the hind legs are alternately drawn up in the form of a Z and quickly extended. As they are pushed back, the toes are spread apart, and as the web between them affords a considerable resistance to passing through the water, this motion gives the body a forward impulse. The fore limbs are held back against the body, after the stroke, and if the frog does not make several strokes in quick succession, the hind limbs are held extended behind the body, so that the animal affords as little resistance as possible to gliding through the water. The fore limbs are also used in swimming, taking strokes sometimes together and sometimes alternately. To a certain extent they aid in propelling the animal forward, but they are also employed, as in locomotion on land, to guide the direction of movement. When the animal starts to swim downward, the fore legs beat backward and upward, the hand being twisted so as to press its broad surface against the water. This naturally pushes the anterior part of the body down. In starting to swim upward, the fore legs beat downward, elevating the anterior part of the body, which is then pushed upward by the strokes of the hind legs. The fore legs are also used in causing the body to move from side to side, and unequal movements of the hind legs are employed for the same purpose. Bendings of the body are also used to help steer the course of the animal. The hind legs usually make a stroke at the same instant, but the frog not infrequently uses them alternately, especially when struggling near an obstacle.

Attitude when Floating on the Surface.—When frogs are kept in water beyond their depth, they spend a considerable portion of their time at the surface with just the tip of the nose exposed, for the purpose of breathing air. The distance which the head projects from the water may be varied at will, as it depends upon the amount of air taken into the lungs. The more the lungs are inflated, the less the specific gravity of the animal becomes, and the higher, therefore, it rises in the water. When at the surface the frog usually lies quiet, hanging obliquely with the hind legs in a state of moderate extension. The fore legs generally are held out from the body. In such a position the frog may rest for a long time without performing any other movements besides those involved in respiration. The extended, sprawled-out attitude of the frog when resting at the surface contrasts markedly with its resting position on land, when its hind legs are closely doubled up and already set for a spring. One probable reason for the extension of the hind legs is that there is nothing to support them from below, and they would naturally hang down, when relaxed, from their own weight. However this may be, the extended condition of the hind limbs is of service in enabling the animal to suddenly draw itself downward whenever danger threatens from above.

Diving.—If a frog is approached when it is resting at the surface of the water, it will dive downward with great celerity and make several strokes, carrying it some distance away from its resting place. The action is performed so quickly that it is not easy at first to see how it is accomplished. At one moment the frog is resting in perfect quiet and at the next instant we perceive him making vigorous kicks and rapidly swimming away. By experimenting with frogs kept in a glass dish and concentrating our attention on one feature of their behavior at a time, we may gain an idea of the way this feat is accomplished. To swim downward through the water the animal has to reverse its position, as an extension of the hind legs in its normal resting attitude would tend to throw it out of the water. The first movement is that of withdrawal from the surface, which is accomplished by suddenly bringing the hind legs forward, thus giving the body a backward impulse. This brings the hind limbs up into a position for making the ordinary swimming stroke. Along with the withdrawal of the body from the surface the fore legs make a sudden stroke backward and upward, thus throwing the anterior end of the body down. Then the hind legs extend and shoot the animal farther downward through the water. The attitude of the body, as the frog rests at the surface, is one of preparation for the act of diving, just as its attitude on the ground is one of readiness for a spring. At the moment the frog leaves the surface, bubbles of air may generally be seen to escape from the nostrils.

Righting Movements.—Like most animals, the frog when placed upon its back will regain its normal position. It does so, too, with remarkable quickness, certainly in less than half a second. A frog will right itself a great many times in quick succession, and in course of time will become so fatigued that it will act slowly enough to give the observer a chance of following its movements. These movements, which involve the coördinated action of several muscles, vary a good deal in different acts, but they commonly occur in about the following way: If the frog rolls over toward its left side, the right hind leg is brought dorsally by a contraction of the muscles of the dorsal side of the thigh; the muscles of the ventral side of the left thigh also contract; both these movements tend to roll the body over to the left. The right hind leg is often brought forward so that the thigh lies at a considerable angle from the body, and this gives the limb a greater purchase in rolling the body over. The left fore leg is brought down alongside of the body, and the opposite member is thrown over to the left side, thus assisting the hind legs in the act of rotation.

The Voice.—The croaking of *Rana pipiens* may be represented, although rather inadequately, by the syllables "au-au-au-au-auk." The voice of the male is louder and deeper than that of the female and is more often heard. In large frogs the notes are deeper than in small ones. The notes of frogs are more often heard during the breeding season, when they are supposed to serve the purpose of a sex call. It has been denied that the female frogs are attracted by the sounds of the male, but it seems fairly well established that the females of tree frogs and toads are guided to the males by this means. In the summer, however, it is not unusual to hear the croaking of frogs, especially in the evening. A damp atmosphere is conducive to their song, and for this reason the voices of these animals are often heard upon the approach of a shower. The tree frogs seem to be especially sensitive to atmospheric changes, and the popular reputation which these creatures enjoy as prognosticators of the weather is not entirely unmerited.

The croaking of frogs is readily evoked by rubbing the back or side of the body. After each stroke the frog usually responds by a croak and then lapses into silence. Croaking is often caused through accidental contact with other individuals. Two frogs which were kept in a dish on my table were in the habit of croaking at frequent intervals, and I observed that each time the back or side of one frog was touched by the other, the individual would respond by a croak. If not disturbed, the frogs would remain silent indefinitely.

Frogs croak as well under water as on land. As the air is forced out of the lungs, past the vocal cords, into the mouth, the external nares are closed so as to prevent its escape. Then the buccal cavity contracts, forcing the air back into the lungs again; and the same process is repeated. If the head of the frog is held under water while the animal is croaking, it may be seen that the air is forced back and forth between the mouth and the lungs, while only a little, if any, is allowed to escape through the nares.

Under conditions which are particularly agreeable, frogs often give out a low grunting sound as if of contentment. On the other hand, when frogs are seized by a snake or other enemy or are severely injured, they sometimes utter a sort of cry which is called the pain scream.

Instincts for Protection.—When a frog is seized in the hands, it usually makes violent efforts to escape. If it is held by the anterior part of the body, the hind legs are used to push against one's hand with considerable force. At the same time the body is generally inflated with air, which enables it to slip away more readily from one's grasp. The sudden ejection of fluid from the bladder, which takes place when the frog is caught, may also be of occasional service in its attempts to get free.

Frogs sometimes swell the body before being seized as if in anticipation of their capture, and they are especially apt to do this after being lightly touched. Touch a frog that is resting quietly, and if the creature does not hop away, one may see the body puff up; and if the body is touched two or three times, the swelling will continue until the lungs contain their maximum amount of air. An animal such as a snake which was attempting to swallow a frog would find the operation somewhat more difficult if the body of its victim were strongly inflated. Frogs often avoid capture better by remaining perfectly quiet than by attempting to get away by jumping. Fear prompts the creatures now to the one and now to the other method of escape. Safety is also sought occasionally by crouching close to the ground, and more often by crawling under some object that promises to afford shelter.

Stimuli that irritate the surface of the body are gotten rid of in different ways. If the eye is touched, it is quickly drawn into the head and covered by the lower eyelid. Curiously enough, the same action is performed if the nose is touched or any part of the head near the eyes. Stimuli on the right side cause the right eye to wink, or if the stimulus is on the left side, the left eye responds. The fore foot is often brought forward to remove the stimulus, the foot on the side stimulated being always employed. Stimuli applied to the side of the body often cause the hind foot to be brought forward to the stimulated spot. There is also a twitching of the muscles of the side of the body near a stimulated spot which reminds one of the twitchings produced by the skin muscles of a horse. If the tip of the urostyle is irritated, the heels of both hind legs are brought up to that point. A frog may be caused to repeat these reactions many times, as a rule, but after a while it attempts to avoid further persecution by hopping away.

Seasonal Changes.—The frog undergoes an unusual amount of change in relation to the different periods of the year. One reason for this is the fact that it is a cold-blooded creature and cannot maintain itself in the same condition winter and summer, as is done, for instance, by man. A frog's condition changes markedly with reference to differences in temperature to which it adapts itself. Another reason for periodic changes is the ripening of the reproductive cells, which, especially in the female, makes extensive draughts upon the stored-up nutriment of the body. Then there are the changes correlated with the recurrence of the period of sexual activity, such as the development of the nuptial excrescences on the thumb of the male, the occurrence, in some species, of papillæ on the back and sides of the female, and the breeding instincts, which appear only at this time.

In the fall of the year the body is richly stored with nutriment accumulated during the summer while food is abundant. During the winter this material is employed not only in maintaining the temperature of the body and furnishing the energy necessary to carry on the various activities of the organs, but it is drawn upon to contribute to the growth of the reproductive cells. A part of this material is stored in the muscles, which during the winter decrease in weight in relation to the rest of the body. Gaule[1] found that in female frogs killed in July the gastrocnemius muscle weighed on the average 32.6 mg. for every gram of body weight. In August the ratio rose to 34.8. In December it sank to 26.1. In January it was 26.4, and in June, the laying period, 27.1. In the male the decrease in relative weight of the muscles is not nearly so great, as there is much less material to be employed in the development of the sexual products.

The liver undergoes marked seasonal changes which will be more fully described in connection with the account of that organ. In the winter it contains a large amount of glycogen, which almost entirely disappears by the end of the breeding season. Until early spring, however, the glycogen suffers comparatively little loss. The color of the liver also varies between winter and summer, owing probably to differences of nutrition. In winter there is an accumulation of pigment which gives the liver a dark appearance. In summer this pigment in most frogs largely disappears and the liver becomes lighter in color. The size of the cells varies, increasing through the summer, reaching its maximum in *Rana temporaria* in November, then decreasing through the winter and early spring, reaching the minimum in April (Leonard)[2] or May (Funke).[3] The size of the liver in relation to the rest of the body, according to Langendorff, Ploetz, and Funke, even increases during the winter months. At the close of the breeding season the minimum size is reached, after which there is a gradual increase during the summer. Apparently, therefore, there is either a growth of the liver during the winter at the expense of the rest

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[1] Gaule, *Arch. ges. Phys.* Bd. 81, 1900.

[2] Leonard, *Arch. Anat. u. Phys.*, phys. Abth. Suppl., 1881.

[3] Funke, *Denkschr., Wien Akad.* math. nat. Cl. Bd. 68, 1900.

of the body, or the various other organs decrease more rapidly than the liver in size.

The blood of the frog undergoes in the spring, after the animal has begun to take food, a rapid regeneration, a process which in higher animals takes place at all times of the year. There is a great increase in the number of blood corpuscles, both red and white. The marrow of the bones, where the new blood cells are mainly produced, shows in the spring a lymphoid structure, becoming more and more fatty toward fall, after the production of new blood cells has mainly ceased.

The changes in the fat body at different times of year have been studied by Ploetz and Funke, both of whom found in the two species studied (*Rana temporaria* and *Rana esculenta*) that this organ changed but little during the winter months, but suffered a marked diminution in size just before and during the breeding period in the late spring. After this there is a gradual increase in the size of the fat body until fall, when it reaches its maximum.

The advent of the breeding season is marked by great changes in the reproductive system, both in the gonads, or organs which produce the sex cells, and the various accessory organs. The variation in the size of the ovary before and after the discharge of the ripe ova is enormous. After the eggs are laid in the spring, the ovary shrivels to a small fraction of its previous dimensions. During the summer it increases in size, and in the fall it may fill most of the body cavity. The oviduct is also enlarged before and during the breeding season. The glands in its wall reach a high degree of development and secrete an enormous amount of a mucus-like substance around the eggs as they pass down the lumen. After the eggs are discharged, the glands diminish in size and activity, and the size of the whole duct is much reduced. There is a diminution in the size of the testes after the escape of the spermatozoa and then a gradual increase in size until mid-summer or fall.

Correlated with the ripening of the spermatozoa and the appearance of sexual instincts of the male frog there is an increased development of the base of the inner digit of the fore arm and an enlargement of certain muscles which are concerned in the clasping reflex. Both the inner digit and clasping muscles are larger in the breeding period than at other times, and it is probable that their increased development is dependent upon changes taking place in the sexual glands. Sometimes there are certain external characters developed in the female also during the breeding season. In the females of *Rana temporaria* Huber has described dermal papillæ which occur especially upon the back and sides of the body and the upper surface of the legs. On the back they are usually confined to the posterior half of the body, but on the sides they extend forward nearly to the tip of the nose. In the male the skin is entirely smooth or possesses in a few cases only very small papillæ. The color of these papillæ is a whitish or light rose, and they are rounded or cone-shaped in outline, and four to five millimeters in diameter. They are richly supplied with blood, but are entirely devoid of dark pigment. When sectioned they are shown to be due mainly to a thickening of the outer portion of the cutis and to be made up largely of connective tissue. The overlying epidermis is not noticeably thicker than it is elsewhere. Since these organs appear during the breeding season, it is probable that they have some function in relation to reproduction. If they do not directly serve to enable the male to retain his hold of the female, they may act as stimuli, causing him to clasp more tightly when he feels the female slipping from his grasp.

Color Changes.—One of the most remarkable adaptations of many kinds of frogs for concealment from their enemies, is the power of changing their color in harmony with their surroundings. The tree frogs possess this property in the highest degree. When these animals are among the green leaves of a tree, they assume a bright green color. When on the bark, their skin turns to a gray or brown. In both cases the color of the frog closely resembles that of the surroundings and serves to make its possessor difficult to distinguish. The value of such a power as a means of protection from enemies is obvious. No frog, however remarkable may be the changes in color it may undergo, is able to assume all shades and hues. Frogs possess the property of adapting themselves only to the predominant colors of their environment, which are green, the color of vegetation, and some shades of gray or brown, the usual color of the soil and the bark of trees. They cannot turn red or blue or violet, and, in fact, the power to do so would be of little value to them if they possessed it.

Rana pipiens, like most of the members of its genus, possesses a much lesser range of color variations than the tree frogs; nevertheless it can change its color to quite a marked degree. If in a dark environment, its skin becomes much darker; the black spots contain so much pigment that they remain unchanged under all conditions, but the lighter regions between them are subject to marked changes. Exposure to bright light gives the skin a much lighter color, the green and golden colors come out to a much greater extent, and the black pigment cells become less conspicuous. There is little doubt that power of color change in *Rana pipiens* is of service to the animal as a means of concealment. The frog is less conspicuous in a dark environment, when its skin assumes a darker hue, and when in the grass or weeds its green coloration serves the same purpose. The mechanism of color changes, and the various stimuli by means of which they are set up, will be treated of in the description of the skin.

Enemies.—As frogs are among the most defenseless of animals, they fall an easy prey to a variety of carnivorous creatures, who devour them in great numbers. First of these enemies in order of destructiveness is doubtless to be counted man, who, on account of his fondness for frogs' legs, to say nothing of his scientific curiosity, has almost exterminated some species in many localities. It is in the breeding period in the early spring that the destruction of frogs is greatest, since the animals then appear most abundantly and are most easily caught. They are devoured by water rats, mink, weasels and skunks. There are many birds which prey upon frogs, such as cranes, herons, hawks and crows; but their greatest enemies, next to man, are the various species of snakes, of which, according to Fischer-Sigwart, they have an intense instinctive fear. When in the water they may also fall a prey to the larger species of turtles. In Europe several fishes, such as the larger herring and trout, prey upon frogs; and smaller fishes are very destructive to the tadpoles.

To a certain extent frogs are preyed upon by other members of their own class. The large Cryptobranchus devours frogs, and even toads. I have several times found large bullfrogs with *Rana pipiens* in their stomachs, and it frequently happens that small individuals fall victims to larger members of their own species.

Among the invertebrates there are few species that actively prey upon the frog if we exclude those forms which are parasitic. Many aquatic bugs, such as Belostoma, Benacus, Zaitha, Ranatra, and even the small back-swimmers, Notonecta, catch the young tadpoles and suck out their blood. Water beetles, such as Dytiscus, and the stealthy larvæ of the dragon flies make use of the same source of food. Mortality among the tadpoles is naturally high, as they are preyed upon by many forms which are unable to cope with the adult frog. Water fowl, fishes, and aquatic insects prevent the great majority from reaching maturity; and the young frog is exposed to many dangers from which older and larger individuals are exempt. Probably only a few even of the adults are allowed to die of old age. The stomach of some larger animal forms the inevitable destination of all but a small per cent of the product of any brood.

The crayfish is often found devouring the dead bodies of frogs, and it is not improbable that occasionally it may capture an unwary specimen alive; but, for the most part, it probably makes use of frogs killed by some other means. Certain species of Glossiphonia (Clepsine), among the leeches, live upon frogs and turtles; but they do not require a very large quantity of food, since one meal may suffice to keep them alive for over a year. Like higher animals, frogs are attacked by mosquitoes, but it is uncertain how much inconvenience arises from this source.

Parasites.—The frog, like most of the higher animals, is afflicted by a large number of parasitic forms, belonging both to the animal and the vegetable kingdoms. The leeches mentioned in the previous section might almost be said to be parasitic, since they remain attached to the frog for a long period. The larvæ of blowflies (Calliphora, Lucilia) sometimes infest the intestine of frogs; but they usually prove a greater pest to toads. The female lays its eggs in the nostrils of the toad, and the larvæ feed upon the membranes of the nasal cavity, and may work their way into the brain and sometimes the eyes of their host. I have found no record of their occurrence in the nasal cavities of frogs, although it is not improbable that they are occasionally found there.

Of the several species of Nematodes (round worms) found in the frog, *Rhabdonema nigrovenosa,* which occurs in several European species, is, perhaps, the best known, since its life history presents several exceptional and interesting features. A kind of alternation of generations occurs in this species, there being a free form living outside the body, and a parasitic form which is usually found in the lungs. The latter is hermaphroditic, and produces eggs which give rise to rhabditiform embryos which pass into the alimentary canal and thence outside the body. These embryos develop into the free form, which consists of both males and females. The eggs produced by the female are fertilized and develop within her body. Here the embryos live and grow by devouring the internal organs of their mother, after which the young matricides make their escape into the water. When opportunity offers, they crawl into the lungs of a frog, and there develop into the parasitic hermaphroditic form. An allied species, according to Leidy, occurs in this country in the lungs of *Rana pipiens.*

Other nematodes (Strongylus, Nematoxys, and Oxysoma) are occasionally found in the intestine of frogs, and the ventricle of the heart and the blood vessels may be infested by species of Filaria. The hair worm, Gordius, occurs in the frog among other forms during a part of its larval life.

The Acanthocephali are represented by one species, (*Acanthocephalus ranæ = Echinorhynchus hæruca* Rud.) parasitic in the intestine of the frog. Another species, *A. lesiniformis* (Malin), has been described in an encysted state in the peritoneum.

Tapeworms (Cestodes) are rarely found in frogs. *Tænia dispar* Goeze, which occurs in the intestine of several European species of Rana, has been found by Leidy[1] in this country in the intestine of *Rana pipiens* and *Bufo lentiginosus.*

Frogs harbor several species of Trematodes, or flukes, which occur chiefly in the intestine and bladder, but they are sometimes found also in the lungs and other parts of the body. Loos[2] describes eight species of Distomum from frogs found in Europe and Stossich[3] mentions ten species of Distomum occurring in *Rana esculenta* and nine in *R. temporaria,* but some of these forms have been united by subsequent writers. Several species of Distomum are common to the frogs of both Europe and North America. The peculiar genus Polystomum, characterized by having a circle of several distinct suckers at the posterior end of the body, is often found in the urinary bladder of frogs.

Frogs harbor several species of protozoan parasites most of which are described or referred to in Wenyon's monumental work on Protozoology. Among the Infusoria one of the commonest species is the well known *Opalina ranarum* which is frequently found in the rectum. This species has a flattened, ciliated body and many small nuclei. Like the other members of the Opalinidæ, it has no mouth. At times it becomes enclosed in a cyst and it may be conveyed in this form from one host to another. Several genera and species of Opalinidæ occur in frogs and other amphibians in various parts of the world. The Opalinas differ so much from other

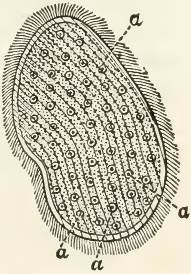

FIG. 14.—*Opalina ranarum; a, a,* nuclei. (From Hegner.)

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[1] Leidy, "Researches in Helminthology and Parasitology," Smithsonian Inst., 1904.

[2] Loos, "Die Distomen unserer Fische und Frösche, 1894.

[3] Stossich. "I Distomi degli Anfibi," 1889.

members of the Infusoria that some writers remove them from that class entirely. So far as known they do little damage to their hosts and should probably be regarded as commensals intsead of true parasites.

Of the parasites belonging unquestionably to the Infusoria there are several species of Balantidium. In the frog they appear to live upon the intestinal contents, although a species in man, *B. coli,* actively invades the tissues and becomes pathogenic. *Nyctotheres cordiformis,* a form related to the species of Balantidium, is a common parasite of the frog's rectum.

Of the flagellate Protozoa there are several species which infest the intestine. *Copromonas subtilis,* whose life history has been worked out by Dobell,[1] is frequently found in the rectum of frogs and in the fæces outside of the body. *Hexamita intestinalis,* which commonly occurs in the intestine, may invade the tissues and is sometimes found in the blood. Several species of trypanosomes occur in the blood of various kinds of frogs in which they may become strongly pathogenic. A common species, *T. rotatorum* (Mayer), is transmitted from one animal to another by a leech which preys upon tadpoles. The parasites multiply in the digestive canal of the leech and are conveyed to other tadpoles during the act of sucking blood.

A few parasitic rhizopods have been reported from the intestine of the frog; one of these, *Entamœba ranarum,* is allied to one of the amœboid organisms which attacks the human intestine. Another rhizopod, *Chlamydophrys ranarum,* which is often enclosed in a thin shell, occurs in the frog's intestine. Whether either of these parasites causes much damage to its host is not known. Other rhizopods

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[1] Dobell, "Researches on the Intestinal Protozoa of Frogs and Toads." *Quart. Jour. Mic. Sci.,* Vol. 53, 201. 1909.

have been observed in the frog, but little is known of their life history.

The largest number of protozoan parasites of the frog fall within the exclusively parasitic class of Sporozoa. The order Coccidiida is represented by two species of Eimeria, *E. ranarum* (Labbe) and *E. ranæ* Dobell, which infest the cells of the intestinal epithelium. *Isospora lieberkühni* is found chiefly in the cells of the kidney.

Of the blood infesting Sporozoa the curious parasite *Lankestrella minima* (= *Drepanidium ranarum*) occurs at first in the endothelial cells of the blood vessels and finally comes to live in the red blood corpuscles. These parasites may be conveyed from one frog to another by the bite of a leech. *Cytamœba bacterifera* and *Dactylosoma ranarum* also occur in the red corpuscles.

Leptotheca ohlmacheri, one of the Myxosporidia, has been reported in the tubules of the kidney both in European toads and frogs, and in *Rana clamitans* and *R. pipiens* in North America (Kudo).

Of plant parasites, there is a species of Saprolegnia which sometimes attacks the skin of *Rana pipiens,* and probably of other species of frogs. It forms large, light-colored blotches which may spread over a considerable part of the body. Necturus and other amphibians are liable to attacks from the same fungus. Eidam [1] has described a species of fungus, *Basidiobolus ranarum,* which inhabits the alimentary canal of *Rana esculenta* and *R. oxyrhina.*

Frogs have so many other parasites that they deserve to be relatively free from bacterial diseases, but they are at least not completely exempt. Lichtenstein [2] has reported a case of a frog whose liver was badly infected with tu-

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[1] Eidam, "Cohn's Beiträge zur Biologie der Pflanzen," Bd. 4, p. 181.

[2] Lichtenstein, *Zeit. f. Bakt. Parasit. Infektionskr.*, Orig. Bd. 85, 249, 1920.

bercle bacilli, and he succeeded in making a culture of these organisms which caused the development of tuberculosis when injected into other frogs. A fairly common bacterial infection which is often a source of trouble to raisers of frogs, is the disease known as red leg. This fatal malady causes a reddish color of the legs and under side of the body due to the congestion and hemorrhage of the cutaneous blood vessels. The animals often become bloated from the accumulation of fluid in the lymph spaces. Emerson and Norris[1] have made cultures of a bacterium (*Bacillus hydrophilus fuscus*) derived from infected animals, and have found that it produced red leg when injected into healthy frogs.

Times and Places of Breeding.—The breeding period of frogs is in the early spring, soon after the animals have emerged from their winter quarters. As in most amphibians, the eggs are laid in the water, usually among the vegetation near the shore, and receive no attention from the parents after they have been deposited. When the breeding season is over, the frogs scatter and resume an active predatory life. In exceptional cases, however, they have been known to resume for a time their winter sleep after the breeding season is over. At Dorpat, Marquis observed that in one year *Rana fusca,* immediately after the breeding season, crawled back into the mud and remained two weeks before again emerging.

The commencement of the breeding depends in a great measure upon the temperature. In general, a late spring delays the time of breeding, and warm weather, on the other hand, hastens it. The breeding period depends to a certain extent upon local conditions. In shallow ponds which are exposed to the sun, and where consequently the water becomes warmed early in the season, frogs breed much

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[1] *Jour. Exp. Med.*, Vol. 7, 32, 1905.

earlier than in water which on account of its depth or the lack of sunshine is heated only very slowly. In masses of water fed by cool springs the breeding of frogs and of other forms of life is much delayed.

The different species of frogs breed at different times, and the breeding period of a species naturally varies with the latitude, coming on later as we pass northward and earlier as we pass south. Thus *Rana temporaria,* whose breeding season in England and middle Europe is in March, does not breed until May in Norway, but in southern countries it may breed even as early as January.

Dr. Morgan[1] has recorded the results of four years' observations of several American species of frogs in the vicinity of Baltimore, Maryland. "The first frogs to lay, and among the very first (*Acris gryllus* excepted) to appear, are the wood frogs (*Rana sylvatica*). A few warm days in early spring suffice to bring them out. The following records give a general idea of the time. February 23, 1891, and March 8th, 9th, and 10th, 1880. The eggs of these had been laid several days. The egg bunches are found in small pools on the edges of weeds, generally among the low hills, and are often stuck to twigs of bushes. The bunches are generally large, four to six inches in diameter, and contain very many good-sized eggs. In the same pools it is quite usual to find the firmer egg bunches of Amblystoma, for this Urodele also lays its eggs very early.

"Somewhat later two species of tree frogs appear in the small pools in the woods, generally in quite small, and, therefore, during the day often quite warm, puddles; sometimes in the same pools as the wood frogs, oftener in the ditches by the side of the road. These two frogs are *Hyla pickeringii* and *Chorophilus triseriatus.*[2] The eggs of these

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[1] Morgan, *Am. Nat.,* Vol. 25.

[2] Now *Pseudacris triseriata.*

species are very similar, and I know of no certain method of distinguishing the one from the other. The bunches are small, attached to bits of grass, or lie simply on the bottom, and each bunch contains from five or six to fifteen or twenty eggs. I have the following record of the times at which the eggs were found: Hyla, March 9, 10, 13; April 5, 1890. Chorophilus, February 23, 1891; March 13 and 24, 1890.

"The eggs of *Rana halecina* are found still later, sometimes in the same localities as the wood frogs, oftener in pools in the open ground quite away from the woods. The following are the records: March 25, April 15, 1890. Eggs of *Bufo lentiginosus* were reported from the same region on April 14, 1890, and April 5 and 6, 1891."

Duration of the Breeding Period.—The duration of the breeding period, like the time of its first appearance, is very dependent upon external conditions, especially temperature. The period of copulation, or the time during which males may be found clasping the females, often considerably exceeds the period between the first and last deposition of eggs. This is due to the fact that the males seize the females often several days before the first eggs are laid. According to Fischer-Sigwart's observations of *Rana fusca,* the females may lay eggs, if the weather is warm, three days after the beginning of copulation; but in cold weather the laying may be deferred for twenty or thirty days. The duration of copulation in frogs kept in the terrarium was found to vary between six and twenty-three days. The less variability of the breeding period in this case is doubtless due to the more uniform conditions under which the animals are kept. The period between the appearance of the first egg mass and the time when all the females have extruded their eggs was found to vary in different localities, between four and twenty-seven days, according to the temperature; in the terrarium a variation between ten and twenty-eight days was observed. According to Pflüger, the laying period in *Rana esculenta* lasts only two days. It is quite probable that a single copulation extends through the whole breeding season. In *Rana fusca* Pflüger has observed that a male may clasp a female for several weeks, and in *Rana esculenta* the same observer has recorded an embrace which lasted a month. Steinach records a still longer period for *Rana fusca,* the pairs remaining united for as much as seven weeks. In these cases the weather was cool, otherwise the discharge of the sexual products would have occurred much more quickly.

Copulation.—In copulation the male clasps the female just behind her fore legs, where he hangs tightly and maintains his hold persistently against all efforts to dislodge him. Often the thumbs are interlocked to increase the firmness of his hold. The body of the female is very much compressed in consequence of this, but it apparently causes her little inconvenience. The labor of locomotion of the pair falls mainly upon the female, the male exerting himself only occasionally for the maintenance of equilibrium. With the exception of the effort necessary to enable him to retain his hold, the male during copulation is singularly inactive, and will endure very unfavorable conditions rather than make any effort to seek a better situation. Sometimes several males will be found clasping different parts of the body of one female, forming masses, "Begattungsklumpen," in the midst of which the female can scarcely be seen. Males will often clasp females which are dead, or females of another species, or even toads. The males of *Rana fusca* have been observed clasping carp and being carried around by the fish, which were unable to divest themselves of their burden. The eyes of many of these fishes are destroyed by the thumbs of the clasping frogs. Males will usually clasp one's finger, or almost any object they can seize, although they will not as a rule retain hold of objects other than female frogs for a very long time. The clasping instinct to a large extent overcomes fear. A frog which will make violent efforts to escape from the hands will often hold to one's finger and entirely desist from its efforts to escape during the period of copulation. The clasping instinct is so strong that the animal may be severely injured without showing any diminution of its ardor. The body of a male frog may even be cut in two in the middle and the fore part will still cling tenaciously to the female for hours, only desisting when the creature becomes so weak from loss of blood that it can no longer retain its position. Further data on the clasping reaction and the recognition of sex are given in the chapter on the nervous systems (p. 320).

Egg Laying and Fertilization.—The extrusion of eggs usually occurs only after the male has clasped the female for several days. The eggs, which are discharged from the ovaries rather slowly, are conveyed from the body cavity into the oviduct, through which they pass into the uteri, where they finally all collect, distending the thin walls of these organs to an enormous degree. As Spallanzani discovered long ago, females killed in the first part of the breeding season have most of the eggs still in the ovary. Later many eggs are found in their passage down the oviduct, although they are not often met with in the body cavity. Females killed near the end of their breeding period have nearly all the eggs in the uterus. At the beginning of the breeding period the seminal vesicles of the males are empty, or contain very little seminal fluid. Steinach found on examining a large number of copulating specimens of *Rana temporaria,* which he received March 5, 1893, that the seminal vesicles contained no traces of spermatozoa. Only on March 8 were the seminal vesicles in some specimens partly filled, and there were yet several males in which the vesicles were empty on March 9. Copulation may begin, therefore, several days before the sexual products of either sex are ready for discharge.

When the eggs are extruded through the cloaca of the female, the male discharges his spermatic fluid over them, and the spermatozoa penetrate the jelly around the eggs and complete the act of fertilization. The operation is somewhat similar to the fertilization of the eggs of most fishes, where the male who accompanies the female during the breeding period discharges his milt or sperm over the eggs at the moment when they are extruded. The clasping instinct of the male frog serves to insure the proximity of the two sexes when the proper moment for fertilizing the eggs arrives. When this time approaches the pair sink to the bottom of the water, where they remain quiet until the sexual products are discharged, when they separate. The male then loses his clasping instinct and is totally indifferent to the other sex. As a rule he fertilizes but one batch of eggs a year.

Fischer-Sigwart is of the opinion that all of the eggs are not generally fertilized at the time of their extrusion, but that many are fertilized later by other males, which are usually found among the masses of eggs in the breeding places. This observer has often seen males discharging their fluid over masses of eggs. The supernumerary males, therefore, play a part in fertilizing the eggs, as well as those which have succeeded in obtaining a mate.

What the stimulus is that prompts the male to discharge his sperm at the same time the eggs are extruded from the female is not altogether evident; the same problem presents itself in the case of fishes.

Congregating at Breeding Grounds.—During the breeding season frogs usually congregate at certain points in shallow water in considerable numbers. At this time there seems to be manifested a gregariousness which does not appear under ordinary circumstances, and which is not entirely accounted for by the tendency of the animals to seek a similar habitat for breeding. According to Fischer-Sigwart's observations on *Rana fusca,* if only a few pairs occur in any locality, they get as closely together as possible, and their egg masses form almost a continuous sheet. The laying grounds are the scenes of lively activity, "Alles hastet und drängt." The supernumerary males crawl over and work through the masses of eggs and, according to Fischer-Sigwart, effect the fertilization of the ova which may not have been reached by spermatozoa at the time of their discharge.

When the sexual products are discharged, the frogs go back upon the land and scatter in all directions. Most frogs leave the breeding grounds at nearly the same time. At one day a place may be teeming with these creatures, while on the following day not a single individual can be found. Henceforth the frog is a solitary animal, having lost all its sexual instincts and social proclivities. It leads its life as if no other member of its species were in existence.

Egg Laying without the Presence of the Male.—The question whether or not the female frog will lay eggs without the embrace of the male has been investigated by Nussbaum[1] in *Rana fusca.* Females were isolated soon after they came out from their winter quarters, when the eggs were still in the ovary. The eggs were found to leave the ovary, pass down the oviduct, and collect in the uterus as they do under normal conditions. They were not extruded from the uterus all at once, but were passed out slowly, a few at a time, some eggs often being retained until considerably after the breeding season. In a female killed late

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[1] *Arch. mik. Anat.,* Vol. 46, 1895.

in the summer one uterus was found to contain a large amount of jelly, but the eggs themselves had broken down and disappeared.

Egg laying in *Rana esculenta* is apparently more dependent upon external conditions. While *R. fusca* readily lays its eggs when in captivity, *esculenta* does so only if the eggs have accumulated in the uteri at the time of capture. When the females are taken earlier, the eggs that are in the ovary are not extruded, but are retained there until they are finally resorbed.

Proportions of the Sexes.—A male frog, as a rule, pairs with only one female during the breeding season, and it is advantageous to the species that the sexes should be nearly equal in numbers. This relation is, in fact, usually found to obtain among adult frogs. Born,[1] in studying the proportion of the sexes in young frogs, came to the conclusion that the females often greatly preponderate over the males. In one brood the females were found to constitute ninety-five per cent of the total number. Pflüger[2] and Griesheim,[3] who investigated the subject with considerable thoroughness, found that in young frogs it is often very difficult to distinguish the sexes. The gonads of the males frequently contain numerous egg follicles and have the general appearance of ovaries, and many frogs which would naturally be taken for females show only male characters at a later period of development. Estimates based on the appearance of the sex organs of frogs during the first year of their life gave a very large percentage of females. This percentage was found to vary greatly in lots of frogs taken at different localities. The degree of development of the sex organs does not closely correspond with the development of the

[1] Born, *Breslauer ärtzl. Zeitsch.*, 1881.
[2] Pflüger, *Arch. ges. Phys.*, Bd. 29, 1882.
[3] Griesheim, *Ibid.*, Bd. 26, 1881.

other parts of the body, and there is consequently a great variation in the appearance of these organs in specimens of the same age. As there is no evidence that the mortality of the young females greatly exceeds that of the young males, and as the proportion of the adults of the two sexes is nearly the same, it is probable that many of the young frogs which would ordinarily be diagnosed as females are "juvenile hermaphrodites" in which the female characters predominate for a time but which later develop into males. This conclusion is supported by the fact that there are many cases in which the sex glands are intermediate in appearance between ovaries and testes. Egg follicles are often found in the testes of frogs at a later period of development.

Witschi and Swingle have found that different local races have quite different sex ratios. In some races the differentiation of sex is distinct, and males and females occur in approximately equal numbers. In other races there is a longer indifferent period and the eventual determination of sex may depend upon external conditions. Frogs are creatures in which the distinctions of sex are apparently not so sharp as in most other organisms.

Copulation in Late Summer.—Fischer-Sigwart has observed that in July and August the sexual instinct of the males kept in terraria often asserts itself a second time, especially if they have been well fed and are in good condition. No sexual products are extruded at this time from either sex, although the males show a strong proclivity to clasp the female and will even clasp other males. A case is related of a male who observed a female which had seized an earthworm, and in attempting to share the morsel clambered over her back, when the clasping instinct suddenly took possession of him, and he remained clasping her body. Later in the season this clasping instinct disappears.

Hibernation.—In the late fall frogs betake themselves to water and bury themselves in the mud out of reach of frost. Here they lie in a dormant condition until the next spring. The general vital activities of the animal run down so low that little expenditure of energy is required to maintain life. There is need, therefore, for only a small amount of oxygen, and skin respiration then suffices. During the whole winter the frog does not breathe air with the lungs. The temperature of the body sinks until it is only a few degrees above that of the surrounding medium. As the frog takes no food during this time, it must keep up its vital activity at the expense of material stored in its tissues. Its temperature, even if only a little above that of its surroundings, requires the use of a certain amount of combustible material for its support. During the summer the frog feeds voraciously, and when cold weather ensues, its system is stored with a rich supply of food material which is gradually expended through the winter months. This food must keep the heart beating and support the various activities of the physiological machinery of the body. And in addition to supplying energy for this purpose, it must afford the substance for the growth of the sexual products, which increase during the winter at the expense of the other parts of the organism.

Life in Summer.—After the eggs are laid in the early spring, the frog leads an active predatory and solitary life. After its long winter sleep and the expenditure of substance and energy during the breeding season which closely follows the awakening in the spring, the frog is naturally in great need of food, and it becomes a very voracious feeder. During the early part of the summer it is busily engaged in the attempt to satisfy its hunger. In midsummer, when the body has compensated for its losses, the frog often betakes itself to a place of concealment, coming out only at intervals to obtain food. This period of comparative inactivity has been spoken of as a summer sleep, but according to Fischer-Sigwart a true summer sleep does not occur either in frogs or toads. There is only a period of comparative rest after the need for a large amount of food has ceased.

Injuries; Power of Regeneration.—As the frog is preyed upon by several enemies, specimens are often found in which fingers or toes, or sometimes the entire hand or foot, are missing. In most cases they are doubtless individuals which have had these parts bitten off and were fortunate that only a portion of their body was left in the possession of the enemy. Even severe wounds in the frog heal very readily. Fischer-Sigwart has observed that if a frog is wounded it betakes itself to the water, and if an individual keeps in the water during the summer, one may be pretty sure that it has received some injury.

The power of regeneration possessed by some of the lower amphibia is very marked. Triton is able to regenerate its tail or limbs, or even its eye, if a small portion of that organ is left. But in the frog, and, so far as is known, in the other Anura, the power of regeneration is almost entirely lost. Even in the tadpole stage it is much reduced. The tadpoles of the higher amphibia are able to regenerate the tail if it is cut off, but their power of regenerating the limbs is very limited. The regeneration of the limbs of tadpoles was first recorded by Spallanzani. Fraisse, however, who cut off the limbs from both young and old tadpoles, arrived at entirely negative results. Later Barfurth carried on several experiments on both old and young tadpoles, and found that if the legs were cut off from young specimens these organs would be frequently regenerated, although slowly. The power of the tadpole to regenerate missing limbs was found to decrease rapidly with age.

Effects of Heat and Cold.—The frog belongs among those animals which are commonly spoken of as cold-blooded. This expression doubtless takes its origin from the fact that the temperature of such forms is usually low. The higher vertebrates, such as the mammals and birds, have a high bodily temperature, and, what is most remarkable, the temperature in most of these keeps nearly constant under most diverse conditions. A bird or a mammal may live in extremes of climate below 40° and 50° below zero F. and considerably over 100° F., and yet the temperature of the blood will not vary more than a very small amount. These animals have an almost perfect mechanism for the regulation of the bodily heat. With a rise of temperature there is, in the mammals, an increase of perspiration and an increased evaporation from the surface of the body which tends to cool the blood. When the temperature sinks, there is less evaporation from the surface, and the cold acts indirectly as a stimulus to increase metabolism and causes the combustion of the bodily fuel to proceed at a more rapid rate and thereby to compensate for the loss of heat by radiation. By virtue of this mechanism the higher animals are able to keep in an active condition in both winter and summer. With the cold-blooded animals it is different. Their temperature rises and falls in correspondence with the temperature of their environment. In the cold their metabolism is slow, their temperature runs down, and consequently they become sluggish and inactive. As it becomes warmer, their temperature rises, their metabolism increases, and they become more active and alert. A lizard which is made almost stiff when the weather approaches the freezing point becomes the most agile of creatures in the sunshine of a hot day.

The temperature of the cold-blooded animals is not, however, entirely at the mercy of the environment. Evaporation from the surface of the body tends to keep the temperature of the animal in warm weather below that of the surrounding atmosphere. And as the weather approaches the freezing point, the small amount of metabolism in the animal serves to keep its temperature somewhat above that of its environment.

The effect of high temperature on the frog has been studied by Maurel and Lagriffe.[1] At 26° to 30° C. the frogs become active and restless. At 31° to 33° C. they show evident signs of discomfort. From 34° to 36° C. they jump about wildly without any apparent sense of direction. At a temperature of 37° to 39° C. they lose their sense of equilibrium, and if exposed to a temperature of 39° to 40° C. they die. If, however, they are exposed only for a short time at the latter temperature, they may subsequently recover, although they may at first appear as if dead. The cause of death is probably the coagulation of certain protein compounds in the blood and tissues.

Frogs have little power of withstanding extreme cold for the reason that they have no means of keeping their temperature very much above that of their surroundings, and their tissues consequently become frozen. On the other hand, they can withstand a reduction of their own bodily temperature far below the point which would be quickly fatal to any warm-blooded animal. They may be even frozen in ice for a short time and subsequently recover if gradually thawed out. Knauthe[2] found that frogs which were exposed to a temperature of from —1° to —5° C. for twelve hours became stiff and the limbs lost their pliability. The animals were then laid in wet moss and kept for several days slightly above the freezing point (.2° to .5° C.), under which condition they gradually came back to

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[1] Maurel and Lagriffe, *Comp. rend. Soc. Biol.* Paris, tom. 52, 1900.

[2] Knauthe, *Zool. Anz.*, Bd. 14.

activity. The bodily temperature of the frogs in the experiment sank to from —.2° to —.8° C. Examination of the web of the foot and the tongue revealed no signs of circulation of the blood, which seemed to be no longer in a fluid state.

The bodies of some specimens were cut open and the heart was found to have entirely stopped beating. According to Knauthe,—and other observers have obtained the same results,—if the tissues of the frog become entirely frozen, the animal will not recover. The bodily temperature cannot be lowered much below —1° C. without producing a fatal result. The animal may, perhaps, be frozen and then recover, but it cannot be frozen hard.

Müller-Erzbach[1] performed the experiment of placing the frog in a dish of water, which was gradually cooled off until it froze. As a film of ice began to form, the frog attempted to keep up at the surface of the water, but it was pushed down below and forced to remain there until frozen in a solid cake of ice. Here it was kept for five hours, while the surrounding temperature ranged from —6° to —8.7° C. When the ice was then thawed, the frog was stiff and showed no signs of life, but after an hour and a half it had revived.

Frogs from warm countries cannot endure so low a temperature as those from higher latitudes. But the frogs in northern regions are often killed by cold, especially during severe winters. If they are prevented from burying deep enough in the mud, the frost may overtake them. In some localities the frogs may be largely exterminated during a period of severe cold, so that few are found the next spring. In regions of high latitude, where the ground is permanently frozen below the surface, thawing out only for a few feet during the summer, frogs do not occur, since no means are

[1] Müller-Erzbach, *Zool. Anz.*, Bd. 14.

afforded to escape from being solidly frozen during the winter.

It was observed by Knauthe that the color of frogs exposed to the cold became very dark, even when they were placed in sunlight, which under normal conditions causes the skin to assume a lighter hue.

Absorption of Water. Frogs do not drink like the higher animals, but absorb the water they require through the skin. The meager and shriveled condition of a frog which has been kept some time in dry air contrasts markedly with its plump appearance after it has just been taken from the water. The skin is loosely attached to the body, and a considerable quantity of water may collect in the large subcutaneous lymph spaces. Donaldson found that a group of frogs after being kept in dry air for several hours lost 14 per cent of their weight. When placed back in the water again they regained very nearly their previous weight in twenty-four hours. Both the loss and absorption of water were found to take place more rapidly in the summer than in the winter. F. G. Hall placed *Rana pipiens* in very dry air and found that they lost 41 per cent of their total weight, but although they were apparently dead they revived upon being placed again in water. An experiment by Townson on a species of tree frog showed that a specimen weighing ninety-five grains increased in weight by seventy-six grains after being kept in the water for an hour.

Shedding of the Skin.—At certain periods the frog casts off its cuticle or outer layer of skin. The part shed consists merely of a very thin transparent membrane only one or two cells thick. This comes off in large patches which may be seen adhering to the animal here and there, the skin covering the toes usually coming off last. The first molt takes place in the spring at about the time of the breeding season. In *Rana fusca* Fischer-Sigwart found that after the first molt, which occurs from late in February to early in April, a second molt follows in the latter part of May or the first part of June, a third in July, and usually a fourth in August. In colder seasons the period of the molt comes later, and the fourth molt may then not occur. Five molts were not observed even during the warmest summers. Frogs often eat their shed skin after they have rubbed it off with the aid of their feet. The same habit has been observed in toads and in the large salamander, Cryptobranchus.

FIG. 15.—*Rana temporaria* in the so-called hypnotic state. The upper figure shows the position assumed when the back is rubbed with the finger. The same attitude is maintained when the frog is placed on its back, as is shown in the lower figure. (Modified from Verworn.)

Hypnotism.—A frog may be thrown into the so-called hypnotic state in several ways. If it is seized in the hands, laid upon its back, and held a few moments until it has ceased its struggles, it will usually remain motionless for a considerable time, sometimes for hours. The position taken is a variable one. There is a tendency to assume an attitude such as would be produced if the movements of the frog were checked sometime during its efforts to regain an upright position. According to Verworn,[1] the muscles involved in the righting movements are in a state of tonic contraction as if these movements were suddenly inhibited. The breathing movements and the heart beats are at first accel-

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[1] Verworn, "Die sogenannte Hypnose der Thiere," 1898.

erated, but at a later stage their rate falls below the normal (Heubel), and there is a decreased responsiveness to external stimuli. Different frogs vary greatly as regards both the ease with which they may be hypnotized, and the duration of the hypnotic state. In some cases if a frog is simply placed on its back without being held, it may become hypnotized after it has righted itself a few times, and lie for a long time in some phase of the process of turning over. Specimens of *Rana esculenta*, according to Verworn, when laid on their backs, sometimes quickly draw the hind legs close to the body, close their eyes, and lie with their muscles in a state of tonic contraction,—a condition which suggests the death feigning of certain insects.

Tonic contractions of different parts of the body may often be induced by rubbing the back and sides. If the frogs are in a normal resting position, they frequently raise themselves up on their legs and remain motionless and rigid for some time. If when in this state they are laid on their backs, the legs still retain the same attitude as before.

Frogs may be awakened from their state of hypnosis by any sudden stimulus, and their recovery is often immediate. The duration of this state may be much prolonged if all sensory impressions are so far as possible removed.

REFERENCES

See especially the works of Abbott, Allen, Boulenger, Brehm, Duméril et Bibron, Dickerson, Dürigen, Fischer-Sigwart, Hay, Gadow, Leydig, Rösel von Rosenhof, Spallanzani and Wright cited in the references to the preceding chapter.

CHAPTER III

EXTERNAL CHARACTERS OF THE FROG

It will be convenient to begin our study of the frog by a description of the principal external features of its structure. The flattened more or less triangular *head* is broadly united to the *trunk,* there being no region that can be properly called a neck. The large *eyes* commonly protrude considerably, but can be withdrawn into the orbits. Press upon one of the eyes with the fingers, and it will be found that it can be forced inward even beyond the general surface of the head. If now the mouth of the frog be opened, it will be seen that there is a marked prominence in the roof due to the fact that the eye is pressed against the membrane lining that portion of the cavity. The *orbit* or *eye socket* of the frog, therefore, is not separated from the mouth by any of the bones of the skull, which is a very different condition from what we find, for instance, in ourselves. In the center of the eye is a dark oval opening, the *pupil,* which is surrounded by a brightly colored ring, or *iris.* The eye, as in ourselves, can be covered by a pair of *eyelids.* The *upper eyelid,* however, is capable of but little movement, but the *lower lid,* which is thin and more or less transparent, can be drawn up so as to cover nearly the whole eye. It will be noticed that each time the frog closes its eyelids the eye is pressed into the head, a fact which gives the winking of the frog so peculiar an appearance. The lower lid of the frog is not quite the same organ as the lower eyelid of most animals. It corresponds rather to the lower eyelid proper, plus a *nictitating membrane.* The latter structure in most animals in which it occurs is very distinct from both the other eyelids. In a bird, for instance, it appears as a thin membrane which can be drawn over the eye from the inner angle of the orbit. In the frog, however, it is situated just above the lower lid, of which it appears to form a continuation. It is thinner and more transparent than the lower lid and separated from it by a shallow groove.

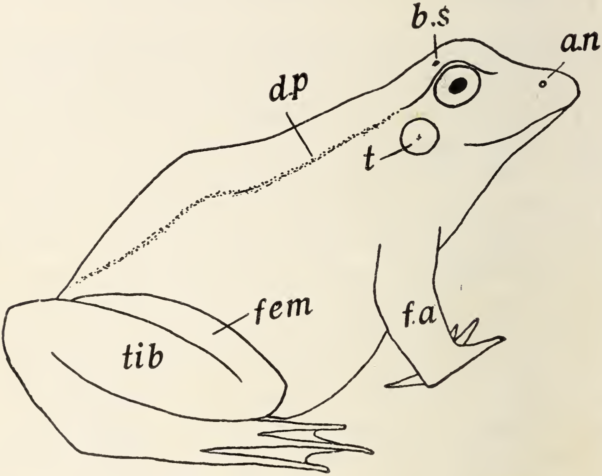

Fig. 16.—Outline of frog. *a.n.*, anterior nares; *b.s.*, brow spot; *d.p.*, dorsal plicæ; *f.a.*, fore arm; *fem.*, femur; *t.*, tympanum; *tib.*, tibia.

Behind the eye is a nearly circular area covered by a tense membrane, known as the *tympanic membrane,* which forms the covering of the *drum* of the ear. Near the center of this membrane may be seen a small prominence caused by the end of the *columella,* or bone which connects at its inner end with a small opening in the skull which communicates with the inner ear. When the tympanic membrane is set in motion by the waves of sound which strike it, the vibrations thus caused are communicated to the internal ear, and thus give rise to the sensation of hearing, as will be treated more in detail in a later chapter. On the inner side of the tympanic membrane lies a cavity, the *Eustachian tube,* which opens internally into the mouth. If a bristle be passed through this membrane, it will be seen to emerge through a rather large rounded opening near the angle of the jaw. The external features of the auditory organ of the frog differ markedly from those of man in that all traces of an external ear are absent, and the tympanic membrane lies exposed at the surface of the body instead of lying at the inner end of a long passage.

Above and behind the blunt tip of the snout lie the *nostrils* or *external nares.* These openings are guarded by *valves* which open and close in connection with the movements concerned in respiration. The tip of the upper jaw is slightly movable, and if it be pressed upward, the valves of the nostrils become closed, and prevent the passage of air through the nares. Pass a bristle through the nostril and it will be found to emerge into the mouth through one of a pair of rounded openings, the *internal nares,* situated somewhat behind the corresponding external openings. The *anus,* or opening of the *cloaca,* lies somewhat dorsal in position at the posterior end of the body.

On the upper side of the head, in front of the eyes, there usually occurs a small, light-colored mark, the *brow spot.* In some specimens this spot may be entirely concealed by pigment; but in most cases it may be detected, although it is often quite inconspicuous. The brow spot is a feature of considerable interest, from the fact that in the embryonic development of the frog it is connected with a peculiar outgrowth of the brain known as the *epiphysis* or *pineal gland.* When the outer or distal portion of this structure becomes constricted off, after the bones of the skull have developed, it is quite widely separated from the basal portion, which persists in connection with the brain even in the adult frog. The pineal gland is found in almost all vertebrates, including man, in whom it was given by the philosopher Descartes the important function of being the seat of the soul. It has been ascertained that this structure is a rudiment of a stalk which formerly connected with a median eye; in fact, there are certain reptiles (Hatteria) in which this eye is fairly well developed, containing a cornea, lens, retina, coats of pigment, and other structures characteristic of a well-developed visual organ; but in most vertebrates the eye no longer appears, or is represented by the merest rudiment. The connection of the pineal gland with the surface in the development of the frog, and the persistence of the brow spot marking the point of this former connection, are facts of considerable significance in relation to the evolution of this form.

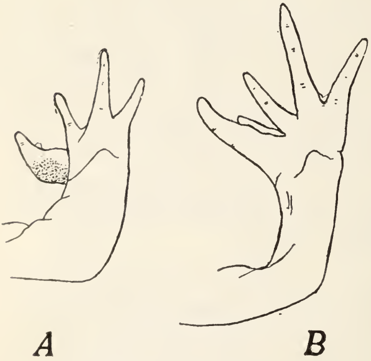

Fig. 17.—Hand and forearm of frog. *A*, male; *B*, female. (After Storer.)

The two pairs of legs are very different in form and in function. The *fore limbs* are short, and consist of three divisions, the *upper arm*, the *forearm*, and the *manus*, or hand. The hand has four fingers, and the rudiment of an additional digit on the inner side which can be felt under the skin. This rudiment corresponds to the thumb of our hands. The two inner digits contain three joints each, the two outer ones, four. There are no claws or nails on the digits of the frog in either pair of limbs. The fore limbs, when the animal is in a resting position, are held in a peculiar twist; the forearm, and to a greater extent the hand, are turned inward, so that the large inner finger often points backward. The fore limbs of the male frog differ in a peculiar manner from those of the female, being modified in relation to the clasping instinct of the male which appears at the breeding season. The forearm is relatively thicker than that of the female, owing to the greater muscular development of that portion of the limb. The inner finger of the hand also becomes much larger in the male and swollen at the base. The swelling is due mainly to a thickening of the glandular portion of the skin in this region, and becomes reduced in size when the breeding season is past.

The *hind limbs* are longer and admirably adapted for jumping and swimming, but are of little service in walking, as the frog can scarcely be said to employ this method of locomotion. Like the fore limbs, the hind limbs are divided into three parts: an upper portion or *thigh,* a middle part, *crus* or *shank,* and the *foot,* or *pes.* The latter is very well developed and has the ankle remarkably elongated; there are five toes and the rudiment of a sixth toe, termed the *prehallux,* which is situated on the inner side of the foot. The toes increase successively in length from the first, or inner one, to the fourth, the fifth toe being commonly a little shorter than the third. The first two toes contain three joints each, the third and fifth, four each, and the elongated fourth toe, five joints. On the under side of the articulations between the bones of the toes are small cushions termed *subarticular pads.* The toes are connected together by *web,* which serves to make the foot an efficient paddle as the animal swims through the water. The amount of web between the toes varies greatly in different species of frogs, and is a character which is therefore made use of for purposes of classification.

The ordinary resting position of the frog is a squatting posture, with the anterior part of the body elevated on the fore limbs, which are bent at the elbows and turned inward. Near the middle of the back is a sort of hump due to a bend at this place in the vertebral column. The hind limbs are folded together, the knees pointing outward and forward, and the ends of the ankles lying near each other at the hind end of body. In this position the frog is in readiness to leap, when alarmed, by the sudden extension of the hind legs.

The *skin* of the frog is almost everywhere smooth, with the exception of small scattered prominences occurring mainly on the back and on the dorsal side of the hind legs. Nothing corresponding to true hair or scales is to be found in the frog; in fact, with the rare exception of rudimentary scales in some forms, such structures are entirely absent from all of the recent Amphibia. The general looseness of the attachment of the skin is a feature which cannot fail to be noticed.

Behind the eyes there extend two, usually light-colored, ridges formed by a thickening of the skin, and known as the *dorso-lateral dermal plicæ* or *folds*. There are usually several smaller and somewhat irregular longitudinal folds of skin between these. The color of the skin is much darker on the upper or dorsal side than below, where it is usually white. In *Rana pipiens* the large black pigment spots which occur on the dorsal side of the body and legs are subject to much variation in size and shape. There is usually a pair of large spots between the eyes and a single median spot in front of these. The spots between the dorso-lateral folds show a tendency to arrange themselves in two rows. The spots on the hind legs are frequently elongated so as to form transverse bands. In addition to the black pigment there are green and golden colors, which are present in varying proportions. The changes in color which the skin may undergo under certain conditions will be discussed in a later chapter.

CHAPTER IV

PRELIMINARY ACCOUNT OF THE INTERNAL STRUCTURE

Mouth Cavity.—If the mouth of the frog is held widely open, the following parts will appear. In the *roof* of the mouth there is a pair of rounded prominences caused by the eyes, as has already been mentioned. Around the margin of the upper jaw is a row of fine, sharp, closely set *teeth* which are conical in shape and curved inward more or less at the tip. External to the teeth is a fleshy fold, or *upper lip,* and on the inner side is a groove, the *sulcus marginalis,* which receives the lower jaw when it is closed. Anteriorly this groove is crossed on each side by a low elevation, the *pulvinar rostrale;* immediately behind the tip of the jaw the sulcus is deepened again, forming the *median subrostral fossa;* on each side of the pulvinars are the *lateral subrostral fossæ,* which are mere deepenings of the sulcus marginalis. The lower jaw is entirely devoid of teeth and is held tightly pressed against the upper jaw, the mandibular muscles being normally in a state of tonic contraction; the tip of the lower jaw is flexible and is capable of being elevated or depressed independently of the rest of that structure, the joints of the movable part, *pars mentalis,* lying under the pulvinars of the upper jaw. The elevation at the extreme tip of the lower jaw (*tuberculum prelinguale*) fits into the median subrostral fossa, and there is a slight depression on either side of this tubercle corresponding to the pulvinars. The two jaws, therefore, fit together, part for part, with great nicety. In fact, they form an air-tight joint which, as we shall see later, is a necessary feature in relation to the peculiar mode of breathing which the frog is forced to employ. The tip of the upper jaw is likewise movable, its free portion corresponding in extent to that of the lower jaw, so that the two parts can be raised and lowered together. It may be noted that the elevation of the tip of the jaw effects the closure of the nares, a point of considerable importance in relation to the process of respiration.

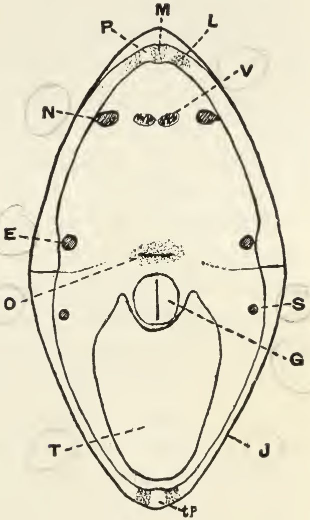

Fig. 18.—Mouth of the frog widely opened. *E*, Eustachian tubes; *G*, glottis; *J*, lower jaw; *L*, lateral subrostral fossa; *M*, median subrostral fossa; *N*, posterior nares; *O*, œsophagus; *P*, pulvinar rostrale; *S*, opening of the vocal sac; *T*, tongue; *tp*, tuberculum prelinguale; V, vomerine teeth.

If a bristle is passed into one of the anterior nares, it may be seen to emerge into the anterior portion of the mouth cavity by one of a pair of rounded or oval openings, the *choanæ*, or *posterior nares.* Between the choanæ is a pair of prominences which bear the *vomerine teeth.* At the posterior end of the buccal cavity near the angle of the jaw are the large openings, *Eustachian tubes,* which lead outward to the *tympanic membrane,* as may easily be demonstrated by means of a bristle. In the male frog another and a smaller pair of openings may be seen on the lower side of the buccal cavity, a little in front of the Eustachian tubes; these are the openings of the *vocal sacs,* and their continuity with these organs may be shown by passing a bristle into them or by inflating them by means of a blowpipe. Posteriorly the buccal cavity presents two openings in the middle line. The ventral opening, or *glottis,* is a narrow longitudinal slit in the middle of a prominence caused by the cartilages and muscles of the larynx; it is kept closed except during the passage of air into or out of the lungs. The dorsal opening marks the beginning of the *esophagus,* which leads to the stomach. Although capable of great distention, the esophagus is kept closed except when food is being swallowed.

The floor of the mouth is very distensible and undergoes continuous movement in respiration. In the middle part may be seen the *hyoid cartilage,* which gives attachment for the tongue and several muscles that move the floor of the mouth. The *tongue* of the frog is attached in front to the lower jaw and below to the hyoid cartilage. Its shape is subject to great variation according to the degree of contraction of its various muscles, but in its normal relaxed condition it is oblong, flattened, somewhat narrowed in front, and produced at its posterior angles into two lobes which extend backward on either side of the glottis; the posterior margin is concave, and the sides, which project over the attachment at the base, leave a considerable space of the floor of the mouth uncovered. In the mucous membrane covering the tongue there are numerous glands which secrete the mucus by which this organ is always covered. There is also a large number of *papillæ,* of which there are two kinds: the filiform, which are conical or threadlike in shape, and the fungiform, which are larger and less numerous than the former. The latter are narrow at the base and expanded at the distal end. In an average specimen of *R. fusca* Fixsen found two hundred and thirty-eight of these papillæ. In a specimen of *R. pipiens* I have found as many as six hundred and forty.

The tongue of the frog can be readily thrown out of the mouth, as it is in capturing an insect, and withdrawn again with great quickness. The sticky secretion with which it is covered causes it to adhere to insects or other prey with which it comes in contact. The victims are then drawn back into the mouth, where the tongue may assist in pushing them back into the throat, where they can be swallowed. The sticky substance on the frog's tongue is not produced by the mucous glands, but is derived, in part at least, if not entirely, from the *intermaxillary gland,* which lies above the anterior part of the roof of the mouth. This gland is partly inclosed by the premaxillary bones just in front of the nasal cavities. It really consists of an aggregate of several small glands (twenty to twenty-five in *Rana esculenta*), with as many independent ducts leading into the cavity of the mouth. Wiedersheim has shown that the secretion of these glands is remarkably adhesive.

The mouth cavity in general is lined by a mucous membrane which varies considerably in structure in different regions. Posteriorly it is thrown into folds which converge toward the esophagus. The epithelium which forms the superficial portion of this membrane is ciliated over a large part of the mouth, and there are numerous goblet cells scattered about among the others. The action of the cilia may be demonstrated in a live or recently killed frog by scattering powdered carmine over the roof of the mouth. The carmine grains will be seen to be carried very slowly backward, and eventually they will be drawn into the esophagus. The whole membrane of the mouth takes part to a greater or less extent in the production of mucus.

The Teeth.—The teeth of the frog are very numerous, but of small size and uniform structure. With the exception of the two patches of vomerine teeth, they are confined to the upper jaw. The jaw teeth rest against the dental processes of the maxillary and premaxillary bones, to which they are attached by cement substance. They are embedded in the mucous membrane of the mouth, beyond which they project only for a short distance. Each tooth is approximately cylindrical in form, tapering slightly toward the upper end, which is somewhat incurved. The basal portion of the tooth which is fastened to the jaw is called the root. Upon this rests the *crown,* which is separated from the root by a transverse furrow. In the center is a cavity filled with the *pulp,* which is a very vascular tissue in which the cells (*odontoblasts*) are situated that produce new material for the growth of the tooth. The greater portion of the crown is composed of substance called *dentine* which forms a hard calcareous wall, traversed by numerous fine branching canals which lead from the pulp cavity. The upper half of the crown is coated with a very hard, resistant layer of enamel which is considerably thickened over the tip. The enamel shows a stratified structure, but it does not contain the vertical prisms found in higher forms. Outside of the enamel there is a thin, resistant membrane, the *cuticula dentis.* The root of the tooth is composed of a substance resembling bone.

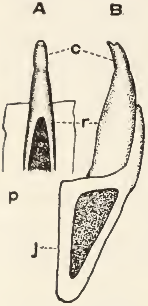

FIG. 19.—Teeth of the bull frog. *A*, view of inner face; *B*, lateral face; *c*, crown; *r*, root; *j*, section of lower jaw; *p*, pulp cavity.

The teeth of the frog are not used for mastication, but only for holding prey, which is the primitive function of teeth among vertebrate animals. There is a continual replacement of old teeth by new throughout most of the life of the animal, the process ceasing only in old individuals. The walls of the old teeth become partly absorbed by means of large multinucleate cells, the *osteoclasts;* in this way they become freed from their attachment to the jaw bone, and are then cast out. New teeth are producd below the old ones, whose place they finally take.

Organs in the Body Cavity.—If the ventral body wall of the frog be cut through and the cut edges be spread apart and pinned down, there will be opened up a large cavity containing the principal internal organs of the body. This space is called the body cavity, or *cœlom.* It lies ventral to the *vertebral column,* or backbone, which may be seen when the internal organs are pushed aside. If the middle part of the *pectoral girdle,* or bony support of the fore limbs, is cut away, the exposure of the parts will be made more complete. Near the anterior end of the body cavity lies the *heart,* not on the left side of the body, as in ourselves, but very nearly in the middle line. It is inclosed in a transparent sac, the *pericardium,* through which one may see the two *auricles,* which are thin-walled and appear dark red from the blood they contain, and a posterior cone-shaped division, the *ventricle,* which has a very thick muscular wall and is of a pink or light reddish color. The pericardium is united to the ventral body wall by a thin sheet of membrane, the posterior edge of which is free and incloses the *anterior abdominal vein,* which runs along the mid-ventral line and finally empties into the liver.

The *liver* is a large, reddish brown organ lying above and partially surrounding the pericardium; it consists of three lobes,—a median, a right, and a left. On the ventral side of the median lobe lies the *gall bladder,* which is connected with the intestine by means of the gall duct. Projecting into the body cavity from in front are two thin, very distensible sacs, with a reticulated appearance, the *lungs.* With a blowpipe they may be inflated from the glottis and swell enormously. When the air is expelled from them, they contract to a very small size.

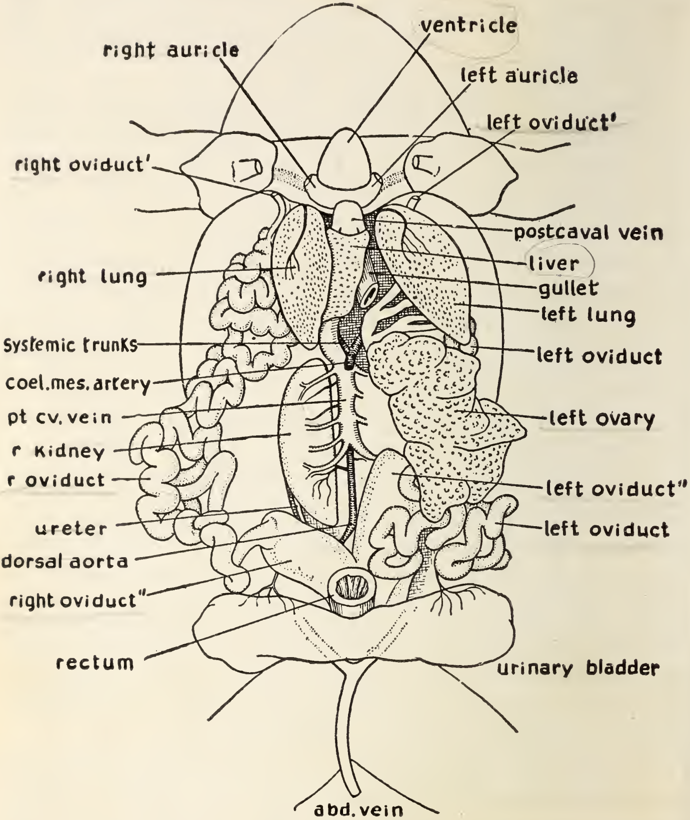

FIG. 20.—Organs of a female frog. The alimentary canal has been cut off at the gullet and rectum and most of the liver has been removed and the ventricle of the heart turned forwards. The abdominal vein has been cut and turned back. (From Newman, redrawn from Parker and Parker.)

The different parts of the alimentary canal vary considerably in size and texture. Above and projecting behind the liver is the *stomach,* a thick-walled, muscular organ which tapers toward the posterior end where the *pyloric constriction* marks its point of separation from the small intestine. Anteriorly the stomach is connected with the short *esophagus* leading from the posterior end of the buccal cavity. The *small intestine*, which proceeds from the pyloric end of the stomach, at first bends forward and runs nearly parallel with the stomach; this portion is called the *duodenum;* the portion behind this, or the *ileum,* curves abruptly backward, and, after forming several coils, suddenly widens out into the *large intestine.* The anterior portion of the large intestine is called the *rectum;* posteriorly it narrows into the *cloaca,* which passes above the ventral part of the pelvic girdle and terminates in the *anus,* or *vent.* Along its whole extent the alimentary canal is suspended from the mid-dorsal portion of the body cavity by a thin, transparent sheet of membrane, the *mesentery.*

In the U-shaped loop made by the stomach and intestine lies an elongated, light-colored organ of irregular shape, the *pancreas.* There is a dark red, rounded body, the *spleen,* attached to the mesentery near the anterior end of the large intestine.

The *reproductive organs,* or *gonads,* lie on either side of the alimentary canal and are supported from the dorsal body wall by special sheets of membrane like the mesentery. The gonads of the female, or *ovaries,* during the breeding season are greatly enlarged, and may be recognized by the small, globular, dark-colored eggs which form the greater part of their mass. External to the ovaries are the large, white convoluted tubes, the *oviducts.* These are also suspended to the dorsal body wall by thin sheets of membrane; they have no connection with the ovaries; anteriorly they open into the body cavity near the base of the lung by a wide funnel-shaped mouth into which the eggs find their way after they have been discharged into the cœlom. The walls of the oviducts are thick and glandular except toward the posterior end, where they become expanded into thin, very distensible sacs, the *uteri,* in which the eggs collect before being laid. The uteri open separately into the dorsal side of the cloaca.

The gonads of the male, or *testes,* are very different in size and appearance from the ovaries. Each testis is an ovoid, whitish organ, occupying a similar position to the

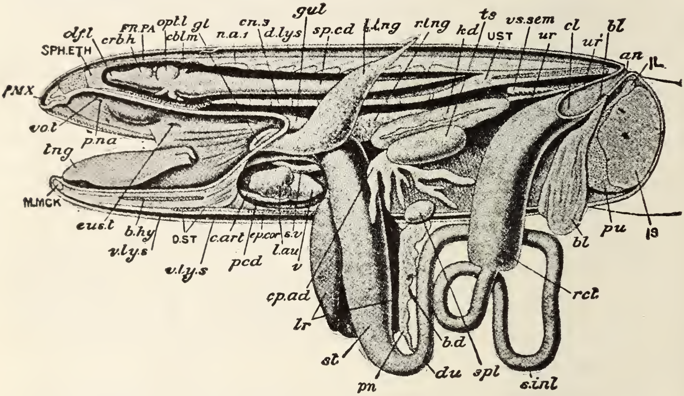

FIG. 21.—*Rana temporaria.* Dissection from the left side; the viscera somewhat displaced. *an*, anus; *b. d*, bile duct; *b. hy*, body of hyoid; *bl*, urinary bladder; *bl'*, its opening into cloaca; *c. art*, conus arteriosus; *cblm*, cerebellum; *cl*, cloaca; *cn. 3*, centrum of third vertebra; *cp. ad*, corpus adiposum; *crb. h*, cerebral hemisphere; *d. ly. s*, dorsal lymph sinus; *du*, duodenum; *ep. cor*, epicoracoid; *eus. t*, Eustachian tube; *FR. PA*, fronto-parietal; *gl*, glottis; *gul*, gullet; IL, ilium; IS, ischium; *kd*, kidney; *l. au*, left auricle; *l. lng*, left lung; *lr*, liver; M. MCK, mentomeckelian; *n. a. 1*, neural arch of first vertebra; *olf. l*, olfactory lobe; *opt. l*, optic lobe; O. ST, omo- and episternum; *pcd*, pericardium; *PMX*, premaxilla; *pn*, pancreas; *p. na*, posterior naris; *pu*, pubis; *rct*, rectum; *r. lng*, right lung; *s. int*, small intestine; *sp. cd*, spinal cord; SPH. ETH, sphenethmoid; *spl*, spleen; *st*, stomach; *s. v*, sinus venosus; *tng*, tongue; *ts*, testis; *ur*, ureter; *ur'*, its aperture into the cloaca; UST, urostyle; *v*, ventricle; *v. ly. s*, ventral lymph sinus; *vo. t*, vomerine teeth; *vs. sem*, vesicula seminalis.

ovary in the body cavity and suspended in a similar way by a membrane, the *mesorchium,* to the dorsal body wall. At the anterior end of both the ovaries and testes are attached the *fat bodies, corpora adiposa,* which are easily recognizable on account of their yellow color and their division into a number of finger-like lobes.

The *kidneys* are reddish, flattened, oblong organs lying against the dorsal body wall on either side of the vertebral column. Their position is somewhat behind the middle of the body cavity, and they are brought into view when the other abdominal viscera are removed or pushed aside. Each kidney is connected with a tube, the *ureter,* which runs along its outer edge and empties, near the opening of its fellow, into the dorsal side of the cloaca. In the male the ureters are expanded distally to form *seminal vesicles,* which in some species of frogs reach a considerable size. The *urinary bladder* is a large, bilobed sac lying in the posterior end of the body cavity, and opening into the ventral side of the cloaca just below the openings of the ureters. If the bladder is inflated by means of a blowpipe inserted into the cloaca, it will swell to a large size, and an accurate idea may be gained of its form and connections.

The walls of the body cavity and the various organs contained in it are covered by a thin, moist, glistening membrane, the *peritoneum.* This membrane is perfectly continuous throughout, and is simply reflected over the various organs. If we imagine that the body cavity were originally empty, and that the organs it contains were pushed into it from the outside, carrying the peritoneum in front of them, it will help us to understand the relation of this membrane to the structures it surrounds. It is not to be inferred, however, that these relations were brought about in just this way, but the device will be useful in enabling us to get the conditions clearly in mind. The alimentary canal, the liver, the lungs, the gonads, oviducts, bladder, fat bodies, and other organs are covered with peritoneum, which usually adheres closely to the surface. The mesenteries and the similar sheets of membrane supporting the ovaries, oviducts, and testes are double, as would naturally be the case if these organs were pushed in in the way mentioned. The peritoneum passes down from the body wall, covers these organs, then passes back to the body wall again, the two sheets of membrane coming close together except where they are separated by the organ they surround. The arteries and veins supplying the organs generally run between the two layers of the supporting membranes. The portion of the peritoneum surrounding the alimentary canal and its appendages is called the *visceral layer;* the part applied to the body wall, the *parietal layer.* For the most part the parietal layer is grown fast to the

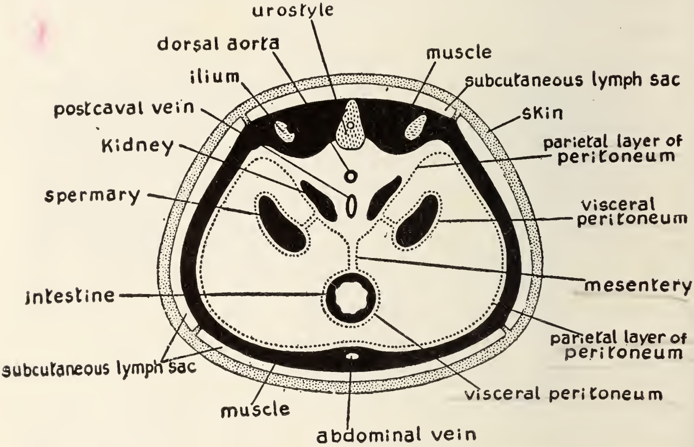

FIG. 22.—Diagram of a cross section of the body of a frog showing the course of the peritoneum by a dotted line. (After Parker and Parker.)

body muscles, but on the dorsal side of the body it is separated from the wall, forming a large *lymph space,* the *cisterna magna,* or *subvertebral lymph sinus.* The kidneys lie in this space; hence they are covered with peritoneum only on the ventral side, and not completely invested by it like the other viscera. The membrane previously mentioned, which extends between the ventral body wall and the pericardium and liver, is a portion of the peritoneum, forming a sort of ventral mesentery; it is reflected upon the ventral body wall on the one hand and spread out over the pericardium and liver on the other.

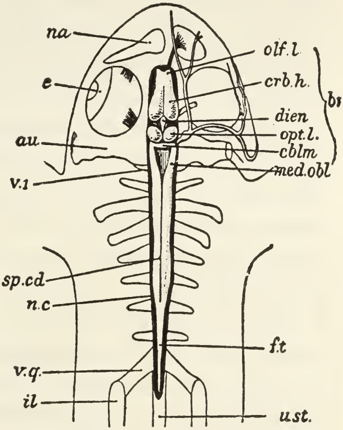

Fig. 23.—Organs in the neural cavity. The anterior part of this cavity contains the brain, which is composed of the olfactory lobes, *olf. l;* the cerebral hemispheres, *crb. h;* the diencephalon, *dien;* the optic lobes, *opt. l;* cerebellum, *cblm;* and medulla oblongata, *med. obl.* *n. c,* neural canal; *sp. cd,* spinal cord ending in the filum terminale, *f. t; e,* eye. (After Parker and Parker.)

The cœlom is filled with a transparent fluid, the *cœlomic* or *peritoneal fluid,* which is essentially the same as the lymph found in other portions of the body. Owing to the fluid in which they lie and the smoothness of their peritoneal coating, the organs in the body cavity are enabled to glide over each other with little friction.

Organs outside of the Body Cavity.—Above the cœlom there is a second cavity surrounded by the bones of the vertebral column and skull and containing the *central nervous system.* This *neural cavity,* as we may well call it, extends farther forward than the cœlom, and is separated from the latter by the bases, or centra of the vertebræ. The anterior portion of the central nervous system, or *brain,* lies in the skull, and is continued posteriorly as the *spinal cord,* which is inclosed within the vertebral column. If we make a cross section through the frog somewhere near the middle, we shall find that the body contains two longitudinal cavities separated by the centra of the vertebræ,— the cœlom below, and the neural tube above. Around both of these is a layer of muscles which is much thicker dorsally although it completely surrounds the cœlom below. And outside of the muscles, from which it is separated by large lymph spaces crossed by a few bands of connective tissue, is the skin.

With the exception of the loose attachment of the skin, all the features of structure mentioned in the last paragraph belong to the vertebrate animals in general. We have next to see how these fundamental features of structure came to be established.

CHAPTER V

THE DEVELOPMENT OF THE FROG

The frog, like all higher animals which are developed through sexual reproduction, begins its existence as a single cell, the *ovum* or *egg*. The eggs or ova arise in the ovary, and, when full grown, break out into the body cavity, where they float around freely until they are carried by the action of cilia into the funnel-shaped mouths of the oviducts. They are then carried down the oviducts by the action of cilia lining the walls and, during their passage, they become surrounded by a thick coating of gelatinous substance. From the oviduct they pass into the large, thin-walled uteri, where they remain until they are discharged into the water, where they are fertilized and undergo their development.

There is perhaps no phenomenon in nature more marvelous than the formation of a complex organism from a single and apparently simple cell. At the one end of the process we have a small mass of seemingly lifeless material with only the simplest visible features of structure, and at the other a creature with a complex organization composed of parts beautifully coadapted and working in harmony, with numerous instincts by which it adjusts itself to the various objects in its environment, and most remarkable of all, with volition and intelligence which, in the highest forms, may attain a high degree of development. The production of even the simplest animal seems almost a miracle, and our wonder is only increased the more we attempt to understand how and why the process takes place.

Many of the older writers who speculated on the problem of development were of the opinion that the egg contains in miniature all of the organs of the body in the same form and relation in which they occur in the adult, and that the parts simply expand as nutriment is absorbed until the embryo attains its maximum size. The process of development was compared to the unfolding of a flower from a bud in which the parts occur in the same relative position as in the expanded blossom and simply unfold through the absorption of sap until the flower reaches its final form. This view, which is known as *evolution,* or *preformation,* was championed by such men as Haller, Leibnitz, Bonnet, and Spallanzani; it really amounted to a denial of development. What appears to be such, according to this interpretation, is simply growth, the expansion of something preformed. The Abbé Spallanzani, who made extensive and most excellent studies on the breeding habits of Amphibians, considered the eggs of these animals to be small embryos of tadpoles whose parts through the influence of the spermatic fluid were stimulated to growth and activity. Other writers, among whom C. F. Wolff occupies the most prominent place, regarded the egg as a mass of simple unorganized material which becomes more and more complex as development proceeds. This doctrine, which is generally known as the theory of *epigenesis,* has become more widely accepted in recent times, although no one at present espouses either epigenesis or preformation in the forms advocated in the eighteenth century.

The cell theory, or the doctrine that animals and plants are composed of living units, or cells, which was promulgated by Schleiden and Schwann in 1839, did much to correct the extravagant forms of the older theories of preformation, and started investigators on the road to a truer conception of development. A farther step in advance was made when it was ascertained that the egg is a single cell. Not many years afterward it was discovered that the spermatozoön is likewise a single cell, and that in fertilization there is a union of the nuclei of the ovum and spermatozoön, each contributing an equal share of chromatin to the nucleus of the fertilized egg, and thence to all the cells of the body of the embryo. The whole aspect of the problem of development is very different from what it appeared to the older naturalists. However we may regard the modern forms of the doctrines of preformation and epigenesis,—for both points of view are still held,—it is certain that development actually proceeds from a single cell to a body consisting of a multitude of cells of great variety of form and function. This cell may be enormously complex, containing somehow features which represent all the different organs of the body, or it may be comparatively simple in structure, and the differentiations appearing in the embryo may be the results of the interactions of its parts and the influence of external conditions. Preformation and epigenesis both have their advocates, but their differences have become less wide as knowledge of embryology has advanced.

The Jelly and its Uses.—The egg of the frog when it is laid in the water is surrounded by a spherical mass of transparent jelly. At first the coat of jelly is less than the diameter of the egg in thickness, but through the absorption of water it gradually swells until it becomes two or three times this diameter. The jelly consists of three layers, a thin *inner layer* closely applied to the egg, a thick *middle layer* of more fluid consistency, and a thick *outer layer*. The coats under the microscope show a concentric series of fine lines, indicating the stratification of the material. The function of this jelly is primarily the protection of the eggs. It keeps them free from dirt, bacteria, and the spores of fungi, and also from the attacks of aquatic insects and snails, and various mechanical injuries which would otherwise affect them. Bernard and Bratuschek[1] consider that the jelly also serves to keep the eggs warmer than the surrounding water, which in the spring, when the eggs are laid, is often very cold, and frequently covered with ice. The jelly is supposed to act upon the principle of a hotbed, allowing free entrance to the sun's rays, but checking radiation from the egg. The heat waves that radiate from the eggs are longer, less refrangible, and pass through the jelly less readily than the shorter waves, which are abundant in the direct heat of the sun. Bernard and Bratuschek[2] found in experimenting upon the jelly that the greater the wave length, the less heat passed through in comparison with an equal amount of water under the same conditions. The jelly was thus shown to have the property required to keep the eggs warmer than the surrounding medium. The black pigment of the eggs which readily absorbs the heat rays also functions in the same manner.

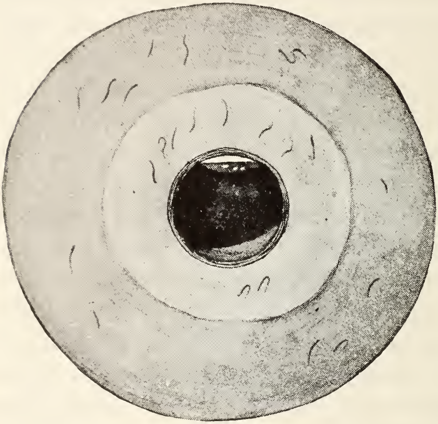

Fig. 24.—Egg in jelly. (After Schultze.)

Resistance of the Sexual Products to Cold.—The egg masses of the frog are laid so early in the spring that the water containing them is frequently frozen. Fischer-Sigwart

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[1] Bernard und Bratuschek, "Der Nutzen der Schleimhüllen für die Froscheier," *Biol. Centrlb.*, Bd. 11, 1891.

[2] *Ibid.*

records finding egg masses which were frozen solid for two days, during which the temperature sank to —8° C. When the eggs were gradually thawed out, they underwent a normal process of development, although somewhat slower than usual, and gave rise to larvæ which left the jelly two days afterward. How long eggs may be frozen and how low a temperature they can endure and still retain their power of development is not determined.

The spermatozoa of the frog may also be frozen without fatal results. The Abbé Spallanzani showed that spermatozoa frozen in ice for half an hour are able to cause eggs to develop, but if kept in ice for several hours, this power is lost. The spermatozoa apparently have less power of resistance to cold than the eggs; careful comparisons, however, have not yet been made.

Structure of the Undivided Egg.—The eggs of the frog as they occur in the body of the female after their discharge from the ovary are surrounded by a very thin *vitelline membrane,* which represents its cell wall. On one side, representing the *animal pole,* the egg is colored by black *pigment,* which, as is shown in sections, is mainly confined to the periphery immediately under the vitelline membrane. This pigment is in the form of minute granules embedded in the protoplasm. The *nucleus* of the egg lies excentrically near the middle of the dark pole. When the egg is in the ovary, the nucleus is large and contains a large amount of fluid known as *nuclear sap,* but just preceding the escape of the egg into the body cavity and during its passage down the oviduct the nucleus becomes shrunken through the exudation of its fluid, and undergoes a process of division involved in the formation of the *first polar body.* As Schultze has shown, along with the shrinkage of the nucleus there appears a mass of fluid beneath the animal pole which he considers to be the nuclear sap. The place is marked by a light-colored spot near the center of the dark cap. The great mass of the frog's egg is made up of *yolk,* which occurs in the form of granules embedded in the cytoplasm. The yolk is a semi-fluid nitrogenous substance which is employed for the nutrition of the developing embryo. It is more abundant toward the light-colored or vegetal pole of the egg, the region around the animal pole containing relatively more cytoplasm. The yolk granules are of various sizes, and are usually spherical or oval in form. By the action of certain reagents they may be broken up into flattened plates which, according to Schultze, do not exist as such in the living egg.

Maturation.—The process of maturation consists in two successive divisions of the ovum, resulting in the formation of the two polar bodies. These bodies are minute globules extruded at the animal pole of the egg. Morphologically they are cells, produced by very unequal divisions of the egg, which is only a cell of very large size. The first polar globule is given off while the egg is within the body, the preliminary steps of the process occurring just before the egg leaves the ovary. The large watery nucleus shrinks, the chromatin becomes aggregated into definite bodies, or chromosomes, a spindle forms at right angles to the surface of the egg, and half the chromatin, with a small amount of cytoplasm, is extruded as the first polar body.

In *Rana fusca* the second polar body is given off after the egg has been laid, and within half an hour after fertilization; no resting stage of the nucleus intervenes between the two maturation divisions. The two polar bodies in *Rana fusca* are of about equal size, and are either attached to the animal pole or float in the fluid which accumulates between the egg and the vitelline membrane. If the jelly is removed from a freshly laid egg, and the light spot, or fovea, at the animal pole observed with a hand lens, the extrusion of the second polar body may be witnessed.

When the maturation divisions are completed, the amount of chromatin in the egg has become much reduced and the number of chromosomes diminished by one half. That the number is not reduced to one fourth is due to the fact that only one of the two maturation divisions is a true reducing division. Just previous to maturation a pairing of the chromosomes occurs which is known as *synapsis*. The chromosomes come to lie side by side in pairs, and one of the maturation divisions consists in separating the chromosomes which had previously been joined. The other maturation division involves a longitudinal splitting of each chromosome, and is hence of the non-reducing type which is found in the ordinary process of mitosis.

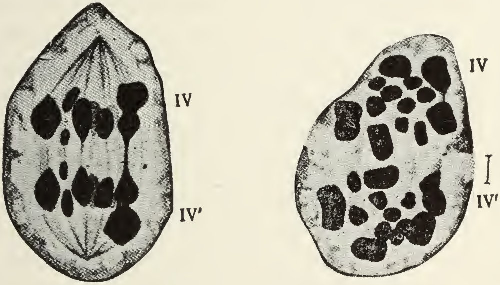

Fig. 25.—Division of the spermatocytes of *Rana temporaria*. The figure at the right shows the chromosomes of two daughter cells. (After Witschi.)

A corresponding pairing and reduction of chromosomes takes place during the development of the sperm cells, so that these finally contain half the usual number of chromosomes. When fertilization occurs there is restored the full number of chromosomes characteristic of the species. In *Rana pipiens*, according to Swingle, and in *Rana tem-*

poraria, according to Witschi, the number of chromosomes is 26 and therefore 13 in the mature sex cells. In the bullfrog Swingle finds 28 chromosomes.

The sperm cells of the frog fall into two classes, one containing a large X chromosome and the other a smaller Y chromosome. There is probably an X chromosome in every egg, and, in accordance with the usual scheme for the determination of sex, if an egg is fertilized with a sperm cell containing an X chromosome it produces a female; if it is fertilized by a sperm cell containing a Y chromosome it produces a male.

FIG. 26.—Spermatozoön of *Rana esculenta.* (After La Valette St. George.)

Fertilization.—The act of fertilization consists in the union of two cells, the *ovum* from the female and the *spermatozoön* from the male. As bearers of hereditary qualities these two cells are equal, but in size and form they are as dissimilar as they can well be. The sperm cell is a minute, elongated body consisting of a narrow, pointed *head* formed mainly of the nucleus, a short *middle piece* just behind the head, and a long, very slender *tail.* As before described, the seminal fluid of the frog is shed over the egg masses as they are extruded into the water from the body of the female. The spermatozoa which swarm in the seminal fluid are active, and swim about by the movements of the tail, working their way through the jelly of the egg mass until one comes in contact with an egg. Then the spermatozoön slowly penetrates the egg substance. The entrance of one spermatozoön seems to cause some change in the substance of the egg whereby other spermatozoa are prevented from entering it, as normally an egg is fertilized by only one sperm cell, although there may be thousands of others in the immediate vicinity. When the head of the spermatozoön has entered the egg, it begins to enlarge, and its nucleus, which is now known as the *male pronucleus*, assumes a spherical form. It migrates slowly toward the central part of the egg, dragging in behind it a mass of pigment granules from the periphery, so that its course comes to be marked by a dark streak. Before the male pronucleus has penetrated very far the process of maturation is brought to completion by the formation of the second polar body. The nuclear material remaining in the egg after this second maturation division goes into a resting stage, forming the *female pronucleus*, or the nucleus of the matured ovum. The male and female pronuclei approach and finally fuse into one, which is called the *copulation nucleus*. The number of chromosomes contributed by both parents to the nucleus of the fertilized egg is the same, and this has doubtless a fundamental relation to the fact that, on the average, offspring inherit qualities from both their parent forms in an equal degree. This correlation of equality of inheritance from the two parents with the equality of their contributions of chromatin material to the fertilized eggs lends strong support to the view that it is to the chromatin of the nucleus that we must look for the bearer of hereditary qualities; and especially since the cytoplasm in the two germ cells differs so enormously in amount.

Very soon after the spermatozoön has entered the egg a mass of fluid collects between the egg and vitelline membrane. This is called the peri-vitelline fluid, and is doubtless derived from the egg itself. Owing to the accumulation of this fluid the egg becomes free to rotate, and the dark pole, which has a less specific gravity than the light-colored yolk-laden region, soon comes to lie uppermost. Before fertilization the eggs lie in all possible planes, but soon after fertilization they all assume the same position, with the black pole above.

Cleavage.—Usually between two and a half and three hours after fertilization the egg begins to undergo its first division. The process begins as a small depression at the animal pole, which gradually extends in the form of a groove until it finally surrounds the egg. This groove marks the outer boundary of a cleavage plane which extends through the egg, dividing it into approximately equal cells. The cleavage of the mass of the egg is preceded and accompanied by a karyokinetic division of the nucleus, so that each daughter cell contains a nucleus derived from the copulation nucleus of the fertilized egg; and in all subsequent cleavages of the ovum there is a separation of nuclear as well as cytoplasmic material, and chromatin derived from both parents comes to lie in all the cells of the body of the embryo.

The egg before cleavage is not entirely a radially symmetrical structure, but the dark pole inclines somewhat to one side. There is consequently only one plane which can divide the egg into two symmetrical halves. As a rule the first cleavage furrow lies in this plane of symmetry; more rarely it lies at right angles to it, although it may occur in almost any intermediate position.

The second cleavage appears about three quarters of an hour after the first; the furrow extends gradually from the animal to the vegetal pole, at right angles to the first furrow, and divides the egg into four cells. The first and second cleavage planes stand in a tolerably constant relation to the axes of the body of the embryo, the first cleavage plane marking the median, or sagittal plane of the future animal; but this is a rule not without exceptions.

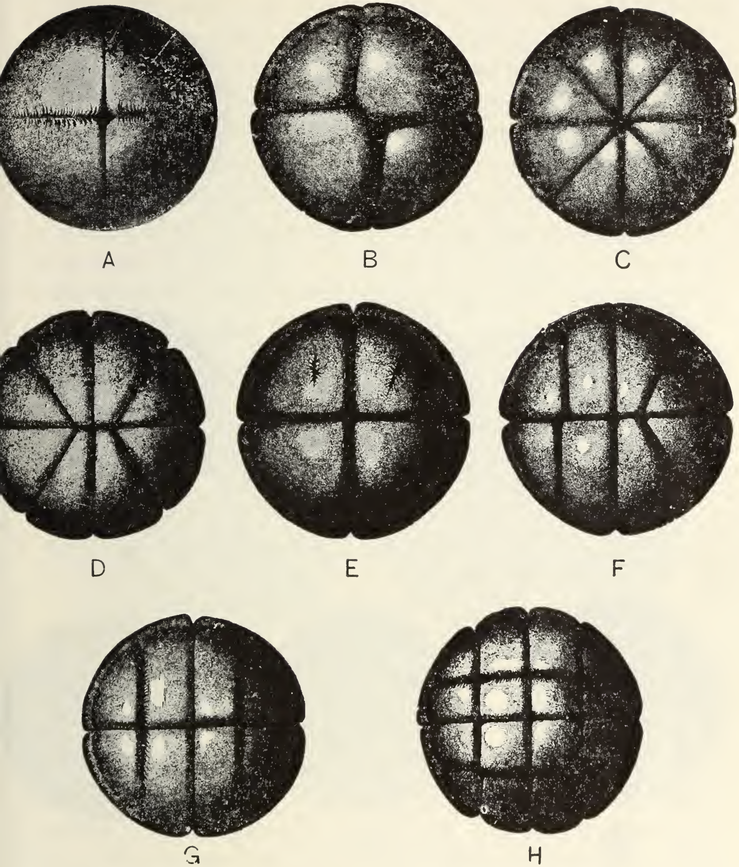

FIG. 27.—Segmentation of egg. (After Schultze.) *A*, two-cell stage, with the beginning of the second furrow; *B*, eight-cell stage, showing the cross furrow at the animal pole; *E*, eight-cell stage; *C*, *D*, *F*, *G*, sixteen-cell stages, showing variations in the plan of cleavage; *H*, thirty-two-cell stage. (From Morgan's "Development of the Frog's Egg.")

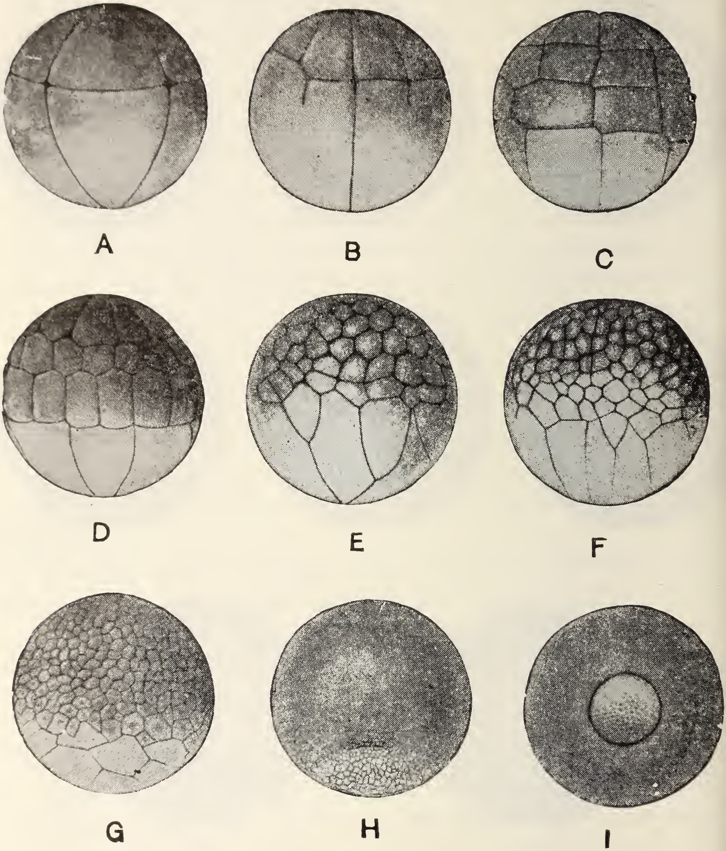

FIG. 28.—Segmentation of the egg and formation of the blastopore. *A*, eight-cell stage seen from one side; *B*, beginning of sixteen-cell stage; *C*, thirty-two-cell stage; *D*, forty-eight-cell stage; *E*, *F*, and *G*, successive later stages of cleavage; *H*, beginning of the blastopore in the form of a small crescent; *I*, circular blastopore on the vegetative side of the egg. (After Morgan.)

The third cleavage furrow comes in a little above the equator of the egg and at right angles to the other two; the four upper cells cut off by this division are a little smaller than the lower four. At the next cleavage the furrows run nearly vertically and hence at right angles to the third cleavage plane. Sometimes the furrows meet at the animal pole, but more frequently they cut through the first or second cleavage furrows, producing thus a bilateral arrangement of the cells. The fourth cleavage furrows are subject to more variation at the vegetal pole of the egg, and the subsequent divisions soon become so irregular that it is impossible to trace out any plan of procedure. A fifth cleavage occurs typically parallel to the third, appearing first in the upper hemisphere and then in the lower. The cleavages thus far usually follow the rule that each cleavage plane comes in at right angles to the previous cleavage plane. Deviations from the typical method of cleavage are apparently of little moment, even in the first few divisions, as such abnormally dividing eggs may nevertheless produce perfect embryos.

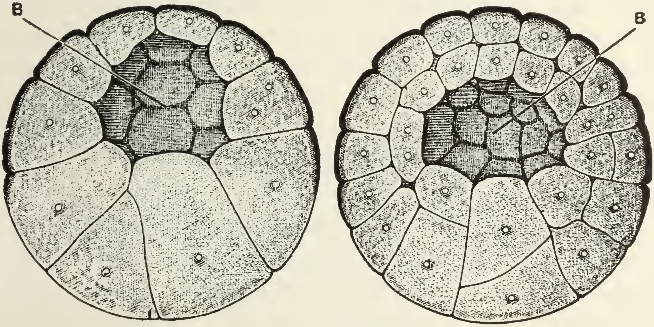

Fig. 29.—Vertical section through the blastula of a frog in different stages. *B*, segmentation cavity or blastocœl. (After Marshall.)

Cleavage takes place more rapidly in the dark or animal pole, since at that place the protoplasm is most dense. Yolk, which is most abundant in the white or vegetative side of the egg, delays cell division, and we find in the later stages of segmentation the cells are much larger at the vegetative pole and gradually become smaller toward the opposite side of the egg. In the first few cleavages the planes of division lie at right angles to the surface of the egg, but subsequently planes of division occur parallel to the surface, so that the egg comes to consist of more than one layer of cells in thickness. A cavity makes its appearance near the center of the egg and gradually increases in size as cleavage proceeds. This is the *blastocœl,* or *segmentation cavity,* and the egg at this time is called the *blastula.* It is essentially a hollow sphere of which the wall on the vegetative side is very much thicker than it is above and composed of large yolk-laden cells.

Gastrulation.—In the embryonic development of most of the many-celled animals a stage is passed through which is known as the *gastrula.* In its typical form a gastrula is a sort of double-walled sac such as may be produced, according to a well-worn illustration, by pushing in one side of a hollow rubber ball with the finger. The mouth of the gastrula is called the *blastopore,* and this opening naturally becomes smaller as the process of inpushing is completed. The process of gastrulation, which is exemplified in its typical form in the development of a starfish or sea-urchin, becomes very much modified in different animals. Such is the case in the development of the frog. The large accumulation of yolk at the vegetal side of the blastula prevents the invagination of this region from taking place in the typical way. The same end is reached partly by a process of in-pushing and partly by the overgrowth of the white pole by the dark. The inpushing and overgrowth take place more on one side of the egg than the other, and these processes are first indicated by the appearance of a crescentic groove a little below the equator of the egg. The crescent represents the beginning of the blastopore. The groove is deepest at the center and thins out towards the edges, which gradually extend around the lower pole of the egg. In this way the crescent becomes converted into a circle, and the circle gradually becomes smaller and smaller until only a small part of the light-colored yolk, known as the yolk plug, appears in the midst of the dark area. The white pole is thus overgrown by the dark, but not with equal rapidity from all sides, the closing-in taking place much more rapidly on the side where the crescentic fold originally appeared, and which subsequent events prove to be the anterior end of the embryo.

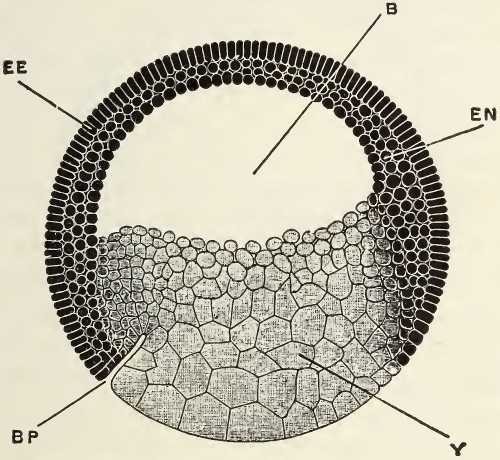

Fig. 30.—Sagittal section through a frog embryo. *B*, blastocœl or segmentation cavity; *BP*, lip of blastopore; *EE*, outer or epidermic layer of ectoderm; *EN*, inner or nervous layer of ectoderm; *Y*, yolk cells. (After Marshall.)

If we make a vertical section through the embryo at right angles to the crescentic blastopore, we shall find the latter is the mouth of a cavity which extends some distance into the egg. Above this cavity, which is called the *archenteron,* is a comparatively thin roof, closely applied to the upper wall of the embryo, and at the floor of the cavity is a large mass of yolk cells. The archenteron represents the cavity produced by the process of gastrulation. It is due, in great measure at least, to the overgrowth of the dorsal lips of the blastopore, the cells forming the floor being formerly at the surface of the egg. According to Marshall, the cavity arises in great part through the splitting apart of the yolk cells, but while this may be a factor in the case, it certainly cannot be the predominant one. (See Robinson and Assheton '91,[1] Assheton '94,[2] Morgan '97.[3]) As the archenteron increases in size, the blastocœl or segmentation cavity necessarily becomes smaller. According to Marshall the former breaks through into the latter, and the two form one cavity. This, however, does not occur in all cases.

The Germ Layers.—The formation of the gastrula produces a two-layered embryo, each layer being several cells thick. The outer of these layers is the *ectoderm;* the inner, the *entoderm.* The cells of the former are small and pigmented; those of the latter for the most part are comparatively large, lighter in color, and contain a large amount of yolk. The two layers are continuous with each other at the lips of the blastopore. Before the process of invagination is completed there appears a third germ layer, the *mesoderm,* or *mesoblast,* between the other two. The mesoderm appears all around the blastopore, and as this opening closes mainly from in front backward, the two masses of meso-

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[1] Robinson and Assheton, *Quart. Jour. Mic. Sci.*, Vol. 32, 1891.
[2] Assheton, *Ibid.*, Vol. 37, 1894.
[3] Morgan, "The Development of the Frog's Egg," 1897.

derm on either side are brought near each other in the mid-dorsal line. The free ventral edges of the masses or sheets of mesoderm extend ventrally until they meet below and come to surround the archenteron, except for a short space along the dorsal side. The sheets of mesoderm soon become split into an inner or *splanchnic* layer, which lies next to the archenteron, and an outer, *parietal,* or *somatic* layer, which lies next to the ectoderm. The space between these two layers of mesoderm is the beginning of the *cœlom,* or *body cavity.* It is at first small, but as development proceeds, it widens out more and more (Fig. 33, C).

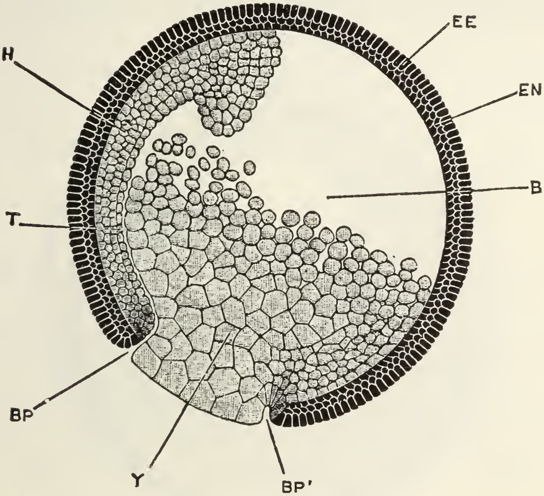

Fig. 31.—Sagittal section through a frog embryo. *B*, blastocœl; *BP*, dorsal lip of blastopore; *BP′*, ventral lip of blastopore; *EE*, epidermic layer of ectoderm; *EN*, inner or nervous layer of ectoderm; *H*, hypoblast or entoderm; *T*, mesenteron or gastrula cavity; *Y*, yolk plug. (After Marshall.)

The cells just above the mid-dorsal wall of the archenteron form a thickening which soon becomes marked off sharply from the mesodermic layers on either side and the wall of the archenteron below. This thickening is the beginning of the *notochord,* a structure forming the beginning of the vertebral column, and occurring in the embryo, when not also present in the adults, of all vertebrate animals. It is always the first part of the skeleton to make its appearance in the embryo, as it was the first part to appear in the evolution of the race. Whether in the frog it is entodermic in origin, as it certainly is in some of the Amphibia and in many other vertebrates, or whether, as maintained by Morgan, it is developed from the mesoderm, is a matter about which there is a difference of opinion. Miss H. D. King[1] has studied the formation of the notochord in *Bufo lentiginosus* and *Rana palustris,* and has come to the conclusion

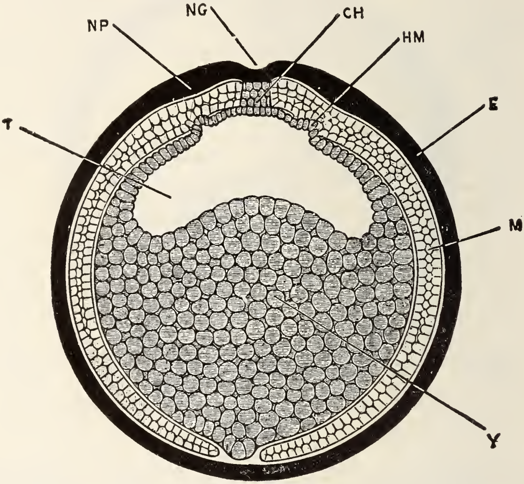

Fig. 32.—Transverse section through the middle of a frog's embryo. *CH*, notochord; *E*, ectoderm; *M*, mesoderm; *NG*, neural groove; *NP*, neural plate; *T*, mesenteron; *Y*, yolk cells. (After Marshall.)

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[1] King, *Biol. Bull.*, Vol. 4, 1903.

that the notochord in the anterior end of the embryo arises from the mesoderm, whereas in the posterior part of the embryo it is developed from both mesoderm and entoderm.

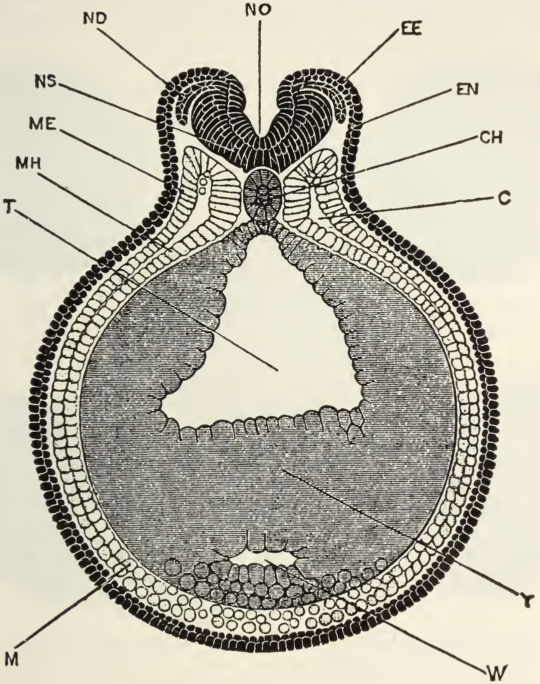

FIG. 33.—Transverse section through a frog embryo before the closure of the medullary or neural folds. *C*, cœlom or body cavity; *CH*, notochord; *EE*, epidermic layer of ectoderm; *EN*, nervous layer of ectoderm; *M*, mesoderm; *ME*, outer or somatic mesoderm; *MH*, inner or splanchnic mesoderm; *NC*, neural groove; *ND*, dorsal root of spinal nerve; *NS*, spinal cord; *T*, archenteron; *W*, liver diverticulum; *Y*, yolk. (After Marshall.)

External Changes.—At the time when the blastopore is nearly closed the egg is still in a spherical form, except that along what is to be the dorsal side of the body of the embryo there is the beginning of a broad depression known as the *primitive groove.* On either side of this are two folds, the inner and the outer *medullary folds,* which are continued as an elevation around the anterior end of the primitive groove and are produced backward on either side

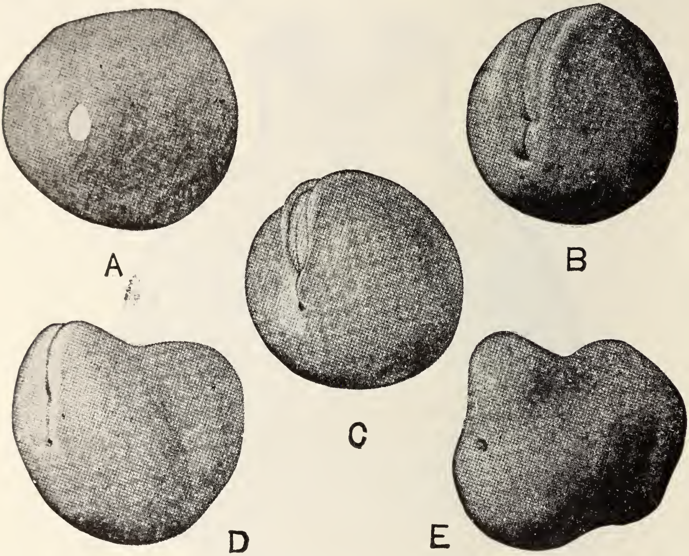

FIG. 34.—Development of the embryo. *A*, yolk-plug stage; *B*, showing the medullary folds, the blastopore nearly closed, and below the latter the invagination which is to form the anus; *C*, *D*, later stages; *E*, the medullary folds have grown together and covered the blastopore. Above the anus is the rudiment of the tail. (From Morgan, after Ziegler.)

of the blastopore. The outer medullary folds gradually fade away, but the inner ones become elevated and arch over the groove between them. Finally the two inner folds meet and fuse along the median line, converting the groove into a tube. The point where they first fuse corresponds to the neck region of the embryo; and the closure of the tube proceeds both forward and backward from this point. The fusion extends backward so that folds on either side of the blastopore close in above that opening in such a way that it becomes no longer visible from the outside. As the medullary tube is completed it is constricted off from the ectoderm above, and the latter becomes continuous over the mid-dorsal line. Subsequently it develops into the brain and spinal cord of the embryo.

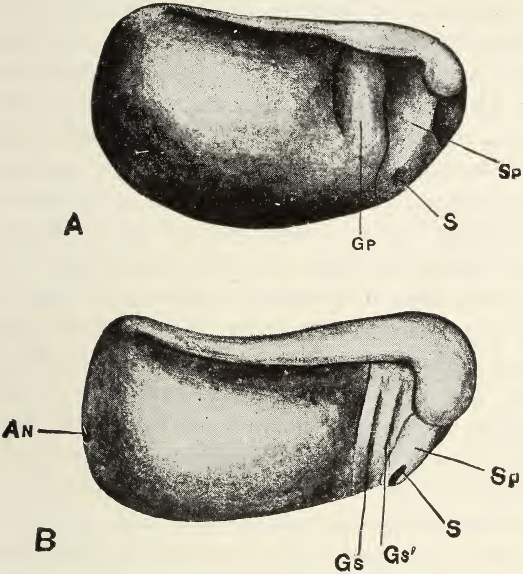

Fig. 35.—Embryos. *Gp*, gill plate; *Gs*, *Gs'*, two gill slits; *S*, suckers; *Sp*, sense plate; *An*, anus. (From Morgan, after Schultze.)

As the above changes are taking place the embryo elongates in the direction of the neural tube, which marks the longitudinal axis of the future animal. On either side of the anterior end of the neural tube there appears a pair of thickenings of the ectoderm. The anterior members of each pair, the *sense plates,* grow forward and meet in front of the end of the neural tube; a depression appears in each plate and marks the beginning of the *ventral sucker* of the tadpole. Subsequently these depressions meet in front and become converted into a U-shaped groove. In the posterior pair of plates, the *gill plates,* there appears tow vertical grooves, which later become converted into the gill slits; later two additional slits appear, one before and one behind the other two, but none of them breaks through until after the tadpole leaves the jelly. In the middle line, just above the ventral sucker, the beginning of the *mouth* appears as a hollow depression of the ectoderm, but it does not communicate with the archenteron until a much later period. The *anus* begins as an invagination of the ectoderm a short distance behind the point where the blastopore was closed over. Later this invagination meets and fuses with a diverticulum from the posterior part of the archenteron, thus establishing an opening between the latter and the exterior. The tail arises as an elevation of the region in front of the blastopore, which grows backward and pushes the anus to a more ventral position. Later it becomes flattened from side to side, and its upper and lower edges become produced into a thin expansion, or tail fin.

The *nostrils* appear as a pair of external depressions or pits a little above the rudiment of the mouth. These pits deepen, and finally communicate with the buccal cavity. Above and to the sides of the nasal pits the beginning of the *eyes* is indicated as a pair of thickenings of the ectoderm. The outline of the enlarged anterior portion of the medullary tube may be observed from the surface. It is bent downward in front, and shows a division into three regions, which become the three primary vesicles of the brain. Near the posterior of these vesicles there is developed on either side an invagination or pit of the ectoderm, which finally sinks in and becomes cut off from the surface and forms the vesicle of the *inner ear.*

At the time the neural tube is formed, the superficial cells of the ectoderm become furnished in many places with cilia by means of which the embryo slowly rotates within the jelly. The general direction of the stroke of the cilia is from before backward. The movement is strongest at the anterior end of the body, and is weaker on the ventral than on the dorsal side. "A tadpole of 6 or 7 mm. will progress, if placed upon its side in water, along the bottom of a flat glass vessel, at the rate of one millimeter in from four to seven seconds." (Assheton '96.) After the tadpole is hatched from the jelly the cilia gradually disappear.

Organs from the Ectoderm.—In addition to forming the outer layer of the skin over the entire surface of the embryo the ectoderm gives rise to certain other structures which come to lie within the body. Chief among these is the central nervous system whose beginning in the medullary groove has already been described. The neural tube into which the medullary groove develops loses its original connection with the surface; anteriorly it becomes enlarged and forms the brain, the remaining portions developing into the spinal cord. The thickening of the walls of the portion of the tube which forms the cord diminishes the central cavity until it becomes reduced to a fine canal, known in the adult as the *canalis centralis.* The anterior portion of the tube becomes divided by slight constrictions into three vesicles, which form, designating them from before backward, the *fore, mid* and *hind brain.* The hindbrain becomes widened from side to side, especially in front; its floor and sides thicken, but the roof, except for a small fold at the end which develops into the *cerebellum,* remains thin and membranous, and becomes thrown into a series of folds which support a mass of blood vessels known as the *choroid* *plexus.* The portion of the hindbrain which does not form the cerebellum is converted into the *medulla.* The central cavity becomes widened out, forming the *fourth ventricle;* which communicates posteriorly with the canalis centralis of the cord and anteriorly with the ventricle of the midbrain.

The *midbrain* grows out dorsally and laterally into a pair of hollow processes, the *optic lobes,* whose cavities or ventricles communicate with the median canal, which becomes narrowed by the thickening of its walls, and forms the *aqueduct of Sylvius,* or *iter a tertio ad quartum ventriculum.* The floor of the midbrain forms the *crura cerebri.*

The *forebrain* soon becomes separated into two parts, the *thalamencephalon* behind, and the *cerebral hemispheres,* which grow out from the latter in front. The floor and walls of the former become thickened to form the *optic thalami,* the roof remains thin and membranous, and the cavity becomes the *third ventricle.* From the roof of the thalamencephalon there arises a median hollow outgrowth, the *pineal gland,* which extends dorsally, reaching the surface ectoderm, where it becomes expanded into a small knob. The knob becomes constricted off when the bones of the skull develop and forms the brow spot, previously described. The floor of the thalamencephalon gives rise to a hollow outgrowth, the *infundibulum,* which extends downward. The extremity of this outgrowth comes into contact with an invagination from the roof of the mouth cavity, the two parts combining to form the *pituitary body* which is therefore an organ of dual origin. The sides of the thalamencephalon give rise to a pair of lateral diverticula, the *optic vesicles,* which grow out until they come in close contact with the surface ectoderm. The distal end of the vesicles widens out to form the *retina* of the eyes, the stalk giving rise to the *optic nerve.*

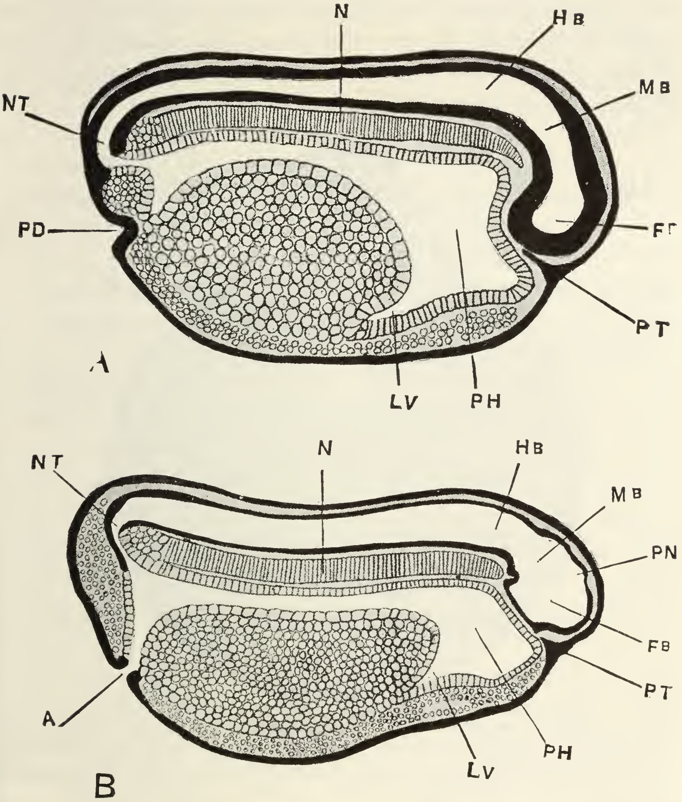

Fig. 36.—Sagittal sections through two embryos. In A the blastopore is overarched and there is the beginning of the proctodæum or anal invagination. In B the proctodæum has met and fused with an evagination of the archenteron. *A*, anus; *FB*, forebrain; *HB*, hindbrain; *LV*, liver diverticulum; *MB*, midbrain; *N*, notochord; *NT*, neurenteric canal; *PD*, proctodæum; *PH*, pharynx; *PN*, pineal body; *PT*, pituitary body. (From Morgan, after Marshall.)

The anterior wall of the forebrain produces a pair of pouches, the cerebral hemispheres, which finally become the largest part of the brain. Their cavities, the *lateral ventricles,* communicate with the third ventricle by an opening, the *foramen of Monro.*

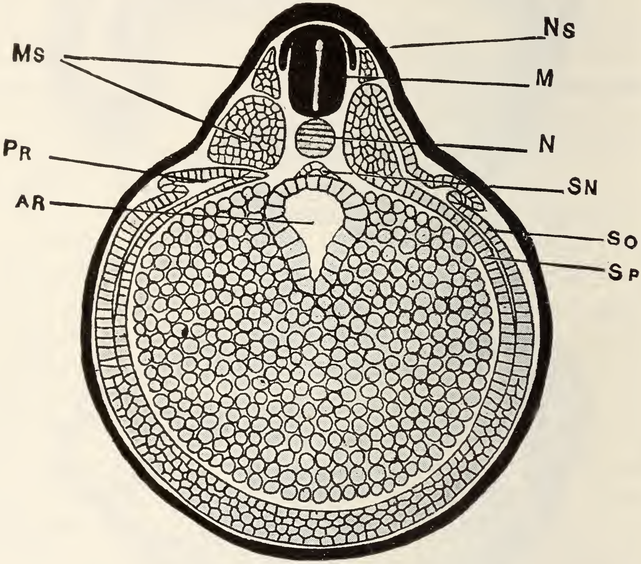

FIG. 37.—Cross section of a frog embryo. *AR,* archenteron; *MS,* mesoblastic somites; *N,* notochord; *NS,* neural crest; *M,* medullary tube; *PR,* pronephros; *SN,* subnotochordal rod; *SO, SP,* somatic and splanchnic mesoderm. (From Morgan, after Marshall.)

The nerves arise as paired outgrowths both from the brain and cord, pushing their way between the cells of the other organs, dividing and ramifying, as they push outward toward the various parts they supply. The spinal nerves begin as two independent outgrowths, representing the dorsal and ventral roots; these soon unite into a single nerve.

The lining of the mouth cavity is formed from an invagination of ectoderm, the *stomodeum,* which pushes in until it breaks through into the archenteron. A similar ectodermal invagination, the *proctodeum,* forms the lining of a small part of the posterior end of the alimentary canal. The lens and cornea as well as the retina of the eye, and the vesicle of the inner ear, also take their origin from this layer.

Organs from the Entoderm.—The entoderm, or the germ layer which is invaginated within the egg, gives rise to the lining of the alimentary canal and of all organs which arise as outgrowths from it. The first of these to be formed is the *liver,* which at the beginning appears as an outpocketing of the ventral side near the anterior end. The outpocketing becomes folded and branched, being converted finally into a number of clusters of tubules, all emptying into the common canal, the *bile duct,* which is produced by a lengthening of the neck of the original outgrowth. A lateral outgrowth of the bile duct forms the *gall bladder.* The cells lining the terminal branches of the hepatic diverticula become the secreting cells of the liver. The connective tissue, blood vessels, and outer coating of the liver are derived from the mesoblast.

The *pancreas* arises much in the same way as the liver, but as a pair of outgrowths instead of a single one. They form, however, a single organ, and their ducts later become connected with the bile duct. Only the secreting portion of the pancreas and the lining of its ducts are of entodermic origin, the connective tissue, blood vessels, etc., arising, as in the liver, from the middle germ layer.

The *bladder* arises as an outgrowth of the ventral side of the alimentary canal, near the posterior end; its lining, therefore, is of entodermic origin.

The *lungs* appear as a pair of pouches from the sides of the esophagus. They make little growth until quite late in

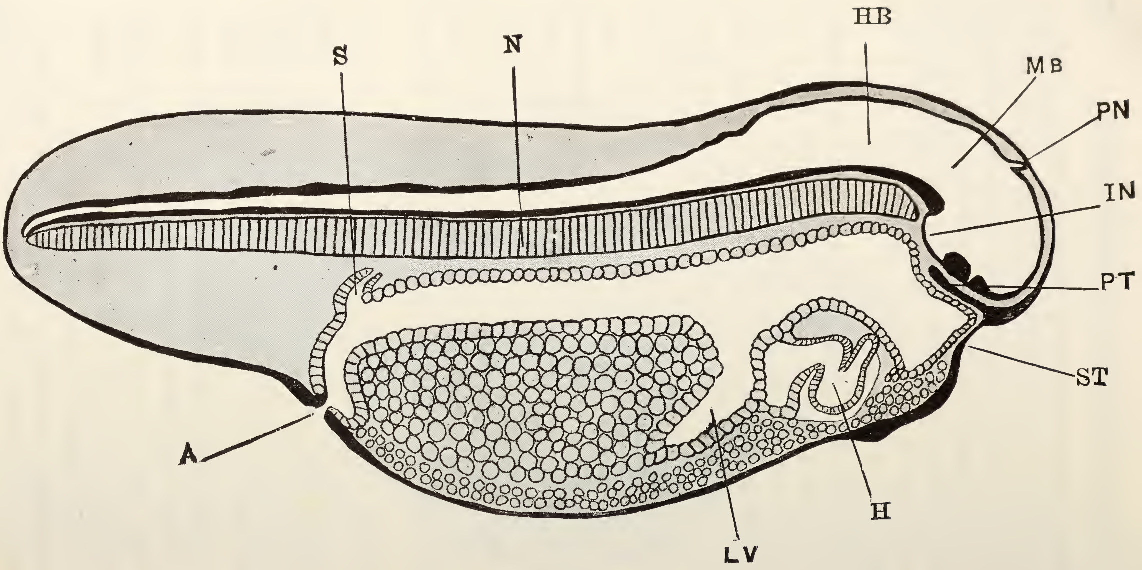

FIG. 38.—Sagittal section through the embryo of a frog. *A*, anus; *H*, Heart; *HB*, hindbrain; *LV*, liver; *MB*, midbrain; *N*, notochord; *PN*, pineal body; *PT*, pituitary body; *S*, segmental duct; *ST*, stomodæum; *IN*, infundibulum. (After Morgan.)

the life of the tadpole. The region of the esophagus from which the lungs arise becomes depressed and partly separated off from the part above to form the *larynx,* the mouth of the depressed portion going to form the *glottis* of the adult.

The *gill slits* in the frog appear in the form of five solid outgrowths on each side of the anterior portion of the archenteron. In section they are shown to be in the form of a double fold such as would be produced if the walls of a pouch-like diverticulum were brought into contact. At their outer ends the slits come into contact with the ectoderm, with which they fuse. The first two slits are the first to form; the others appear in order from before backward. When the tadpole escapes from the jelly into the water, the walls of the solid gill slits separate, the ectoderm breaks through at the outer end, and a free communication is established between the throat and the outside. The first slit, the *hyomandibular,* does not break through to the outside; its entodermic lamellæ separate and form a pouch which communicates with the pharynx. In most forms the hyomandibular cleft forms the *Eustachian tube* and its covering over its outer end, the tympanic membrane; but in the frog, according to Marshall, the Eustachian tube has a different method of origin. (See "Vertebrate Embryology," p. 143.) The four following slits are known as the *branchial clefts;* of these the second and third open first, then the first, and finally the fourth.

The *thyroid gland* begins as a longitudinal groove along the floor of the pharynx. It gradually sinks below the surface and becomes converted into a solid, elongated mass of cells. Later it divides into right and left portions, which are completely separated.

The *thymus,* according to Maurer, arises by a sort of budding process from the epithelium of the dorsal end of the first branchial cleft. The end then separates from its point of origin and becomes carried backward, finally lying behind the tympanic membrane. The thymus is relatively larger in young frogs than in older ones. Other bodies of similar epithelial origin from the gill clefts are, according to Maurer, the post-branchial bodies, the epithelial bodies, and the pseudothyroid ("ventraler Kiemenrest").

The entoderm forms only the inner portion of the alimentary canal and its diverticula. The connective tissue, muscular, and peritoneal layers are derived from the mesoblast. For the most part it is composed of but a single layer of cells. The epithelium of the mouth and a small portion of the cloaca are produced by the ectoderm, these being the only portions of the lining of the alimentary canal not of entodermic origin.

Organs from the Mesoderm.—The development of the mesoderm has been traced to the stage in which it consists of two double-layered sheets of tissue extending from the notochord above to the ventral side of the body. The two sheets of mesoderm are separated by the notochord except for a short distance in front of and behind this structure, where they become continuous across the middle line. A division soon occurs in the mesoderm, separating a dorsal portion, known as the *vertebral plate,* from a ventral part, called the *lateral plate.* The former becomes divided transversely into a number of blocks called *myotomes,* or *muscle segments.* Each of these becomes thickened so that the central cavity becomes reduced in size and finally disappears. The division of the vertebral plate into segments begins in the neck region of the embryo and proceeds backward. The segments soon become separated from each other by septa of connective tissue which assume the form of a V with its apex pointing toward the anterior end of the body. The myotomes are easily seen at the sides of the body of a young tadpole, especially in the region of the tail. The cells of the myotomes elongate in a direction parallel with the long axis of the animal and become converted into muscle fibers.

The two layers of the lateral plates become widely separated by the enlargement of the intervening body cavity or cœlom. The inner or *splanchnic layer* becomes closely applied to the entoderm of the archenteron and forms the supporting tissue and musculature of the alimentary canal and its diverticula. The outer or *somatic layer* comes to lie against the outer ectoderm and forms the inner portion (connective tissue, muscle, and peritoneum) of the body wall. The innermost portion of both the somatic and splanchnic layers of mesoblast become differentiated as a separate layer, the *peritoneum,* which is continuous all around the body cavity. As the right and left halves of the cœlom arise independently and gradually extend toward the mid-ventral line, they are separated for a time by a median ventral partition. This subsequently breaks down along most of the length of the alimentary canal, putting the two sides of the body cavity in connection with each other. The median partition persists, however, for a short distance anteriorly, forming the vertical membrane which extends from the liver and pericardium to the ventral body wall. A still smaller portion occurs between the body wall and the ventral side of the cloaca.

The *heart* and *pericardium* take their origin from the mesoderm near the anterior end of the ventral side of the body. A pair of fissures appears in the sheet of mesoderm in this region; these gradually enlarge and extend toward the middle line. The layer roofing over these fissures becomes raised up on either side, and the two folds thus formed meet each other above, forming a sort of tube. Within this tube are inclosed some scattered cells which arrange themselves into a layer that becomes the endothelial lining of the heart. The cavity outside the tube becomes the cavity of the pericardium, and the tube itself thickens and becomes transformed mainly into the heart, but its outer layer gives rise to a thin sheet of tissue, the visceral portion of the pericardium. The tissue which at first connects the heart with the ventral side of the pericardium becomes broken through, and the two sides of the pericardial cavity become continuous; the dorsal connection of the heart disappears at a later period. The visceral layer of pericardium which closely invests the heart becomes reflected upon the sides of the surrounding cavity, where it becomes continuous with the parietal layer, the relations of the two parts being essentially the same as that of the portion of peritoneum surrounding the alimentary canal and that lining the cœlom. Owing to its increase in length the heart becomes bent in the form of an S; anteriorly it becomes continued into the *truncus*

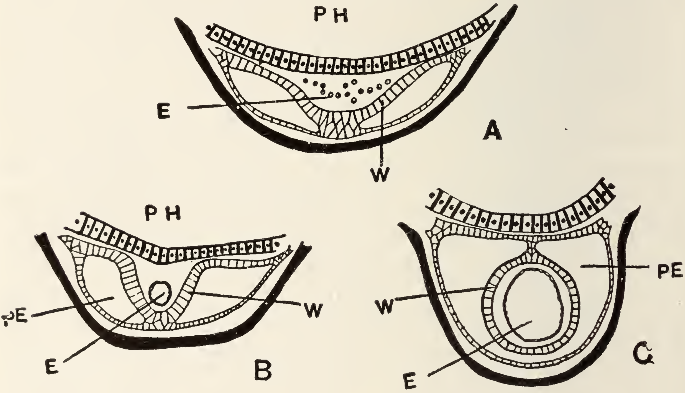

Fig. 39.—A, B, C, three stages in the development of the heart. *E*, endothelium; *PE*, pericardium; *PH*, pharynx; *W*, wall of heart. (After Morgan.)

arteriosus, which divides into two branches which proceed toward the gills, where they break up into the *aortic arches,* which distribute branches to the gill filaments. The blood vessels first appear as lacunæ or spaces between the cells of the mesoderm; the spaces enlarge, become continuous, and the cells surrounding them take on a definite arrangement and form the walls. The blood corpuscles arise either from cells originally inclosed in the vessels or from cells budded off from the lining membranes.

In the development of the renal organs there first appears on each half of the body a temporary organ known as the *pronephros,* which later disappears without contributing to the formation of the permanent kidney. The duct of the pronephros, or *segmental duct,* arises, according to Field,[1] as a thickening of the mesodermic wall of the body cavity. It becomes hollowed out secondarily, and at its anterior end it divides into three tubules which open into the cœlom. Posteriorly the duct joins the cloaca. The tubules increase in length and become more convoluted, and the duct itself in the region of its tubules becomes bent and twisted owing to its increase in length, but its hinder portion remains straight. The mouths (*nephrostomes*) of the tubules become lined with cilia which carry material into the canals.

The pronephros, which is the functional kidney of early larval life, is replaced by the *mesonephros,* or *Wolffian body,* which is the renal organ of the adult. The mesonephros makes its first appearance as a series of small tubules on either side of the body, between the aorta and the segmental duct. The tubules are at first solid, but they soon acquire a lumen which communicates with that of the segmental duct, with which they fuse. Their distal ends become swollen out into a sort of sac, one wall of which becomes pushed in by a knot of blood vessels or *glomerulus* derived from the renal

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[1] Field, *Bull. Mus. Comp. Zoöl. Harvard,* Vol. 21, 1891.

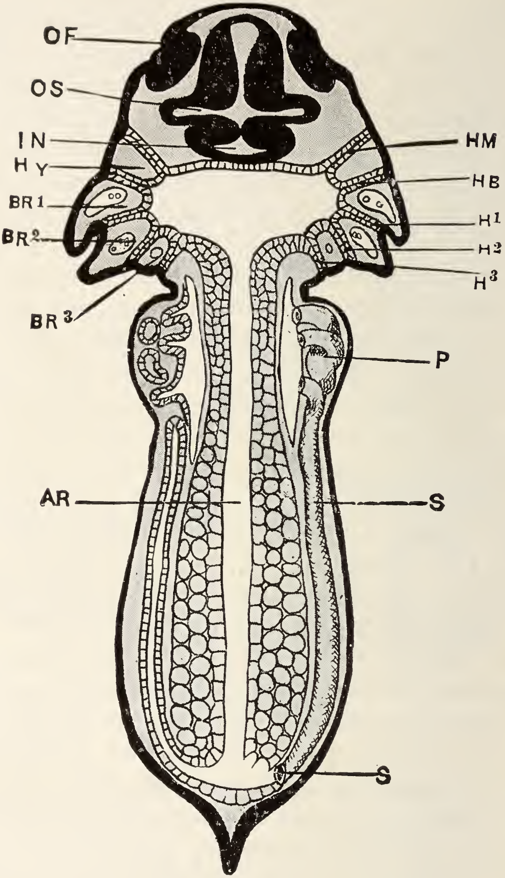


FIG. 40.—Horizontal section through an advanced embryo. *AR*, archenteron; *BR*¹, *BR*², *BR*³, branchial arches; *H*¹, *H*², *H*³, gill slits; *HB*, hyoid slit; *HM*, hyomandibular cleft; *HY*, hyoid arch; *IN*, infundibulum; *OF*, olfactory pit; *OS*, optic stalk; *P*, pronephros; *S*, segmental duct. (From Morgan, after Marshall.)

arteries, thus forming the *Malpighian bodies* found in the adult kidney. Owing to their growth in length the tubules become contorted; branches are given off which later open into the cœlom by funnel-shaped ciliated mouths, or nephrostomes, but the latter soon lose their connection with the tubules and acquire secondarily an opening into the branches of the renal veins in the ventral part of the kidney. The tubules increase to a very large number and become richly supplied with blood vessels; they form with the connective tissue which binds them together a compact mass which assumes the form of the kidney of the adult. The segmental or pronephric duct which served as the outlet of the pronephros is worked in to form the *Wolffian duct* or *ureter* of the adult. The Müllerian duct was formerly supposed to arise by a splitting of the segmental duct, but according to MacBride,[1] Marshall,[2] Gemmill,[3] and more recently Hall,[4] it develops quite independently of that structure.

The reproductive organs first appear as ridges of the peritoneum near the base of the mesentery (Marshall). As the genital ridges increase in size they become constricted at their points of attachment, and finally hang supported by a peritoneal membrane. In the male the testis becomes connected with tubes which grow out of the renal tubules and form the vasa efferentia. The genital ridges in the two sexes have a similar appearance until near the close of larval life, when those of the female undergo a much more rapid growth.

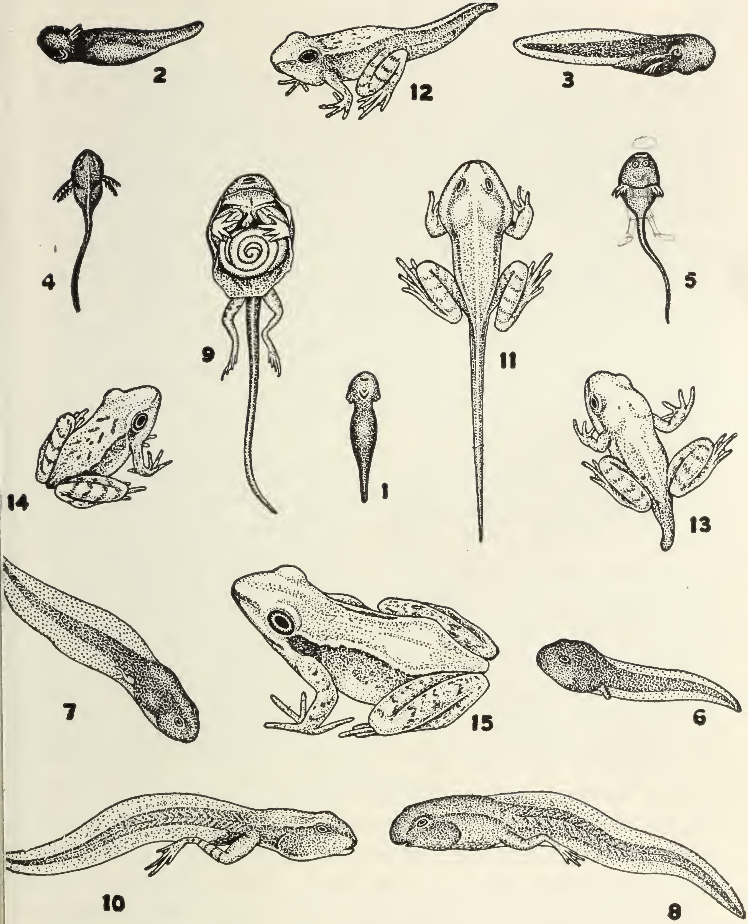
The beginning of the vertebral column is represented by the notochord, but this structure forms but a relatively small portion of the backbone of the adult frog. Loose mesodermic cells, or mesenchyme, produced from the periphery of the somite, collect around the notochord, forming a tubular

[1] MacBride, *Quart. Jour. Mic. Sci.*, Vol. 33, 1892.
[2] Marshall, "Vertebrate Embryology."
[3] Gemmill, *Arch. f. Anat. u. Phys.*, Phys. Abth., 1897.
[4] Hall, *Bull. Mus. Comp. Zoöl. Harvard*, Vol. 45. 1904.

investment. From the dorsal side of this mass ridges or folds grow up and surround the spinal cord. The mesoderm covering the notochord then becomes divided by transverse septa which alternate with those between the somites, but these do not cut across the notochord itself. The segments they cut off represent the vertebræ; they soon become cartilaginous, and finally ossify. The cartilaginous sheath grows inward at the ends of the vertebræ, constricting and finally cutting through the notochord, so that in the adult all that remains of this structure are small portions inclosed within the centra of the vertebræ.

Metamorphosis.—At the time of hatching the tadpole is a fish-like creature, having a long, vertically flattened tail, by means of which it swims through the water. The sides of the tail show the markings of the muscle segments through the skin. The flattened expansions of the integument on the upper and lower sides of the tail are thin and nearly transparent, so that one may easily observe with a microscope the blood flowing in the capillaries.

The mouth breaks through into the archenteron a few days after hatching, the larva, previous to this time, living at the expense of the food yolk in the alimentary canal. The intestine increases very rapidly in length, and becomes coiled in the form of a spiral, which may often be seen through the ventral body wall. The external gills grow rapidly after the tadpole is hatched, and soon are converted into long, branching tufts. Three pairs of external gills are developed, the posterior pair making its appearance after the first two. The gill slits grow about the time the mouth is fully formed, and the water which is taken in at the mouth is passed through the gill slits to the exterior. In addition to the external gills there are developed somewhat later four pairs of *internal gills,* which are produced by foldings of the membrane lining the gill slits. Both external and internal



IG. 41.—Metamorphosis of *Rana temporaria.* 1, tadpole just hatched, dorsal aspect; 2, 3, older tadpoles, side view; 4, 5, later stages, dorsal views showing external gills and development of operculum; 6, older tadpole, left side, showing single opening of operculum; 7, older stage, right side, showing hind leg and anus; 8 and 10, lateral view of two later stages showing development of hind legs; 9, dissection of tadpole to show internal gills, spiral intestine, and anterior legs developed within operculum; 11, advanced tadpole just before metamorphosis; 12, 13, 14, stages in metamorphosis, showing gradual resorption of tail; 15, juvenile frog after metamorphosis. (From Newman, redrawn after Leuckart-Nitsche wall chart.)

gills receive an abundant blood supply from the vessels that form the aortic or branchial arches. The disappearance of the external gills is associated with the growth of a fold, the *operculum,* which arises on either side of the head and gradually extends backward. The free posterior edge of the fold fuses with the body behind and below the gill region, leaving only an open space on the left side of the body, which is known as the *spiracle.* The water which passes out of the gill slits comes into a chamber bounded externally by the opercular wall, and thence passes through the spiracle to the outside. Soon after the completion of this chamber the external gills disappear and the internal gills function in their stead.

The jaws of the tadpole are furnished with horny coatings which function as teeth, but these are shed in later larval life. In addition both upper and lower lips also contain transverse rows of fine teeth, which vary in number and arrangement in the different species. Around the outside of the lip there are numerous small papiliæ, which also vary considerably in tadpoles of different species of frogs. The nasal pits do not break through into the mouth until some time after hatching. The eyes are situated on the dorsal side of the head, and look obliquely upward. There are several rows of sense organs on the skin of the tadpole, but these disappear when the animal assumes a terrestrial mode of life. The ventral sucker in the recently hatched larva is in the form of a horseshoe. The ectodermic cells covering it are partly glandular, and they form a mucous secretion by means of which the larvæ adhere to various objects. Later in larval life the sucker becomes divided in two in the middle. The two parts become carried farther back on the ventral side of the head, and gradually decrease in size, and finally disappear.

The hind limbs, which are the first ones to appear, bud out as small papillæ on either side of the base of the tail. They gradually increase in size, become jointed in structure, and later bud out the toes at the distal end. The fore limbs develop in much the same manner; the left limb passes through the spiracle, the right one pushing through the wall of the operculum.

Toward the end of the larval period the tail begins to disappear; its tissues break down and are resorbed, serving, doubtless, as food material for building up the other organs of the body. During the transformation of the tadpole into the young frog, the intestine shortens, the mouth becomes much wider, and the horny jaws are shed, the tongue increases greatly in size, the legs grow rapidly, the rounded body changes in form, and the gills become resorbed; the lungs then develop rapidly, and the tadpole frequently comes to the surface for air.

The food of the tadpole is mainly vegetable matter. Spirogyra and other algæ are common articles of diet; animal food, however, is greatly relished. Tadpoles will feed eagerly on decaying insects, earthworms, or almost any kind of meat. They will also eat bread or fruits; there are few things, apparently, in the way of food, which they disdain.

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CHAPTER VI

HISTOLOGY OF THE FROG

Since Schleiden and Schwann promulgated the cell theory in 1838-1839 we have been accustomed to regard organisms as composed of little units or cells. Most cells of the body of the higher organisms are united to form *tissues* which are aggregations of cells of similar character bound together by means of an *intercellular substance.* In the bodies of animals the classes of tissues commonly distinguished are the following:—

1. *Epithelial.*
2. *Connective.*
3. *Muscular.*
4. *Nervous.*

These broad divisions include nearly all the manifold variety of cells occurring in the body. The blood and lymph are sometimes added as forming a distinct class of tissues, sometimes classed as a form of connective tissue with fluid intercellular substance, and sometimes treated of as if they were not tissues at all. They will be described in a later chapter.

In the *epithelial tissues* the cells lie in layers with only a small amount of intercellular substance. We meet with this class of tissue on the surfaces of organs, or lining the cavities of organs, and forming the lining of glands, blood vessels, and ducts of all kinds. The various kinds of epithelium are distinguished according to the shapes of the cells. An excellent example of *flattened* or *squamous epithelium* may be obtained in the outermost skin which is cast off during the molt. The cells of this layer are broad and exceedingly thin, and show a rounded nucleus near the center. The cells of the peritoneum are mostly of the same flattened type. In *columnar epithelium* the cells are elongated perpendicularly to the surface and are usually prismatic in outline, owing to mutual pressure; such epithelium is common in the mucous layer of the intestine. In many places, as in the outer skin, there may be all transitional stages between columnar epithelium and squamous epithelium. Layers such as this which are several cells deep are called *stratified epithelium.*

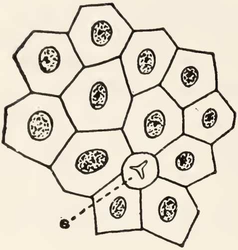

FIG. 42.—A portion of the epidermis of *Rana pipiens. s,* stoma cell.

In some parts of the body there occurs a peculiar variety called *ciliated epithelium* in which the cells are furnished with cilia at their outer ends. Usually such cells are columnar, but they may be cuboid or even somewhat flattened. Ciliated epithelium occurs in the mouth and throat of the frog, in certain parts of the peritoneal lining of the body cavity, on the inner lining of the oviducts, in the mouths of the ciliated funnels of the kidney, in the ventricles of the brain, and, in early larval life, on the outer surface of the body. If the roof of the mouth of a frog be scraped with a knife and the cells removed and examined under a microscope, a shimmering movement may be seen on one side of each cell. This is due to the rapid movement of the cilia or fine hairlike processes on the surface. The cilia of all the cells of a particular area beat most strongly in one direction, and the effect of this common movement is to create a current which carries small objects in the direction of the ciliary beat. The action of cilia may easily be demonstrated by sprinkling some powdered carmine on the roof of a frog's mouth. Soon one may observe that the substance is slowly carried backward down the esophagus into the stomach.

The *connective tissues* embrace a large number of tissues whose general function it is to support and hold together the various other parts of the body. While in the other kinds of tissue the intercellular substance is relatively very small in amount, in the connective tissues it is usually very abundant. Nearly all of the connective tissue is derived from the middle germ layer, or mesoderm. It arises chiefly from scattered cells, or mesenchyme, and in the early stages of its differentiation the amount of intercellular substance is very small, and of a jelly-like consistency. The intercellular substance becomes modified in various ways in the different varieties of connective tissue. In some cases it remains soft, in others it becomes fibrous, in bone it becomes hardened through deposits of carbonate and phosphate of lime. The principal kinds of connective tissue found in the frog are the following:—

White fibrous connective tissue is the variety which has the widest distribution. A good example of this may be obtained from the membranes which connect the skin with the body wall. If a portion is spread out on the slide and examined with the microscope, it will be seen to be made up of a clear homogeneous portion, or matrix, of a gelatinous substance in which are imbedded numerous fibers; the fibers are usually unbranched and have a characteristic wavy appearance. They are frequently united in bundles which run in all directions. When treated with acetic acid, they swell up and disappear, and when boiled, become converted into gelatin. Scattered among the white fibers there are generally a few *yellow elastic fibers;* these are straight and not wavy; they are not affected by acetic acid and do not yield gelatin when boiled; they frequently branch, and when cut across, the ends do not curl like those of the white fibers. Imbedded in spaces of the matrix here and there are the *connective tissue corpuscles* or cells. These cells vary considerably in their form and in the appearance of their cytoplasm; usually they are branched, and the branches of neighboring cells often unite or anastomose, forming an irregular network, the meshes of which are filled with the intercellular substances. These processes of the cells run in canals which allow a circulation of the fluid among the spaces or lacunæ in which the cells lie. White fibrous tissue varies greatly in consistency and texture in different parts. The loose tissue binding the muscles together is called areolar tissue, and is composed of sheets and strands intersecting each other in all planes. It forms a coating or *fascia* for each muscle, and toward the ends of the muscles it is frequently modified into *tendon* which is very dense and inelastic, and mainly composed of fibers, all of which lie in one direction. The loose tissue of lymphatic glands belongs to a variety called *adenoid,* which is composed of an irregular network of sheets and strands forming a fine meshwork which supports the

Fig. 43.—Fibrous connective tissue from the frog. *c*, connective tissue corpuscles; *e*, elastic fibers; *w*, white fibers. (After Parker and Parker.)

cells. The ligaments uniting the bones together are formed of a very dense and inelastic variety of white fibrous tissue. Modifications of the same kind of tissue occur in the cutis of the skin, in the submucosa of the alimentary canal, in the substance of glands and the capsules surrounding various organs.

Adipose tissue may be regarded as a form of connective tissue in which many of the cells have become enlarged through being gorged with fat; the nucleus with a small amount of protoplasm lies to one side of the cell, and the cell wall and a thin pellicle of protoplasm surround the globule of fat. In its early stages the fat cell may contain several isolated droplets of oily substance which as they grow coalesce into a single large mass.

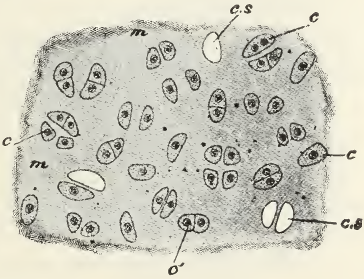

Fig. 44.—Cartilage from the head of the femur. *c*, cells; *c′*, cells in process of division; *c. s*, empty cell space; *m*, matrix. (After Parker and Parker.)

Cartilage is a dense massive variety of connective tissue. In the clear *hyaline* cartilage which is the predominant variety in the frog, the matrix appears transparent and homogeneous, although under proper treatment it may be shown to contain numerous fibers which ordinarily are not evident. The cells are contained in rounded spaces or lacunæ, scattered irregularly through the matrix; in some cases minute channels have been observed connecting the neighboring lacunæ together. Two or more cells are often found in one lacuna, a fact which indicates that they have recently arisen by the division of the parent cell. Each cell causes the deposit around it of intercellular substance; and the cells separated by cleavage soon form a partition between each other which gradually increases in thickness and presses the cells farther and farther apart. The outer surfaces of cartilages are covered by a layer, or perichondrium, which consists of an outer fibrous membrane, below which are connective tissue corpuscles, which, as the cartilage grows, sink into the matrix and become transformed into ordinary cartilage cells. Hyaline cartilage occurs at the ends of the bones of the limbs, between the vertebræ and at the ends of their transverse processes, at the tip of the urostyle, in the pubis of the pelvic girdle, in the hyoid and the cartilages of the larynx, and at both ends of the sternum; it forms the basis of the cranium and the central axis of the lower jaw.

Calcified cartilage, which contains a deposit of lime salts in the matrix, occurs in the suprascapula, the pelvis of old frogs, and at the ends of some of the larger bones of the limbs; viz. the heads of the humerus and the femur.

The structure of *bone* is similar to that of cartilage in that it contains cells imbedded in a solid matrix. In bone the matrix is rendered firm by the deposit of carbonate and phosphate of lime. By immersion in acid the lime salts may be removed and a cartilaginous body having essentially the same histological structure as bone remains. Bone, however, is not merely calcified cartilage; it differs from it both histologically and chemically. Cartilage is often the precursor of bone, but in such cases the former is broken down and bony tissue built up in its place.

Two principal varieties of bone are usually distinguished, —*compact* bone, which is very firm and dense, and *spongy* or *cancellous* bone, which is made up of plates and bars forming a structure which is comparatively loose and lacking in strength. The latter is found within the center of the vertebræ and to a small extent within some of the long bones. A good example of compact bone may be obtained by making a cross section of the femur. The central part of the bone is hollow and filled with *marrow,* and the outer surface is covered by a layer of *periosteum,* which is similar in structure to the perichondrium surrounding the cartilage. The bony substance is arranged in concentric layers, or *lamellæ,* which contain numerous *lacunæ,* in which lie the *bone cells.* From the lacunæ fine branching tubes, or *canaliculi,* containing processes from the bone cells, are given off which extend in all directions and anastomose with the canaliculi of neighboring spaces.

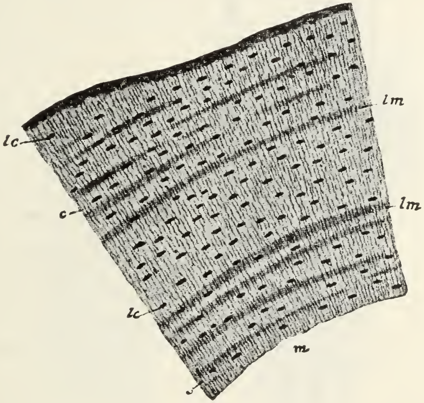

FIG. 45.—A part of a cross section of the femur of the frog. *c,* canaliculi; *lc,* lacunæ; *lm,* lamellæ; *m,* marrow cavity. (After Parker and Parker.)

Bones increase in thickness by the addition of successive layers to the outside. The *osteoblasts,* or cells forming the inner layer of the periosteum, give rise continually to new bone cells which cause the deposition of new layers of bony substances between the periosteum and the old bone. New layers may also be added from within by a layer of cells lining the inner surface of the walls of the marrow cavity.

Muscle is composed of elongated cells or muscle fibers united by connective tissue. Two varieties of muscle are commonly distinguished, the *striated,* or so-called *voluntary,* and the *unstriated,* or *involuntary.* In the latter the cell structure is relatively simple; the fibers are commonly spindle-shaped, with a single nucleus near the center, which is usually elongated in the direction of the fiber. The ends of the fibers are sometimes branched, but they are more commonly entire. The length of the unstriated muscle fibers varies greatly; they may be very narrow and attenuated, as in the walls of the bladder, or short and comparatively thick, as in the walls of the smaller blood vessels. While the fibers usually show no cross striation, the cytoplasm shows delicate longitudinal strands, or *fibrillæ,* which are considered by most investigators to be the contractile elements of the cell. The cell wall is very thin and transparent. In its action unstriated muscle is slow; a considerable time elapses before it responds to a stimulus, and it is also slow to relax. It is found in those parts of the body where there is little occasion for sudden movement. It occurs in the muscular coats of the alimentary canal, in the walls of the blood vessels and of many ducts, in the lungs, urinary and gall bladders, around many of the glands of the skin, and in the iris and ciliary muscle of the eye. It is concerned in the production of slow movements, like the contractions of the intestine, the expansion and contraction of blood vessels, the change in shape of the pupil of the eye.

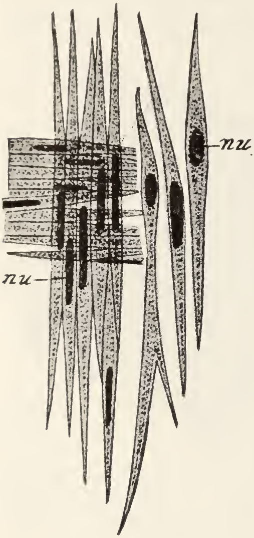

FIG. 46.—Unstriated muscle fibers from the intestine of the frog. *nu,* nucleus. (After Howes.)

The fibers of *striated muscle* are more complicated in structure. They possess several spindle-shaped nuclei, scattered about through the cell, each of which is surrounded by a small amount of unmodified cytoplasm. There is a thin, but well-defined, cell wall, or *sarcolemma,* which is best seen in places where the contents of the fiber are crushed or broken apart. Each fiber of voluntary muscle is to be regarded as a single cell, with numerous nuclei scattered about through its cytoplasm. In its early stages of development a voluntary muscle cell possesses but one nucleus. As the fiber grows, the nucleus divides repeatedly, but as the cytoplasm does not divide at the same time, there come finally to be numerous nuclei within the limits of a single cell wall. The cytoplasm shows both a longitudinal striation, and a cross striation consisting of alternate lights and dark bands. The longitudinal striation is due to the existence of minute strands, the *sarcostyles* or *fibrillæ,* which extend the length of the cell. The fibrillæ, which are supposed to represent the contractile elements of the fiber, are separated by a semifluid substance, the *sarcoplasm.* There is an arrangement of the fibrillæ into bundles, the *muscle columns,* which are separated from each other by a thicker layer of sarcoplasm than that between the fibrillæ.

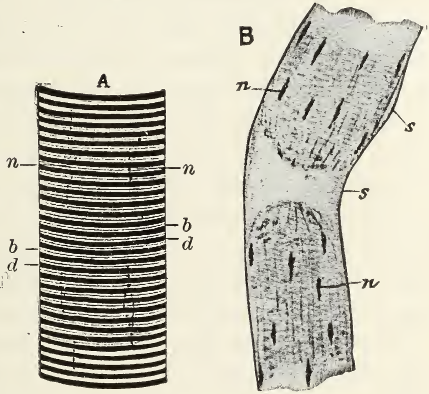

FIG. 47.—A, part of a fresh muscle fiber of a frog; B, the same after treatment with distilled water followed by methyl green. *b*, light bands; *d*, dark bands; *n*, nuclei; *s*, sarcolemma showing more clearly where the fiber is broken. (After Parker and Parker.)

The appearance of cross striation is brought about by the division of the fibrillæ into *segments,* or *sarcomeres.* The sarcomeres are separated from each other by a very fine dark line known as *Krause's membrane,* which extends not only across the individual fibrillæ, but across the sarcoplasm between the fibrillæ of the fiber. Krause's membrane lies in the center of a comparatively clear and lightly staining band formed by the opposed ends of the two contiguous segments. The middle portion of each sarcomere forms the so-called dark band. Across the center of this band there extends a second very delicate membrane, known as the *line of Hensen.* When the fiber is relaxed, this line may be seen to lie in the center of a comparatively light band, which is usually not evident when the muscle is in a contracted state. The dark bands of the muscle fiber are composed of material which is anisotropic, or doubly refracting, while the lighter areas on either side of Krause's membrane are isotropic, or singly refracting, like the sarcoplasm. When viewed with polarized light the differences between these two substances are clearly brought out.

A transverse section of a muscle fiber presents the appearance of a number of polygonal areas called *Cohnheim's fields,* which represent the cut ends of the muscle columns, the spaces between the fields being filled with sarcoplasm. Each of the fields shows a dotted appearance, due to the cut ends of the individual fibrillæ.

The muscle fibers of the heart differ from both of the above classes. They are cross-striated, but each fiber contains but a single nucleus. Each muscle cell is furnished with branches which connect with the branches of contiguous muscle cells, so that the whole mass forms a sort of network.

The tissue of the nervous system consists of *nerve fibers,* and nerve, or *ganglion cells.* Each nerve is composed of usually a large number of nerve fibers, held together by connective tissue and surrounded by a common sheath. A typical nerve fiber presents the following parts: a central strand, or *axis cylinder;* a sheath of fatty substance around this called the *medullary sheath,* or *white substance of Schwann;* and a delicate external membrane, *neurilemma,* or *sheath of Schwann.* At intervals constrictions occur, called the *nodes of Ranvier,* where the white substance is interrupted, although the axis cylinder and neurilemma are continuous. Immediately beneath the neurilemma occur the nuclei, each surrounded by a small amount of protoplasm. Each internodal segment, or space between two nodes of Ranvier, contains several oblique markings across the medullary sheath, which are known as the *incisures of Schmidt.*

The axis cylinder of a nerve is simply the elongated process of a ganglion cell, and under high magnification is found to be made up, much like a muscle cell, of very fine fibrillæ, with an intervening substance of more fluid consistency. The white or medullary substance contains a large amount of fatty material called myelin; if a fresh nerve is placed in water, this substance will swell up and collect in drops, giving the nerve a very irregular outline. The medullary sheath is supposed to act as a sort of insulator, like the coatings that are wound around an electric wire.

The nerve fiber, unlike that of muscle, is a composite structure, being formed of cellular elements of diverse origin. The sheaths of the nerve represent a series of cells which have become applied to but have an entirely different origin from the axis cylinder. The latter is always an outgrowth of a nerve or ganglion cell and is always of ectodermic origin. In the development of a nerve the axis cylinder is always the first part to make its appearance; as it grows out, pushing its way through the other tissues, it becomes surrounded with nucleated cells which flatten out and form the neurilemma; the white substance appears at a comparatively late period. The cells forming the sheath of a nerve are of mesodermic origin; the nerve fiber being therefore a structure derived from two germ layers.

The regeneration of nerve fibers which have been cut in two shows an intimate dependence of the axis cylinder upon the ganglion cell from which it arises. The portion of the axis cylinder distal to the cut, and consequently no longer connected with the nerve cell, degenerates, and becomes replaced by an outgrowth from the proximal part which follows the track of the degenerating fiber until the structure of the whole nerve is restored. This phenomenon is but a special case of the general principle that a portion of a cell

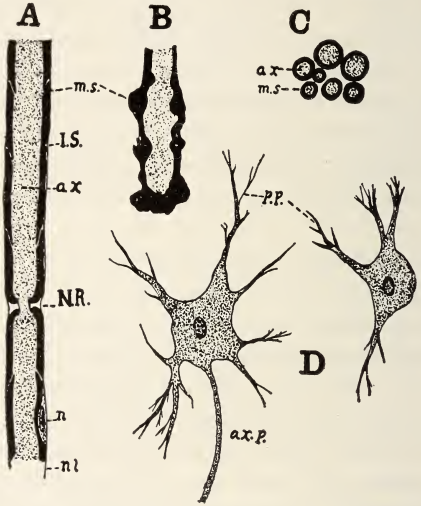

Fig. 48.—Nerve cells and fibers of the frog. A, fresh nerve fiber. B, nerve fiber with the myelin swollen through the absorption of water. C, cross section of nerve fibers. D, ganglion cells. *ax*, axis cylinder; *ax.p*, axis cylinder process of ganglion cell; *I.S*, incisure of Schmidt; *m.s*, medullary sheath; *n*, nucleus; *nl*, neurilemma; *N.R*, node of Ranvier; *p.p*, protoplasmic process of ganglion cell.

cut away from the part containing the nucleus invariably dies.

The nerve or ganglion cells are found in those parts which are spoken of as the nerve centers; viz. the brain, spinal cord, spinal ganglia, and the various ganglionic masses of the sympathetic system. These centers are made up of ganglion cells and their fibers, together with the connective tissue which binds them together and the vessels which supply them with nutriment and carry away their waste products. Ganglion cells are generally irregular in outline, with a nucleus near the center. Their cytoplasm is granular and under proper treatment shows a network, the strands of which are connected with the fibrillæ of the nerve fiber and other processes of the cell. Two kinds of processes are commonly distinguished: the axis cylinder process, which acquires a sheath and forms a part of a nerve fiber; and the protoplasmic processes, often several in number, which are shorter than the former and generally branched. Nerve cells are designated as *unipolar, bipolar,* or *multipolar,* according as they possess one, two, or three or more processes. Unipolar ganglion cells are found in the sympathetic ganglia.

CHAPTER VII

THE DIGESTIVE SYSTEM AND ITS FUNCTIONS

One of the characteristics of all forms of life is the need of food. The matter which composes the bodies of living organisms is being continually broken down and eliminated as waste products. New matter is consequently required to make good the loss if the vital process be kept going. In the frog a part of the material is taken from the oxygen of the air and from the water absorbed through the skin; but neither of these sources supplies the carbon, nitrogen, and other elements which form essential parts of all living substance. Life phenomena are associated especially with certain compounds called proteins. These are complex substances containing carbon, oxygen, hydrogen, and nitrogen, and, in many cases, also sulphur, phosphorus, calcium, potassium, sodium, magnesium, iron, chlorine, iodine, and occasionally other elements. Living substance, or protoplasm, is of protein nature, but it is probable that it is a group of compounds rather than a particular compound which we might express by a definite chemical formula. This living matter is the subject of chemical changes which are spoken of under the general term *metabolism.* The synthetic or building-up processes by which this substance is formed from simpler compounds are called *anabolism;* the opposite, or tearing-down processes by which it is resolved into simpler substances are known as *katabolism.* If an organism grows, it is evident that the anabolic side of the process must predominate over the katabolic. If katabolism predominates, or, in other words, if waste exceeds repair, the organism must diminish in size.

Now the function of food is not merely to compensate for the material which is broken down and eliminated, but to afford the energy necessary to carry on the various activities of the organism. Food is to the body what fuel is to a steam engine. The body is continually expending energy in the form of heat. The amount of energy lost in this way depends upon circumstances, and it may be comparatively small when the temperature of the animal is only slightly above freezing. But so long as life lasts there is some heat produced, and this heat results from the breaking down of some of the constituents of the body. Every movement which the frog performs involves the expenditure of energy, which must come ultimately from its food supply. An organism has often been compared to a vortex which maintains its form, while the material of which it is composed is subject to continual change. The matter composing the tissues of an animal is not the same during successive years, nor quite the same during successive days. It is being continually drawn through the vortex, where it gives up a part of its energy for the maintenance of the vital processes. The substances eliminated by an animal possess, therefore, less energy than the food material taken in. The amount of energy obtainable from a gram of any particular compound, such as cane sugar, when it undergoes decomposition, may be measured with considerable accuracy. If we measure the energy resulting from the splitting up of a certain amount of food substance and compare it with the energy obtainable from an equal amount of material after it has been eliminated from the organism, we should find the energy of the latter to be much less in amount. If now we could measure the energy expended by the organism in radiating heat and performing work during the time this material is consumed, we should probably find it to be equal to the difference between the potential energy of the food and that of the eliminated products. All of our experience goes to prove that the great law of conservation of energy applies as strictly to organisms as to the phenomena of the inorganic world. Living beings are not sources of energy in themselves, but are dependent upon their environment for energy as much as they are for the material composing their bodies.

In order that food material may be assimilated or built up into the tissues of the bodies, it must be rendered soluble, so that it can pass through the lining of the alimentary canal into the blood and lymph, and from these fluids through the walls of the cells in the different parts of the body. This process of converting food into a soluble state ready for absorption is called digestion. There are certain mechanical processes involved in digestion, such as (in higher animals) chewing the food, moving it about by the contractions of the walls of the stomach, and passing it along the intestine by the peristaltic contraction of the walls. The frog, however, like most lower vertebrates, does not chew the food taken into the mouth, but swallows it whole down the very distensible esophagus into the stomach, where it is acted upon by the gastric juice. The principal part of the process of digestion consists in the chemical changes produced in food by the action of the various digestive fluids. These changes are mainly of the nature of fermentations caused by substances called *enzymes*, or *ferments*. What the chemical nature of enzymes is still remains very much in the dark, since they cannot be completely freed from their association with other substances, but it has often been held that they are some form of protein. They have the property of causing chemical changes in other bodies without suffering any, or at least but very little, destruction of their own substance. A very minute amount of enzyme will cause the fermentation of a very large amount of other material. Near the freezing point the action of enzymes is almost nil; but with increase of temperature their action goes on much more rapidly until a maximum is reached beyond which further increase of temperature checks the process. A temperature of 100° C. destroys the action of most ferment entirely.

The substances which may serve as food are the *proteins, fats, carbohydrates,* water, vitamines, salts of various kinds, and a few other substances not falling into any of these categories.

The *proteins* are the most essential of the food materials, since they contain in addition to the carbon, oxygen and hydrogen found in carbohydrates and fats, the element nitrogen, and in many cases a certain number of other elements besides. The white of egg, muscle, in fact most animal foods with the exception of fat, consist largely of different forms of protein. In *fats* only carbon, oxygen, and hydrogen are present, and the proportion of oxygen is small. Chemically, fats are compounds of glycerin with some fatty acid.

The *carbohydrates* are compounds of carbon, oxygen, and hydrogen, the two latter elements being in the proportion in which they occur in water (H^2O); in other words, there are twice as many atoms of hydrogen as of oxygen in each carbohydrate molecule. Sugar and starch are examples of this class of food.

All of these classes of food are acted upon by specific ferments, which render them soluble and capable of diffusing through the walls of the alimentary canal. The action of the different digestive fluids will be described in connection with the organs by which they are produced.

The Esophagus and Stomach.—The esophagus is very short and remarkably distensible, as is proven by the rela-

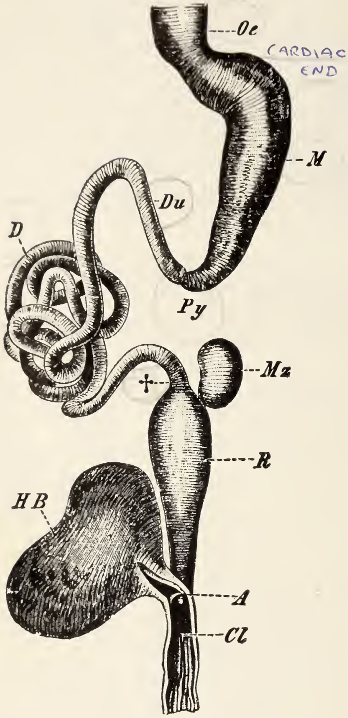

FIG. 49.—Alimentary canal of *Rana esculenta*. *A*, opening of the rectum into the cloaca, *Cl;* *Du*, duodenum; *D*, ileum; †, boundary between the latter and the large intestine, *R; HB*, urinary bladder; *M*, stomach; *Mz*, spleen; *Oe*, esophagus; *Py*, pylorus. (After Wiedersheim.)

tively large animals the frog is capable of swallowing. The inner surface is thrown into longitudinal folds which extend also into the stomach. There is no sharp line of demarcation separating the esophagus from the *pharynx* on the one hand and from the *stomach* on the other. The anterior end of the stomach is considerably wider than the esophagus, and the organ tapers gradually to the posterior or pyloric end, where it is separated by a constriction, the *pylorus*, from the small intestine. The *stomach* lies mainly in the left half of the body, and is curved so that the convex side is toward the left. It is suspended dorsally by a fold of peritoneum, the *mesogaster*, and from the ventral side arises a second sheet of peritoneum (the *gastro-hepato-duodenal ligament*), which extends to the duodenum and liver. The wall of the stomach is much thicker than that of the esophagus or the intestine. The inner surface is thrown into several longitudinal folds, which become less prominent posteriorly, and near the pyloric end entirely disappear.

In a cross section of the stomach one may observe a very thin outer layer composed of much flattened cells; this is the *serous coat* or *serosa,* and it is formed by the peritoneum. Within the serosa is a thicker layer, the *subserosa,* consisting mainly of connective tissue. This layer has been frequently described as a layer of longitudinal muscles, and it has the appearance of such; but if treated with the proper stains, it can readily be shown to be mainly connective tissue. Some writers (Valatour, P. Schultze), have been disposed to deny the existence of longitudinal muscles in the frog's stomach. In sections across the cardiac end of the stomach, however, one may detect a few muscle fibers among the connective tissue, and in the pyloric end, according to Gaupp, there are a few longitudinal fibers which are continuous with those of the intestine.

Within the subserosa is a thick layer of *circular muscles* which becomes thicker toward the pylorus. Internal to the circular muscles is a layer of connective tissue, the *submucosa,* in which there are numerous blood vessels. The tissue of the submucosa extends into the folds of the inner coat. Between the mucosa and submucosa there is a thin muscular layer, the *muscularis mucosæ,* composed of an inner layer of circular fibers and an outer stratum of longitudinal ones.

The *mucosa* of the stomach is a thick layer composed of glands embedded in a supporting matrix of connective tissue. These glands represent invaginations of the epithelium lining the inner surface of the stomach. They are elongated tubular structures set very closely together, and frequently more or less branched. The glands differ in structure at the two ends of the stomach. In the cardiac region the glands are very long, the mouth of the gland is quite deep, and lined with elongated cells whose clear inner ends are filled with a substance which probably forms mucus. Near the outer end of the gland the cells are more elongated, like those of the surface epithelium; behind the clear substance the cytoplasm of the cells is granular, the nucleus is elongated, and the outer ends are drawn out into a long narrow process. Passing down the mouth of the gland the cells become shorter, the nuclei more rounded, and the tail-like processes finally almost disappear. In the neck regions of the gland there are usually a few rather large cells containing a large clear vacuole which pushes the nucleus and most of the cytoplasm to one side. It is usually in the region of these clear cells that the glands branch. The cells composing the body of the gland lie just below the clear cells and present a very different appearance from the cells lining the mouth and neck. They are polygonal in outline, with large round or oval nuclei and granular cytoplasm; the lumen, or central cavity of the gland in this region, is very small and at times almost obliterated. The lower ends of the glands extend as far as the muscularis mucosæ.

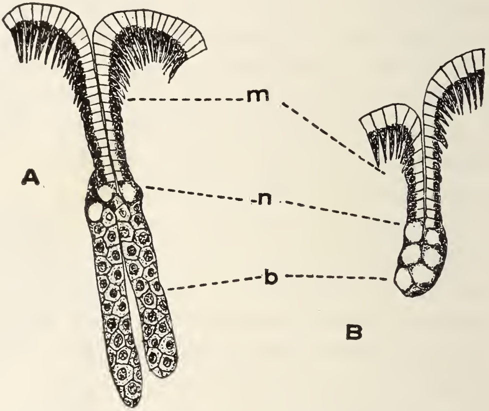

Fig. 50.—Glands of the stomach. *A*, from cardiac end; *B*, from pyloric end; *m*, mouth; *n*, neck; *b*, body of gland.

In the pyloric end of the stomach the glands are less deep. The mouth of the gland, however, is relatively deeper than in the cardiac end, but is lined by much the same kind of cells. At the bottom of the gland there are several large polygonal cells with very large clear vacuoles much like the cells in the necks of the cardiac glands. Occasionally there may be a few polygonal granular cells below these. In general, however, the pyloric glands may be said to correspond to the mouth and neck of the glands of the cardiac end of the stomach. Like the latter, these glands frequently branch, but the branching commonly takes place above the body of the gland.

The histological structure of the esophagus resembles in a general way that of the stomach. There is an external layer of longitudinal muscles and an inner layer of circular fibers, but both are comparatively thin. A muscularis mucosæ is lacking except close to the stomach, where it is represented by a few scattered fibers. The mucosa is well developed; the surface epithelium consists of cylindrical mucous cells with ciliated cells scattered among them.

The glands of the mucous layer are comparatively large and much branched; and in many cases the branches, which may be as many as fifteen in number, redivide. Near the mouth the glands are small in size, and toward the stomach they become smaller again and more simple in structure. The cells of the body of the esophageal glands have a granular appearance much like the corresponding cells of the glands of the cardiac end of the stomach. The mouths of the glands are lined with a short cylindrical epithelium with occasional ciliated cells.

Gastric Digestion.—In the stomach the food is subjected to the action of the gastric juice, which is secreted by the glands of the mucosa. Gastric juice is acid in reaction from the presence of a small quantity of free hydrochloric acid, and it contains also a ferment, *pepsin,* which acts upon the proteins, converting them into soluble *peptones.* Neither the fats nor the carbohydrates undergo digestion in the stomach. By digesting out the protein portion of foods in which fats and carbohydrates are contained the gastric juice helps to render these substances more readily digestible by other fluids.

The action of the gastric juice of the frog may be readily demonstrated by siphoning off some of this fluid from the stomach by means of a bent glass tube and placing in it a small bit of the white of a hard-boiled egg. The piece of egg after a time will be seen to be corroded, and finally it will become entirely dissolved.

The secretion of the esophagus has a strong digestive power, but its reaction is alkaline instead of acid, and it is capable of acting only after it has been rendered acid through mixture with the fluid of the stomach (Nussbaum).

When gastric digestion is completed, the food passes through the pylorus into the small intestine.

Changes in the Glands during Digestion.—The changes undergone by the glands of the esophagus and stomach have been studied by Partsch, Swiecicki, Nussbaum, Grützner, Langley, and Sewall. In frogs which have been kept for several days without food Langley found the cells of the body of the gland to be enlarged so as practically to obliterate the central canal. The contents of the cell are uniformly granular and the cell outlines are very indistinct. "In one to two hours after feeding the lumina begin to be obvious, and the granules to disappear from the inner border of the cells. . . . Up to the fifth hour these changes become more and more marked, and at the same time the cells and the remaining granules they contain become distinctly smaller, and the cell substance stains more deeply. . . . At the period of maximum change the nucleus is much larger compared with the cell substance than it is during rest; it is still surrounded by finely granular protoplasm, and it is sometimes placed near the outer border of the cells. The return to the normal appearance begins about the fifth hour, so that during the greater part of the digestive period the formative processes go on whilst the secretory are still active. In twenty-four hours the glands have nearly or altogether returned to the hungry condition." The time and extent of the changes produced in the glands were found by Langley to vary enormously with the amount of food given and the state of the frog. "If a frog is fed with several worms so that the stomach is much distended with digestible food, the changes are greater and persist for a much longer time. . . . In twenty-four hours the glands, instead of having returned to the hungry state, are still small and consist of somewhat small cells with a more or less distinct inner non-granular border; the lumina are frequently large." The increase in the size of the lumen is accompanied and probably caused by the

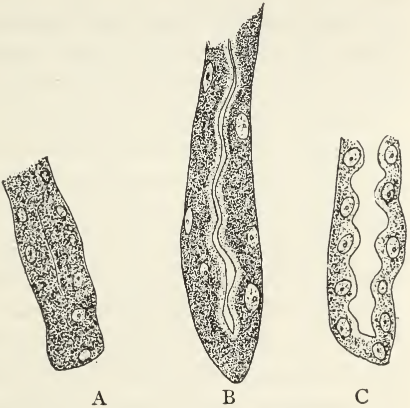

Fig. 51.—Showing changes in the gastric glands of the frog. A, gland from a hungry frog which had not been fed for five days. The cell outlines are indistinct and the granules are scattered throughout the cells. B, gland three hours after a meal; the granules have disappeared along the inner border of the cells; lumen of the gland visible. C, gland twenty-five hours after a heavy meal; the cells are shrunken and not so full of granules. (After Langley.)

decrease in the size of the cells. "In frogs to which an excess of food has been given, the non-granular inner zone is usually most obvious about the eighteenth or twentieth hour after feeding. The cells there have increased and are still increasing in size; the greater clearness with which the non-granular zone can be seen is then probably due to the net increase in the cell granules taking place more slowly than the increase in the cell protoplasm."

Langley found that the effect of fasting in winter is not very great; the cells of the gland become somewhat smaller, but they are fairly well filled with granules. If, however, the winter frogs are kept warm, or if frogs at other times of the year are kept for a long time in a fasting condition, the cells shrink in size and become clear along the inner border as they do after secretion.

The mucigen content of the cells lining the mouth of the gastric glands is large in amount before and for some time after a meal, but during the height of the digestive process it becomes much diminished. The changes in the pyloric glands are much like those in the mouth and neck of the cardiac glands. "The maximum amount of mucigen is contained by the pyloric and similar gland cells after a moderately prolonged fast. The minimum amount of mucigen is contained by these cells twelve to eighteen hours after a heavy meal; it is then only with difficulty that the mucous can be distinguished from the subcubical cells."

The changes undergone by the esophageal glands differ somewhat from those of the glands of the stomach. Langley and Sewall, and also Grützner, found that in normal hungry frogs the cells were granular throughout. Some time after food is taken the granules begin to disappear near the outer end of the cell; *i.e.* the end away from the lumen of the gland instead of in the opposite end as in the gastric glands. The outer clear zone thus produced increases in size as digestion proceeds, and the whole cell grows smaller. "As the outer zone increases, the granules in the inner end become smaller. The diminution in the size of the granules is very marked in cells in which the outer zone takes up the larger part of the cell. . . .

"During the first hour and a half after feeding no distinct change is to be seen. After this period a diminution in the number of granules in the outer half of the cell becomes obvious. Usually this is first seen in the glands close to the stomach. The disappearance of granules in the outer portion of the cell goes on so that a clear zone is formed. The clear zone steadily increases until the sixth to twelfth hour, or even later, the time varying with the state of the animal and the amount of food given. The glands then begin to become more granular, the time of complete recovery varies enormously: in some cases the glands are throughout granular in twenty-four hours from the time of feeding the animal, in others they do not become so for several days."

If the frog is fed with pieces of sponge instead of food, a secretion is set up both in the stomach and the esophagus, the change being as a rule the greater, the larger the sponge. Changes take place in the cells similar to those produced by digestible food, but they occur much more slowly, beginning generally only three or four hours after the sponge is placed in the stomach; the granules begin to increase again in the esophagus only after some days.

Of what significance are these changes in the granular contents of the gland cells? It is evident that they have something to do with the formation of digestive fluids of the esophagus and stomach, and it is probable that the granules are composed of a substance which is transformed into pepsin. That they are not composed of pepsin itself, but of some substance which has been called *pepsinogen,* is indicated by the following experiments. "If the esophagus or stomach of a frog be placed in glycerin as rapidly as possible after removal from the body, the glycerin extract has only a weak peptic power. If the esophagus or stomach of a frog be kept moist for twenty hours before it is placed in glycerin, the glycerin extract has a very much greater peptic power. If the esophagus and stomach which has been extracted with, say, 5 cu. cm. of glycerin for a week be washed free of glycerin and treated with 5 cu. cm. of dilute hydrochloric acid, then an enormously greater amount of pepsin is found in the acid than is found in the glycerin extract."

The amount of pepsin content is greatest in those glands in which there is the greatest number of granular cells. The pepsin content of the esophagus was found by Swiecicki, Langley, and Sewall to be greater than that of an equal area of the stomach. In the pyloric region, where the granular cells are few in number, the pepsin content of the glands is much less than in the cardiac end. Langley found that if pieces of equal size were cut out of the esophagus, cardiac end, middle, and pyloric end of the stomach, and the pepsin content of each estimated, the power of converting protein was much the greatest from the piece from the esophagus, and became less respectively in the pieces from the other regions named. Partsch, Nussbaum, Swiecicki, Langley, and Sewall have all investigated the relative digestive power of the glands well filled with granules and glands from which the granules have mainly disappeared, and all agree that the pepsin content of the former is much the greater.

Rapidity of Digestion.—The digestive processes of the frog compared with those of the higher vertebrates proceed slowly, due probably to the fact that the frog is a cold-blooded animal. The length of time taken to digest a meal varies with the amount of food. Langley found that a small earthworm was digested in somewhat less than twenty-four hours, but if several worms were given, they do not disappear from the stomach until a longer period. The rate of digestion, as Riddle has found,. is rapidly increased by a rise of temperature from 25° C. to 30° C.

Structure of the Intestine.—The small intestine begins just behind the pyloric constriction, and runs forward as the *duodenum* for some distance, when it turns abruptly backward as the *ileum,* which after coiling about in an irregular manner, widens out abruptly into the large intestine near the posterior end of the body. The diameter of the small intestine, which is nearly uniform throughout its course, is much less than that of the stomach, and its walls are much thinner. The intestine is fastened by a mesentery to the mid-dorsal portion of the body cavity, and its duodenal portion is connected to the liver and stomach by the previously mentioned remains of a ventral mesentery, the gastro-hepato-duodenal ligament.

A cross section of the small intestine shows the following layers: At the outside is a very thin coat of *peritoneum* similar to that coating the stomach. Within this is a well-marked layer of *longitudinal muscle fibers;* then comes a thicker layer of *circular muscle fibers,* and within this the *submucosa;* the latter is connective tissue layer containing numerous blood vessels. There is no sharp line of division between the submucosa and the connective tissue portion of the mucosa; the latter is more dense, and contains more cellular elements; between the mucosa and submucosa are large, irregular lymph spaces which frequently extend into the folds. The existence of a muscularis mucosæ has been affirmed by some investigators (Howes, Grimm, Langer, Ecker), but others (Valatour, Heidenhain, Gaupp) were unable to verify the observation. At most this layer can consist of but a few scattered cells. In sections which I have studied there are connective tissue fibers just below the epithelium which give an appearance very much like that of a thin muscle layer, but I have been unable to convince myself of the existence of muscle cells in that region.

The epithelium of the mucosa consists of a layer of cylindrical cells among which two varieties may be distinguished, the *goblet*, or *beaker* cells, and the ordinary type of *absorptive cells.* The goblet cells may be distinguished by the large, oval vacuole, the inner end of which is filled with a transparent, more or less granular substance, which probably gives rise to mucus. The nucleus is situated near the base of the cell, and the part between the nucleus and the inner globule is constricted, and contains several small vacuoles (Bizzozero). The absorbing cells are narrow, with an oval nucleus near the base; the outer free border is thickened, and shows a cross striation. According to Bizzozero the mucous cells do not arise from the transformation of cells of the ordinary type, as Paneth maintains, but are a distinct kind of cell. The young stages of the goblet cells may be seen wedged in between the bases of the other cells, and all intermediate stages between these and the mature type may be traced.

Leucocytes are often found between the epithelial cells, and also wandering cells of larger size with bodies of various kinds in their protoplasm (Heidenhain, De Bruyne). Wandering cells containing pigment have been found to occur in the lower end of the small intestine (Oppel).

The mucosa of the small intestine is thrown into numerous folds, but there are no true villi nor definite glands nor crypts such as occur in the higher vertebrates. Just behind the pylorus the folds take the form of an irregular network, but a short distance farther back they become arranged in two series of transverse semilunar plications the free edges of which are produced backward, forming a double series of pockets which tend to check the flow of food in the direction of the stomach. The pockets are connected by smaller folds which run mainly in a longitudinal direction. Farther back, a little beyond the middle of the intestine, the folds lose their regular arrangement, and in the posterior third they assume a longitudinal direction.

The *large intestine* is composed of the same layers as the small. The inner surface is thrown into folds, which at the proximal end form an irregular network, but in the rectum they become longitudinal. The epithelium of the mucosa consists of cylindrical cells, among which numerous goblet cells are to be found.

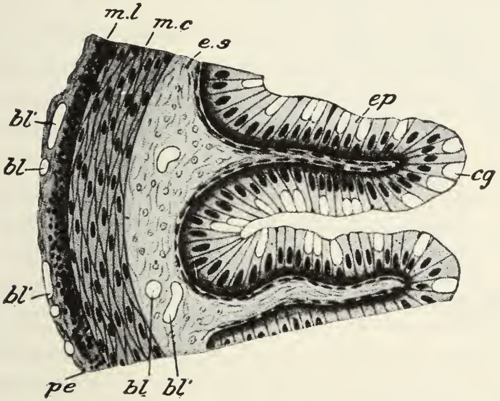

Fig. 52.—Part of a cross section of the small intestine of the frog. *bl*, blood vessels; *cg*, goblet cells; *ep*, ordinary epithelial cell; *e.s*, submucosa; *m.c*, circular muscles; *m.l*, longitudinal muscles; *pe*, peritoneum. (After Howes.)

The Pancreas.—The pancreas is an elongated gland of irregular shape situated between the stomach and the duodenum, and extending from the liver to within a short distance of the pylorus. It is traversed by the common bile duct into which its ducts enter. Of these there is a principal duct, and several smaller ducts from the portion of the gland near the liver.

The pancreas is a much-branched tubular gland, the terminal branches of the glands being often curved and twisted in an irregular manner. The tubules are coated externally with a basement membrane, and held together by a delicate connective tissue in which lie the blood vessels and nerves.

The secretory cells of the tubules contain numerous zymogen granules, which, when the frog is in a hungry state, are found in great abundance, especially at the inner or free end of the cell. These disappear after the animal is fed, like the granules in the glands of the stomach. A peculiar darkly staining body (paranucleus, nebenkern) is usually found near the nucleus toward the outer, or basal end of the cell.

The fluid secreted by the pancreas is alkaline, mainly from the presence of sodium carbonate (Na_2CO_3), and it contains three ferments: *steapsin,* or lipase which causes a splitting of fats into fatty acid and glycerin; *amylopsin,* which converts starch into sugar; and *trypsin,* which converts proteins into various simpler compounds and finally into amino acids. Trypsin carries protein digestion farther than it is carried by the pepsin of the gastric juice. Trypsin differs also from pepsin in that it acts in an alkaline or neutral medium; in a strongly acid medium its action is entirely stopped.

The Liver.—The liver is a massive gland whose secretion, the bile, is conveyed to the intestine through the *bile duct* along with the fluid secreted by the pancreas. The organ is of a dark reddish color, and is divided into a right, a left, and a middle lobe. The middle lobe is small and concealed from view by the heart. The left lobe is divided by an oblique incision into an anterior and a posterior portion, the latter occupying the middle of the posterior part of the liver.

The greater portion of the liver is covered by a closely adherent layer of peritoneum, which is continued to form attachments with the pericardium, ventral body wall, dorsal body wall, and the stomach and intestine.

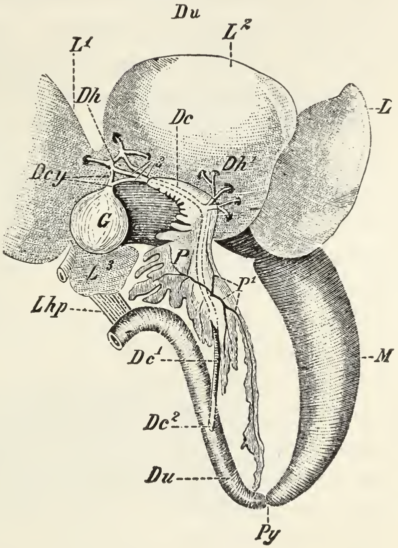

Fig. 53.—Liver and pancreas of frog. *Dc*, common bile duct; *Dcy*, cystic ducts; *Dh*, Dh^1, hepatic ducts, which with the cystic ducts combine to form the common bile duct; *G*, gall bladder; *L*, L^1, L^2, L^3, lobes of the liver turned forwards; *Lhp*, hepatoduodenal ligament; *M*, stomach; *P*, pancreas; P^1, pancreatic ducts entering the common bile duct; *Py*, pylorus. (After Wiedersheim.)

The bile duct is formed by the confluence of the *hepatic ducts* leading from the lobes of the liver. The *gall bladder* lies on the dorsal side of the liver, between the right and left lobes. It is rounded or oval in outline, and usually appears green from the color of the bile seen through its thin walls. The gall bladder is connected with the cystic ducts, the one leading to one of the hepatic ducts, the other joining the common duct farther down, usually within the substance of the pancreas.

The histological structure of the liver differs considerably from that of the pancreas, although both organs are to be regarded as much-branched, tubular glands. The terminal branches inclose the ultimate ramifications of the hepatic ducts, or *bile capillaries.* These capillaries come to branch and anastomose in an irregular manner so as greatly to obscure the original tubular structure of the organ.

The *bile capillaries* may be surrounded by five or six cells in cross section, or they may run between but two cells; they also give off lateral branches which penetrate the cell bodies. The secretory cells of the liver are cubical or polyhedral in form, with large nuclei; the cytoplasm contains protein granules, small drops of fat, lumps of glycogen, and often pigment.

The liver receives blood from two sources: (1) the *hepatic artery,* which conveys arterial blood, and (2) the *portal system,* which includes the *anterior abdominal vein* from the ventral body wall, and the *portal vein,* which receives blood from the stomach, intestine, pancreas, and spleen. The materials absorbed by the blood from the organs of digestion pass, therefore, through the liver before entering the general circulation. All of the blood leaves the liver by the hepatic veins, which lead from the dorsal side of that organ to the posterior vena cava.

The liver is well supplied with lymph vessels which form perivascular lymph spaces around the capillaries.

The liver of the frog generally contains a considerable amount of pigment. Two forms of pigment occur, according to Leonard, the black or dark brown, and the golden. A certain amount of pigment granules occurs in the ordinary cells of the liver parenchyma, but most of this substance is found in pigment cells which are scattered about through the whole organ.

Eberth held that the pigment cells lie within the blood vessels, and that they resulted in large part at least, from the transformation of leucocytes. Ponfick and Leonard regard them as lying outside the blood vessels in the perivascular lymph sinuses. Braus, however, finds pigmented cells both in the blood and in the lymph vessels.

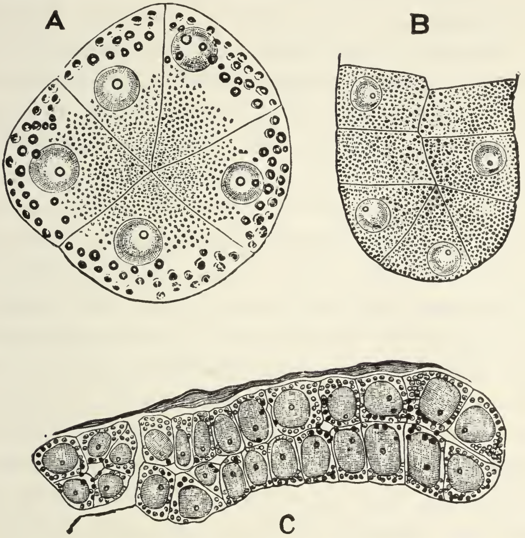

FIG. 54.—Three phases of the hepatic cells of the frog. A, cells rich in glycogen taken from a frog during winter. There are numerous proteid granules around the lumen, and several larger fat globules toward the outer ends of the cells. B, cells poor in glycogen taken from a winter frog that had been kept for ten days at a temperature of 22° C. The proteid granules are scattered uniformly throughout the cell. Much the same appearance is presented by the hepatic cells of a frog in summer. C, cells taken from a frog starved for a long time in summer. The cells are shrunken and the glycogen has almost disappeared. (From Foster's Physiology, after Langley.)

There is no evidence that the pigment cells are derived from the ordinary secreting cells of the liver (Oppel). Colorless amœboid cells have been observed in the lymph spaces of the liver, and it is not improbable that a large part of the pigment cells may result from the accumulation of pigment by such cells which have wandered into the liver from other sources.

The secreting cells of the liver present different appearances in relation to changes in their activity. The granules of the cells were found by Langley to increase in number after a meal. "The changes are much more marked when the cells have, to start with, a small outer non-granular zone; in such cases in the 6th to 8th hour of digestion, the outer zone is large, and in the 24th to 30th, the cells become granular throughout." The decrease of granules was found, as a rule, to be accompanied by an increase in the glycogen in the cells, and *vice versâ.* From analogy with the behavior of similar granules in other gland cells, Langley considers the granules in the liver to be concerned in the secretion of bile. Lahousse finds that granules disappear from the cell almost entirely eleven or twelve hours after feeding. Five or six hours after food is given the liver cells are considerably enlarged, and the capillaries congested. By the eleventh hour after feeding the congestion has disappeared, and the cells diminish somewhat in size.

Functions of the Bile.—The bile, which is secreted by the cells of the liver, makes its way by means of the gall capillaries to the hepatic ducts, and thence into the gall bladder, where it is stored until food passes out of the stomach, when it is discharged through the common bile duct into the intestine. Bile is an alkaline fluid of complex composition. Some of its constituents, such as the fatty substance, cholesterin, and the bile pigments, are simply waste products, but others play a certain part in the digestion. In higher vertebrates it has been shown that the bile helps to emulsify fats and facilitates their absorption from the intestine.

Intestinal Digestion and Absorption.—The food, when it is passed from the stomach into the duodenum, possesses an acid reaction due to the acidity of the gastric juice with which it is mixed. In the duodenum it becomes mixed with the pancreatic juice and bile, both of which are alkaline, and its acidity is neutralized. The proteins which may have escaped the fermentative action of the pepsin in the stomach, together with the peptones which result from peptic digestion, are acted upon by the trypsin of the pancreatic juice and converted into simpler compounds, chief among which are the amino acids. The starchy constituents of the food are converted into sugar by the secretion of the pancreas, and the fats are emulsified and split into fatty acids and glycerin by the pancreatic ferment lipase.

The rôle of the intestinal juice in the frog is little known, but in the mammals it has several important digestive functions. It contains a ferment, erepsin, which converts peptones and other products of protein digestion into amino acids; it contains a ferment which splits the more complex sugars, the disaccharids, into the simpler monosaccharids, dextrose, lævulose and galactose; it secretes a substance which activates the protein-splitting enzyme of the pancreas; and it produces still other substances which play an important part, directly or indirectly, in digestive processes.

When the various constituents of the food are digested, or rendered soluble by the action of the digestive juices, they are absorbed through the walls of the intestine into the blood and lymph. In the higher vertebrates most of the fat is taken up by the lymph vessels of the intestine, and it is generally held that a large part of the sugar and products of protein digestion is absorbed by the capillaries of the blood vessels. Whether the absorbed materials follow the same course in the frog is not certainly known.

Probably but a small fraction of food is absorbed by the stomach; most of the cells of the lining of that organ are of the secretory type. The inner surface of the intestine is especially adapted for absorption on account of the large number of folds it contains which give an extensive surface for contact with the food. The numerous blood and lymph vessels near the epithelium of the mucous layer afford ready means of transport of substances which diffuse into them through their walls.

The Glycogenic Function of the Liver.—One of the principal functions of the liver is the formation of *glycogen,* a carbohydrate, having the same empirical formula as starch, $C_6H_{10}O_5$. This substance is, in fact, often referred to as "animal starch," and it possesses several points of resemblance to the starch found in plants. It is soluble in water, forming a milky white solution. When treated with iodine its solution gives a reddish, port-wine color. In its dry state it forms a white powder.

Glycogen occurs in the cells in the form of granules or even lumps of considerable size. Its presence may be detected by staining with iodine sections of liver prepared by hardening the organ in absolute alcohol and then embedding it and cutting without allowing the tissue to pass through water. In this way the glycogen may be prevented from dissolving out. Glycogen may be prepared by throwing the liver of a recently killed frog into boiling water, then grinding it up with sand in a mortar, extracting with water and filtering. A milky fluid will thus be produced which can then be evaporated until the residue is obtained, which is largely glycogen.

If the liver of a frog be left for some hours before boiling and then tested for glycogen, it will be found that the amount of this substance obtained is comparatively small, and if appropriate tests be applied, it may be shown that a certain amount of dextrose has appeared in its stead. The liver contains a ferment which has the power of converting glycogen into dextrose; as the ferment is destroyed by boiling, a greater amount of glycogen can be obtained from the liver if it is boiled soon after it is removed from the body.

The glycogen content of the liver not only increases in the fall and decreases in the spring and summer, but it undergoes changes in relation to variation in the amount of food, and to changes of temperature of short duration. After feeding there is a slight increase in the amount of glycogen in the liver; this slowly disappears if the frog is kept several days without food. In winter, if frogs in which the liver is well filled with glycogen be kept for a few days in a warm room, the glycogen content of the liver rapidly decreases. On the other hand, if summer frogs, which generally contain little glycogen, be kept at a low temperature for several days, the amount of glycogen in the liver becomes markedly increased.

The glycogen stored in the liver may be given out slowly into the blood in the form of dextrose, into which it is changed by an enzyme in the hepatic cells. The liver acts as a sort of reservoir of food, storing it up in a comparatively insoluble form when it is in excess, and expending it gradually to tide over periods of fasting. The frog begins its long period of hibernation with a large reserve supply of this material, which is slowly used up during the winter and more rapidly consumed in the early spring.

While glycogen occurs in greatest abundance in the liver, forming at times over 8 per cent of the weight of that organ, it is found also in many other organs of the body. The muscles contain a considerably less percent of glycogen than the liver; but owing to their much greater bulk their total glycogen content may exceed that of the liver. although it is usually less. Smaller quantities of glycogen are found in the ovaries. central nervous system, and skeleton.

Periodic Changes in the Liver.—The liver of the frog undergoes important changes in relation to food and temperature. There is a regular seasonal change which affects not only the size and general appearance of the organ, but also the amount of pigment contained in it, and the contents of the secreting cells. In the summer the liver is usually large, comparatively light in color, and furnished with little pigment (Weber, Eberth, Leonard). In the winter and early spring, before the feeding period, the liver becomes relatively small in size and dark in color, the number of pigment cells increases, and there are more pigment granules contained in the secreting cells. Miss Leonard, who has made a study of the percentage of pigment in relation to the whole mass of the organ in different times of the year, arrives at the following result:—

November, .7 per cent
December, 4.13 per cent
April, 11.12 per cent
June, 2.77 per cent
July, .68 per cent

It may thus be seen that the relative amount of pigment contained in the liver increases through the winter, then diminishes in the spring after the period of feeding.

The same observer found that in winter and early spring the average size of the secreting cells and also their nuclei was smallest in early spring, and increased during the summer as is shown in the following table:—

	November	December	April	June	July
Average diameter of cells	.0292 mm.	.0162 mm.	.012 mm.	.0172 mm.	.0274 mm.
Average diameter of nuclei	.006 mm.	.0044 mm.	.0076 mm.	.0065 mm.	.0065 mm.

Similar measurements by Funke gave results approximately the same as those obtained by Miss Leonard. The minimum size of the cells in *R. temporaria* according to Funke occurs in May, the maximum in July and August. In *R. esculenta* the minimum falls in June and the normal size is reached two or three months later, but there is no well-defined period of maximum growth. In both species the minimum size of the liver cells as well as the liver as a whole occurs at the time of breeding.

The fat content of the liver was found by Funke to vary in an irregular manner both in *R. esculenta* and *R. temporaria.* In the first species the fat content of the liver in many instances almost entirely disappeared in June. During the summer fat is stored in the liver, and in the winter it suffers very little diminution if it does not actually increase in amount. In *R. temporaria* the amount of fat in the liver is very small compared with that in *R. esculenta,* and no definite conclusion could be drawn regarding the general course of its seasonal changes. According to Langley's observations upon frogs in England, "the fat in the liver cells reaches its maximum amount in February and March. In January it is as a rule somewhat less. In April it rapidly decreases, from May to December it is present in comparatively small though varying amounts. It is usually present in minimum amount in September and October."

Miss Leonard found that the relative proportion of blood vessels to the whole mass of the liver varies in different seasons. The following table represents the percentage of area of cross sections of blood vessels in relation to the whole areas of the sections studied, during different seasons of the year:—

November, 17.23 per cent
December, 10.105 per cent
April, 7.47 per cent
June, 9.82 per cent
July, 6.58 per cent

Comparing this with the previous tables, it will be seen that as the size of the cells of the liver increases, the relative proportion of blood vessels and pigment to the whole mass of the liver decreases.

Variations in glycogen contents of the liver at different times of year have been studied by several investigators (Langley, Luchsinger, Von Wittich, Barfurth, Langendorff and Mozeik, Athanasiu). In the spring during the breeding season the amount of glycogen is at its minimum, there being often scarcely a trace of this substance in the liver cells. After the frog begins to take food glycogen slowly accumulates, but during the active life of the animal in summer it is not stored in the liver in any great quantity. In the fall, when the weather becomes cooler and the frogs less active, the glycogen becomes much increased in amount. During the winter sleep glycogen is used up only to a slight extent, but as the temperature rises on the approach of spring, and the sexual products are maturing, the store of glycogen is rapidly diminished. Athanasiu, who has investigated the amount of glycogen in the whole body of the frog (*R. esculenta*) at different seasons, finds that the minimum quantity (slightly over one tenth per cent of the body weight) occurs in June, then there is a slow accumulation until September, when there is a rapid increase to the maximum (1.43 per cent of the body weight) followed by a slow diminution during the winter and then a rapid falling off in the spring. The amount of glycogen in the liver alone was found to increase and decrease along with that of the body as a whole. The amount of glycogen in the liver was found to be more variable than the glycogen content of the rest of the body, exceeding the latter in the fall and early winter, while in the spring the reverse relation obtains.

The variations in the weight of the liver as a whole have been studied in detail by Gaule in *Rana esculenta*. The weight of the liver was found to be relatively greater in males than in females and to possess a somewhat greater range of seasonal variations. The following table taken from Gaule's estimates shows the weight of the liver per gram of body weight in the two sexes during the different months of the year:—

	Male	Female
January	.05775	.0430
February	.0436	.0382
March	.0502	.0348
April	.0370	.0323
May	.0370	.0232
June	.0244	.0214
July	.0317	.0311
August	.0360	.0360
September	.0710	.0509
October	.0571	.0574
November	.0723	.05882
December	.06001	.0567

The numbers in the table represent the average weights of the livers and bodies of a number of individuals (usually 15 to 25) sacrificed for each determination. The variations in the size of the livers are thus shown to correspond in general to the variations in the glycogen content. In November the liver may become between two and three times as large as it is in June.

Fate of the Different Kinds of Food.—The functions of food, as we have seen, are to build up tissue and to supply the organism with the energy for carrying on its vital processes. Only the proteins are capable by themselves of forming living tissue, as they alone possess all the necessary elements. The fats and carbohydrates, however, are also to a certain extent tissue builders, but they can supply only three of the elements of living matter; namely, carbon, oxygen, and hydrogen.

The fat stored in the cells of adipose tissue may be obtained from fat contained in the food, but it may also be derived from carbohydrates and even from proteins.

The principal functions of both fats and carbohydrates is the production of energy. These compounds are split up and oxidized to carbon dioxide and water, yielding energy in this way for the performance of bodily movements and the maintenance of the temperature of the animal. Energy is also derived from the breaking down of proteins, so that it may be said that all of the principal classes of foods are tissue builders and also energy producers. After the food stuffs have played their part and become broken down into simpler compounds, they are eliminated from the body through the organs of respiration and excretion.

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CHAPTER VIII

THE VOCAL AND RESPIRATORY ORGANS

In the vertebrate animals the vocal and respiratory organs are intimately associated owing to the fact that the production of sound is caused by the expulsion of air from the lungs. With the exception of the sounds made by a few fishes the voice makes its first appearance in the vertebrate series among the Amphibia. In the Urodeles, or lowest division of the group, the voice is, as a rule, feebly developed or entirely absent. It attains its maximum development among certain of the Anura, but in not a few members of this order it is small and weak.

The Vocal Apparatus:—The sound-producing organs of the frog are located in a sort of box called the *larynx,* situated just below the pharyngeal cavity at the beginning of the entrance into the lungs. The larynx opens into the pharynx through the slit-like *glottis* above, and by a pair of openings behind, into the lungs. It is held between the stout, bony thyroid processes of the hyoid apparatus, to which it is attached by muscles as well as connective tissue. The skeleton of the larynx is composed mainly of the *cricoid* and *arytenoid cartilages.* The former consists of a slender ring surrounding the larynx and lying in nearly the same plane as the thyroid processes of the hyoid, to which it is closely attached; at its posterior end it is produced into a spine which extends backward between the lungs. From near the middle of its ventral surface it gives rise to a sort of loop, the tracheal process, which is bent backward and serves as a means of attachment for the necks or roots of the lungs. The *arytenoid cartilages* are a pair of semilunar valves, which rest upon the cricoid cartilage; their upper edges form the lateral margins of the glottis; they afford attachment to muscles by which the glottis may be opened or closed. The true sound-producing organs consist of a pair of elastic bands, the *vocal cords*, extending longitudinally across the larynx. They may easily be seen from above by spreading apart the two sides of the glottis, or from below by removing the membranous floor of the laryngeal cavity. Their median edges are thickened and lie near each other in the middle line. Sound is produced by the expulsion of air from the lungs which sets the free edges of the vocal cords in vibration. Variations in the

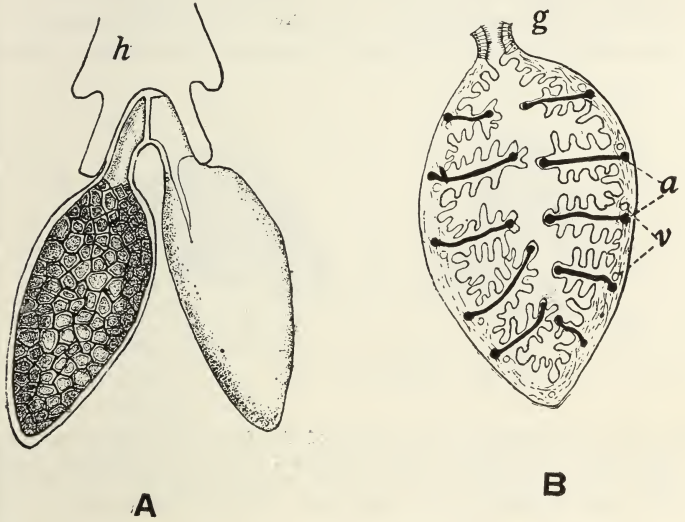

Fig. 55.—Lungs of the frog. A. ventral vein, the right lung cut open to show the inner surface; *h*. hyoid. B, section through lung; *a*. artery; *g*. glottis; *v*. vein. (B, modified from Renaut.)

sound are caused by altering the tension on the cords through the action of the laryngeal muscles. The vocal apparatus of the male frog is much larger than that of the female.

The males of many species of Rana possess a pair of *vocal sacs* situated at the sides of the pharynx. These sacs are out-pocketings of the pharyngeal wall which extend backward between the skin and the body. They communicate with the mouth by small openings in the floor a short distance in front of the angle of the lower jaw. Besides a lining of mucous membrane they possess a muscular coat which consists of fibers drawn out from the subhyoideus muscle. The vocal sacs are distended during the croaking of the frog through the pressure of the air in the buccal cavity. They serve as resonators to reënforce the sound produced by the vocal cords. They are absent in the female. Their size in the males of *Rana pipiens* is very variable; in some of the varieties of this species they are absent entirely.

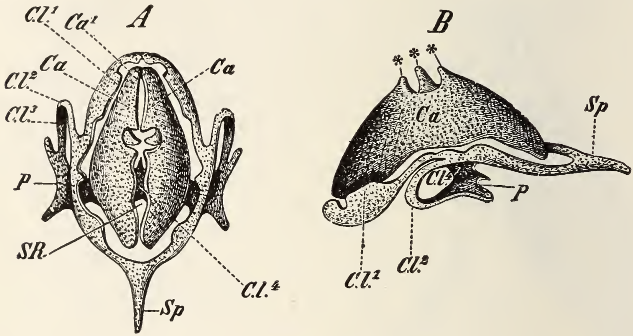

Fig. 56.—Cartilages of the larynx of the frog. A, from above; B, from the side; *Ca*, arytenoid cartilage; $C.\ l^1$ to $C.\ l^4$, cricoid cartilage; *P*, expansion of the cricoid; *Sp*, spinous process of the cricoid; * * *, prominences of the arytenoids. (After Wiedersheim.)

The Lungs.—The lungs are ovoid, thin-walled sacs of comparatively simple structure. They are capable of great distension and may be readily inflated through the glottis; they do not collapse when the body is cut open, owing to the fact that the glottis under ordinary circumstances remains closed. When air is let out of the lungs, they shrivel to an inconspicuous size. The inner surface of the lungs is divided by a network of septa into a series of small chambers or *alveoli*, by means of which the amount of surface exposed to the air is very greatly increased. The walls of the alveoli are richly supplied with blood vessels which break up to form a fine capillary network. The inner surface of the alveoli is covered with a single layer of epithelial cells which are very thin and flattened except on the edges of the septa, where they become cylindrical and ciliated. Outside the epithelium is a connective tissue layer which contains the blood and lymph vessels, and numerous unstriated muscle cells which give the lungs their great power of contraction. The outer surface of the lungs is coated with peritoneum.

The area of the inner surface of the lungs of *Rana esculenta* has been carefully calculated by Krogh. In a specimen weighing 40 g. it was found to be 98 sq. cm. The total surface of the skin was estimated to be 154 sq. cm. in the same specimen.

The Respiratory Movements.—Since the frog has no ribs, it is unable to draw in air by enlarging the cavity containing the lungs as the higher animals do, and it has recourse to a more indirect method of inspiration. If one watches the respiratory movements of a frog, it will be seen that the floor of the mouth rises and falls at quite regular intervals. Usually at somewhat greater intervals there may be seen a contraction followed by a sudden expansion of the body wall; and accompanying the latter movement there is a brief closure of the nares. The respiratory movements of the frog fall into two classes: (1) the oscillatory throat movements, and (2) the movements directly concerned in filling and emptying the lungs. The throat movements may continue for quite a long period, especially if the frog is kept quiet and where it is cool, without any movements of the body or nares. During this time the glottis remains closed and no air passes into or out of the lungs. The nares are kept open, and air is drawn through them into the buccal cavity as the floor of the mouth is lowered, and forced out through them as the floor of the mouth is raised. These oscillating movements per-

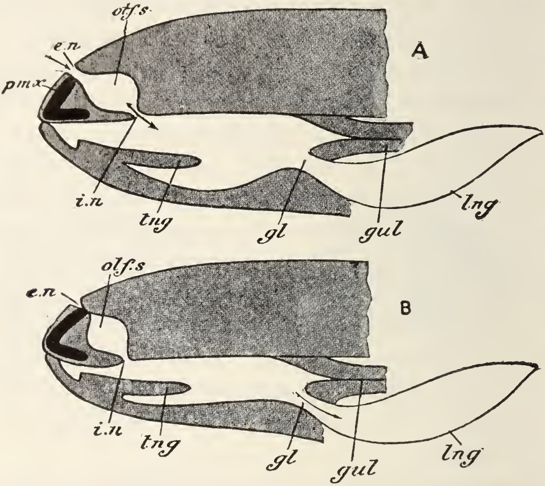

FIG. 57.—Diagrams to illustrate the respiratory movements of the frog. In A the floor of the mouth is depressed, the nares are open, and air rushes through them into the buccal cavity. In B the floor of the mouth is raised, the nares are closed, and air is forced from the buccal cavity into the lungs. *e.n*, external nares; *gl*, glottis; *gul*, gullet; *i.n*, internal nares; *lng*, lung; *olf.s*, olfactory chamber; *pmx*, premaxillary bone; *tng*, tongue. (After Parker and Parker.)

form two functions: (1) they are subservient to the respiration which takes place in the mucous walls of the mouth and pharynx, and (2) by renovating the air discharged into the buccal cavity after each expiration from the lungs they enable comparatively pure air to be forced into the lungs again at the next inspiration. The breathing in which the lungs are involved is indicated by movements of the flanks, or regions above and behind the fore legs. Certain small movements, however, occur in these regions which appear to be incidentally associated with the oscillatory movements of the floor of the mouth and play no part in lung respiration; the true flank movements are quite well marked. After each drawing in of the flank or expiration there follows immediately a swelling of the flank due to inspiration, but there may elapse a considerable interval before the next expiration occurs, so that the lungs are always filled with air during the pause between successive respiratory acts. Expiration is effected by the contraction of the muscles of the body wall aided by the elasticity of the walls of the lungs. During the act of expiration the glottis opens and almost immediately afterwards closes. If the sides of the body are cut open so that the lungs cannot be compressed by the muscles of the body wall, air will be expelled, though more slowly, every time the glottis opens. A frog thus operated on is still capable of both inspiring and expiring air, the mere elasticity of the walls of the lungs being sufficient for the latter function.

In filling the lungs the buccal cavity acts as a sort of force pump. As the floor of the mouth rises, the nares are closed, the glottis opens, and the air in the buccal cavity thus subjected to pressure and having no other avenue of escape is forced through the glottis into the lungs. The glottis then closes, and the movements of the floor of the mouth may continue for some time before the next inspiration takes place. The rising of the floor of the throat and the closure of the nares take place almost at the same time that air is expelled from the lungs; and the expansion of the lungs follows almost immediately afterward. Much of the air expelled from the lungs in expiration does not escape from the buccal cavity, but is forced back into the lungs again at the next inspiration. It is mixed, however, with the comparatively pure air previously in the mouth cavity. The valvular arrangement for closing the nares is an essential part of the mechanism for filling the lungs. It was formerly thought that the nares were closed by special muscles attached to the valves, but it was shown by Gaupp that this function is performed through raising the tip of the lower jaw, thus elevating the premaxillaries and thereby closing these openings. It may be readily shown that the closure of the nares can be brought about in this way by pressing upward against the premaxillaries with the finger. So long as its mouth is kept open the frog is unable to close its nares; being unable to force air into the lungs, such a frog will sooner or later die of asphyxiation. During all of the respiratory movements the mouth of the frog is held tightly closed through the tonic contraction of the muscles of the lower jaw. As has been explained in a previous chapter, the tip of the lower jaw is independently movable, owing to the existence of the small mentomeckelian bones, which are opposed to the premaxillaries. The contraction of the small submentalis muscle, which runs transversely across the tip of the jaw, causes this part to be raised above the general level and by pressing upward against the premaxillaries closes the nares.

As air is forced into the lungs, the pressure in the buccal cavity is indicated by the slight protrusion of the eyes and tympanic membranes. Sometimes, however, when the frog is making strong inspiratory efforts, the eyes are drawn inward during each gulp of air, thus aiding the process by diminishing the size of the buccal cavity.

According to Baglioni the external aperture of the nares does not remain closed during the last phases of the elevation of the floor of the mouth; nevertheless, air does not escape from the buccal cavity, as may be shown by placing the nose of the frog beneath water, when no bubbles arise from the nostrils. The muscles which draw the hyoid apparatus and tongue forward and upward cause the tip of the jaw to be depressed when a certain position of these organs has been reached and the nares open. Why, then, does not air pass out of the nares as the floor of the mouth continues to be raised? As Baglioni maintains, this is because the nasal passages are closed from behind by means of the anterior processes of the hyoid cartilage, which are so formed and situated that they fit neatly into the posterior nares as the hyoid apparatus is drawn upward and forward in the act of inspiration.

Changes in the Blood in Respiration.—The respiratory movements that have been described are subsidiary to keeping fresh air in close relation with the blood. On the one hand we have the organs of respiration and the distribution within them of the blood vessels, which are so arranged that the blood is brought very close to the surface over a large area. And on the other hand we have a complicated and beautifully adaptive mechanism for keeping the large portion of the respiratory surface included in the lungs in contact with pure air. These devices facilitate the exchange of gases which takes place between the air and the blood by means of diffusion across the intervening membranes. The blood receives oxygen from the air and gives off carbon dioxide, so that the air which has been expired from the lungs or buccal cavity always contains less of the former and more of the latter gas. The process of respiration falls into two phases: (1) external respiration, or the exchange of gases between the blood and the surrounding medium, and (2) internal respiration, or the exchange of gases between the blood and the tissues. The metabolism of every cell involves the consumption of oxygen which is received from the blood, and as the result of the oxidation of compounds of carbon which occurs throughout the body every cell produces carbon dioxide, which is given off into the blood. The blood, therefore, acts as a means of transporting oxygen from the organs of respiration to the tissues and of carbon dioxide from the tissues to the organs of respiration. It thus serves as the medium between internal and external respiration. The greater portion of oxygen in the blood is carried by the red corpuscles in combination with hemoglobin. This peculiar substance has the power of forming a weak and unstable chemical union with oxygen. As the blood passes through the capillaries of the respiratory organs, oxygen diffuses into it and combines with the hemoglobin; when the blood reaches the tissues where the partial pressure of the oxygen is diminished, the hemoglobin parts with its oxygen to the surrounding cells. Hemoglobin is a protein compound containing iron; it is readily soluble in water and may be obtained by evaporation from its solution in the form of crystals. When combined with oxygen, it assumes a bright red color, but when it loses its oxygen, it becomes a much darker and more bluish tinge. It is to this change in the hemoglobin that the difference in color between arterial and venous blood is due. Blood that has been oxygenated is bright red, while blood that has not been purified has a much darker color.

The Respiratory Function of the Skin.—The skin of the frog is an organ of respiration of the utmost importance. During the winter when the frog lies buried in the mud it becomes practically the only respiratory organ. Frogs may be kept alive when submerged in water at 0° to 13° C. for several days. At a higher temperature frogs tend to come to the surface oftener for air, and if prevented from doing so, they may die of asphyxiation. The skin functions as a respiratory organ both in water and in air. If the nostrils of a frog be plugged with wax, the animal may be kept alive in cool air for several days.

The experiments of several investigators have shown that more carbon dioxide is given off through the skin than through the lungs. Klug found that the ratio of CO_2 given off by the lungs to that given off through the skin varied in the different specimens investigated from 1:2.5 to 1:4.46. The frogs which Klug experimented upon were put in a chamber divided by a partition which contained an aperture surrounded by rubber. The frog was placed so that its head projected through the partition, and was held tightly by the rubber so that one chamber was completely shut off from the other. Air was passed through both chambers, and the amount of carbon dioxide given off into each measured and compared. The one chamber received the output from the skin only, while the other received that of the lungs together with the small amount exhaled from the skin of the head. The method of Klug was an improvement over those of his predecessors, although not entirely free from objections, the principal one being that the pressure of the rubber necessary to produce an air-tight fit would impede the normal movements of respiration. Experiments of ligating or extirpating the lungs, removing the skin, tying the cutaneous blood vessels, plunging the frog in oil nearly up to its nostrils, etc., in order to eliminate one or the other modes of respiration are all open to the same criticism that they do not tell us anything of the relation of skin and pulmonary respiration under ordinary conditions. If carbon dioxide is prevented from escaping through the skin, more of it will be exhaled through the lungs, or if the lungs are tied, more carbon dioxide will be eliminated through the skin.

The relation between the cutaneous and pulmonary respiration of the frog has recently been quite exhaustively studied by Krogh. The lungs were supplied with air by means of artificial respiration, and the income of oxygen and the output of CO_2 from both the lungs and skin compared under various conditions. In *Rana fusca* at a temperature of 20° C. the average ratio of oxygen income to CO_2 output in several experiments on frogs taken at different times of year was, in pulmonary respiration, O_2 105 : $CO_2$45; in cutaneous respiration O_2 52 : CO_2 129. It is thus evident that in the lungs the oxygen taken in is greatly in excess of the CO_2 given out; while in the skin the reverse relation obtains. In *Rana esculenta* relatively more oxygen is taken in through the skin and relatively less CO_2 eliminated through the lungs. The respiratory quotients (*i.e.* ratio of O_2 to CO_2) in the two species at 20° C. are as follows:—

	CUTANEOUS RESPIRATION	PULMONARY RESPIRATION
R. fusca	2.48 r.q.	.32 r.q.
R. esculenta	1.92 r.q.	.32 r.q.

Influence of External Conditions upon Respiration.— The respiratory functions of both the lungs and the skin vary in different periods of the year even when the animals are placed under the same degree of temperature. The amount of oxygen taken in by the lungs is greatest during the breeding season; then it rapidly decreases during the summer, and reaches its minimum in the winter, the ratios of oxygen absorption at a temperature of 20° C. being as follows: spring, 134.5; summer, 82; winter, 54. The output of CO_2 by the lungs varies in a similar manner (spring, 62; summer, 42; winter, 16.5). The cutaneous respiration is subject to much less seasonal variation; the absorption of oxygen is practically constant; the elimination of CO_2 is considerably increased during the breeding period, but for the rest of the year it varies but little. While the amount of oxygen taken in by the lungs during the spring and summer considerably exceeds that absorbed by the skin, the cutaneous absorption of oxygen becomes much greater than the pulmonary in the winter. In winter, therefore, the skin becomes relatively more important in respiration than during the rest of the year.

Whether the skin functions more efficiently as a respiratory organ in air or in water the few and contradictory results of Bohr and Krogh do not enable one to determine. Few experiments have been made upon the relation between temperature and the rapidity of respiration, although it is known that respiration takes place much more rapidly when the temperature is increased. At low temperatures respiratory changes are slight.

Moleschott and Fubini have shown that light has a marked effect upon respiration of the skin, the amount of CO_2 produced at a given temperature being much greater in the light than in the dark. This was held to be due in part to a direct action of light upon the skin, because the increase occurs in frogs whose eyes have been removed, although to a less extent than in normal specimens. The more refrangible rays have the greatest effect upon skin respiration, as was shown by measuring the CO_2 output in frogs exposed to differently colored lights. The ratios of CO_2 production under violet, yellow, and red light were found to be as 114, 103, and 100 respectively. In red light there is but little more CO_2 output than in the dark. The influence of heat was excluded in the experiments by passing the light through a vessel of water. As frogs which are placed in the light become restless and excited and frequently make efforts to go toward the source of illumination, it is probable that these differences in respiration result from variations in the animal's activity. The fact that the phototactic activities of the frog become greater under the more refrangible rays would naturally lead to a parallel increase in respiration under the same conditions. That differences in respiration occur in blinded frogs under differently colored lights is not inconsistent with this interpretation, since phototaxis still occurs in frogs from which the eyes have been removed.

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CHAPTER IX

THE SKIN

External Characters.—The skin is an organ of unusual importance in the life of the frog, because, in addition to the functions which it commonly performs among other animals, it has a number of special functions which are peculiar to the Amphibia, and which, in most cases, reach their fullest development among the Anura. ① As in most of the Amphibia, the skin of the frog is smooth and moist; it is very loosely attached to the underlying musculature by thin bands of connective tissue, which separate the large subcutaneous lymph spaces. ② It is everywhere very tough, but it is considerably thicker on the dorsal side of the body than it is below. In certain regions it presents special thickenings; such as the dermal plicæ, which extend backward from near the posterior angles of the eyes, the subarticular pads beneath the joints of the digits of the feet, the swelling at the base of the first finger of the arm, the protuberance over the sixth toe or prehallux, and the upper eyelids and lips. Small papillæ often occur, especially on the dorsal side of the body, some of which, the tactile papillæ, are permanent; others, the sexual papillæ of the female, occur only during the breeding period.

Histological Structure.—The skin is composed of two principal layers, the *epidermis*, and the *corium*, or *cutis*. A third layer of subcutaneous connective tissue, not belonging to the skin proper, lies underneath the corium and forms the septa uniting the skin to the body wall.

The *epidermis,* or outer portion of the skin, is composed of several layers of cells. The cells of the innermost layer are columnar; but in passing toward the outer surface the cells become more and more flattened, until those of the outermost or horny layer (*stratum corneum*) become very broad and thin. It is the stratum corneum that is shed during the molting process. The gradual change in shape between the cells of the inner and outer surfaces of the epidermis is due to the fact that there is a continual production of new cells in the inner layer which are gradually pushed outward, becoming more and more flattened the farther they are pressed away from their point of origin.

The epidermis, especially on the dorsal side of the body, usually contains more or less dark brown or black pigment. This pigment is partly within special cells, the *chromatophores,* and partly in and between the typical cells of the epidermis. In certain regions all of the cells of the epidermis may contain small pigment granules. Ehrmann found that in the same region of epidermis pigment would appear and disappear in the course of a few months. The chromatophores of the epidermis resemble the dark pigment cells of the corium. Whether they are derived from cells of the corium which have wandered into the epidermis, or whether they arise through the transformation of cells of the epidermis itself, is a matter of controversy. Loeb and Strong[1] have come to the conclusion that the chromatophores that appear in the regenerated epithelium of the frog are derived from epithelial cells, and not from cells that have wandered in from the cutis. Chromatophores in the epidermis are not usually abundant. The main source of the color of the skin is in the pigment cells of the corium.

The inner layer of the epidermis contains several stellate cells, which, according to Mayer, arise from the modifica-

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[1] Loeb and Strong, *Am. Jour. Anat.*, Vol. 3, p. 275, 1904.

tion of cells of the typical form, and, by acquiring pigment, become later transformed into chromatophores. In the outer portion of the epidermis occur scattered oval or flask-shaped cells, the upper portion or neck of which lies just beneath the stratum corneum. According to F. E. Schultze they produce a secretion which passes between the stratum corneum and the subsequent layer of cells and aids in shedding the skin. Pfitzner, on the other hand, regards them as degenerate epithelial cells which retain the mechanical function of holding the stratum corneum in contact with the underlying layer. Modifications of the outer layer or stratum corneum are found in the small stoma cells, which are situated over the necks of the cutaneous glands. The necks of these glands open to the surface through a small triradiate aperture which is raised slightly above the general level. This aperture has generally been regarded as passing through a single cell (Harless, Ciaccio, Eberth, Engelmann, Heidenhain, Nicoglu), but, according to Junius, what has been heretofore considered as one cell is really made up of several, the boundaries between which have disappeared.

The corium is separable into two layers, an outer comparatively loose layer (*stratum spongiosum*), which contains most of the glands, and an inner layer (*stratum compactum*), which is formed of very dense connective tissue. The stratum spongiosum consists of a loose network of fibrous connective tissue, richly supplied with lymph spaces and blood vessels. Just beneath the epidermis it forms a thin layer which contains numerous pigment cells. In the deeper portion are embedded the glands. Thickenings of the stratum spongiosum form the basis of the dermal papillæ mentioned above.

The stratum compactum is mainly composed of a dense layer of connective tissue, whose fibers run in a wavy course parallel to the surface of the skin. At intervals this layer is crossed by vertical strands, which often extend through the stratum spongiosum into the epidermis. In addition to fibrous connective tissue, these strands frequently contain smooth muscle fibers, elastic fibers, nerves, and blood vessels. It is probably due to the contraction of these muscle fibers that the papillation of the skin is produced after certain conditions of stimulation. The fibers may also aid in squeezing out the secretion of the cutaneous glands.

The subcutaneous connective tissue forms a loose layer beneath the stratum compactum and a second very thin layer next to the muscles, the two layers being separated by large lymph spaces except in the septa, where they become continuous. The outer of the two layers is very vascular and contains numerous stellate cells, within which are numerous grayish white pigment granules. These cells are especially abundant on the ventral side of the body, where they produce the white coloration characteristic of that region.

Glands of the Skin.—The skin of the frog, like that of most of the Amphibia, is richly furnished with glands. These glands are of the simple alveolar type, and lie mainly in the stratum spongiosum of the corium. Only rarely, as in the large glands of the inner finger, do they extend into the deeper portions of the skin. Typically the glands are spherical or oval in form, and open to the surface through a narrow neck which extends through the epidermis and terminates in the triradiate opening of a so-called stoma cell at its outer end.

The skin glands of the frog have been studied by numerous investigators, but there remain the widest differences of opinion regarding many of the most important features of their structure and functions. Two varieties of gland are commonly distinguished which may be designated as the *mucus glands* and the *poison glands.* While Heidenhain, Nicoglu, and others regard these two types of gland as specifically distinct, other investigators (Calmels, Leydig, Sczcesny, Junius) consider them as different phases in the development of one and the same gland. However this may be, the glands of the frog's skin may be grouped into two classes which are structurally and functionally different, and we shall describe them separately without regard to the question as to whether they are genetically connected.

The mucus glands are smaller and much more abundant than the poison glands, and are found over practically the entire surface of the body. In some places they are so thick that they nearly touch. In *Rana fusca,* according to Engelmann, they average about sixty to each square millimeter of surface. Their ducts are narrow, and lined with a layer of small flattened epithelial cells. The body of the gland is lined with epithelial cells which form a single layer except near the opening of the neck, where there are two layers. It is this epithelium which forms the mucus which is discharged into the lumen of the gland, and poured out through the neck over the surface of the skin. The appearance of the secreting epithelium varies greatly in different glands. In some cases, more often in the smaller glands, the epithelial cells are low, clearly marked off from each other, and from the large lumen of the gland, and contain nuclei which take up a large part of the cell. In other glands the cells are elongated so that they fill a large part of the lumen; the nucleus is relatively small, and situated near the base of the cell, and numerous granules occur toward the free ends. During secretion these granules swell up, and become converted into a transparent substance which is discharged into the central cavity (Biedermann), and it is probable that they represent a stage in the formation of mucus. Numerous transitional stages between these two varieties of epithelium occur, and it is quite certain that the differences are due to the age of the glands, and their different states of secretion. Changes in the form of the cells, however, are produced to a certain extent by the contraction of the gland.

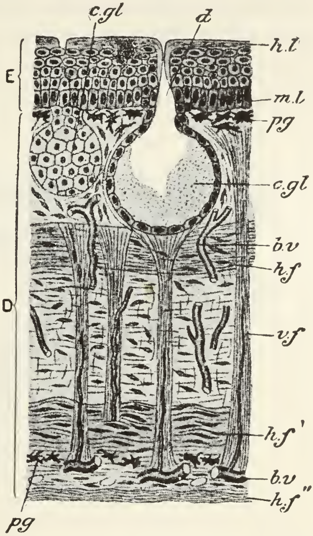

Fig. 58.—Cross section of the skin of the frog. *D*, dermis or cutis; *E*, epidermis; *b.v*, blood vessel; *c. gl*, cutaneous gland cut through the center; *c. gl′*, the same from one side; *d*, duct of gland; *h.f*, *h.f′*. *h.f″*, horizontal fibers of connective tissue; *h.l*, outer or horny layer of the epidermis; *m.l*, Malpighian layer of the epidermis; *pg*, pigment cells. (After Howes.)

Outside of the epithelium is a muscular coat composed of smooth muscle cells which lie in a meridional direction. The outermost coat of the gland is formed by a layer of fibrous connective tissue. The function of the muscle cells is the expulsion of the secretion of the gland. The glands of the skin are in constant motion (Ascherson, Engelmann), as may be seen by an examination of the glands in the web of the foot. They change not only in size, but also in form, being now rounded and now wrinkled and angular. Contraction may be caused by stimulation of the skin with irritant solutions or by the electric current.

The poison glands are larger and less abundant than the mucus glands, and less uniformly distributed over the surface of the body. They are more numerous on the dorsal side of the body and hind legs, and they are especially abundant, and unusually large, in the lateral dermal plicæ. According to

Junius, they occur on all parts of the skin, although they may be comparatively scarce in certain situations. Like the mucus glands they possess a muscular and a connective tissue coat outside the layer of epithelium. The chief differences in the two types of glands, with the exception of size and the thickness of the tunics, lies in the secreting cells. Engelmann described the epithelium as consisting of cylindrical cells nearly filled with granules. The boundaries of the cells apparently disappear under certain conditions of secretion, the epithelial lining forming a continuous irregular layer of protoplasm (Gaupp).

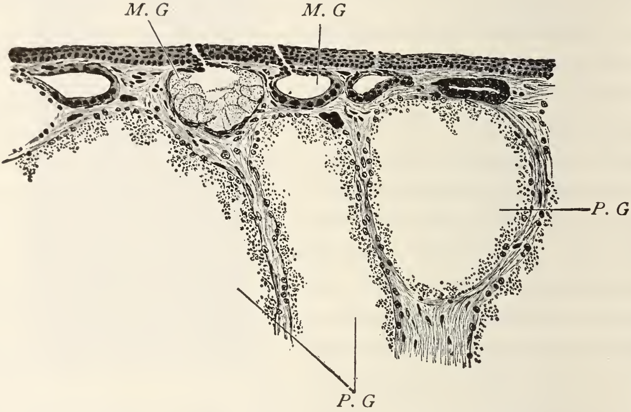

FIG. 59.—Section across a dermal plica of *Rana esculenta*. *M. G*, mucus glands; *P. G*, poison glands; the granular epithelium has an indefinite outline and shows no cell walls. (After Gaupp.)

The secretion of the poison glands is a whitish fluid with a burning taste. It may be caused to exude from the skin, especially of the bullfrog, by placing the animal under chloroform. Of its properties in the frog comparatively little is known. Paul Bert found that a goldfinch which was inoculated with the dermal secretion of *Rana esculenta* died within one minute; a frog inoculated with the poison of another frog of the same species died within an hour and a quarter.

In many other Amphibia, especially the toads and salamanders, poison glands are very extensively developed, and yield an abundant secretion.

Sex Differences.—The skin of the frog presents certain differences characteristic of sex, some of which are permanent, while others occur only during the breeding period. In *Rana fusca,* according to Leydig, and in *R. arvalis,* according to Steenstrup, the web on the hind feet of the males is more fully developed than in the females. The swelling on the inner side of the first finger of the male, which has been mentioned in a previous chapter, is caused by modifications both of the corium and the epidermis. This swelling is much larger in the breeding period than at other times, and it doubtless subserves the functions of aiding the male to retain hold of the female. The cutaneous glands in this region are much enlarged, and become elongated into a tubular form, and extend through the entire thickness of the skin. The epidermis in the breeding period is proliferated to form small papillæ with a thick, rough, horny layer. After the breeding period the epidermis becomes smooth again, and there is also a partial disappearance of the pigment of the corium, so that the swelling loses its dark color.

The occurrence of dermal papillæ in the female of *Rana fusca* during the breeding period has already been sufficiently described (see Chapter II). The males of certain species assume at this time a blue coloration which appears mainly on the ventral side of the body. In *Rana arvalis* (*R. oxyrrhinus*) it has been described by Steenstrup and by Siebold. In *Rana fusca* Falio described a blue coloration appearing on the throat during the breeding period. Leydig found that this color disappeared soon after the animal was taken from the water. Both Leydig and Haller, who studied the same phenomenon in *Rana temporaria,* regard the blue as an interference color produced by minute granules in the skin. It is probable that the appearance of the blue color is associated with the absorption of water. Frogs which have lost the blue color when kept in the air soon regain it when placed in the water again. After the breeding period is over, the blue color quickly disappears. A reddish brown color during the breeding season has been described by Leydig in the female of *Rana fusca,* and Smith has observed a blue coloration of the throat which he regards as characteristic of the female of that species at this time.

The skin of the male of *Rana fusca* in the breeding season becomes swollen and may hang down at the sides. The stratum compactum of the corium becomes more or less gelatinous and the subcutaneous lymph spaces become filled with a material resembling the vitreous humor of the eye.

With the exception of the swollen first finger of the male and the dermal papillæ of the female there is no evidence as to what functional significance the above characters possess, if they possess any. They may be the incidental products of the important constitutional changes which take place during the breeding period, without being of any direct value to the organism.

Seasonal Changes.—Most of the seasonal changes in the skin are correlated with the sexual differences that occur during the breeding season, and have been treated under that head. There are some other seasonal changes, however, which occur apparently without regard to the development of the sexual products. In the winter and early spring frogs are darker in color than in summer, owing probably in large part to differences of temperature. According to

Donaldson the power of the skin to absorb water is greater in summer than in winter.

Color Changes.—The power of the skin to change its color in relation to surrounding conditions depends upon changes which occur in the pigment cells, or chromatophores. Of these there may be distinguished the following varieties: *black pigment cells* (**melanophores**), *interference cells* (**leucophores**), *golden pigment cells* (**xanthophores, xantholeucophores**), and in some species of frogs *red pigment cells.*

The black chromatophores are stellate cells with irregularly branching processes. There is a single nucleus near the center of the cell. The dark pigment is in the form of numerous small brown or black granules of a substance called *melanin,* which is a very resistant compound remaining unaffected by most reagents. The black chromatophores are most abundant on the dorsal side of the body, especially in the black spots where they are massed together very thickly. On the ventral side they are almost entirely absent over a considerable area. They are found mostly in the superficial layer of the corium just below the epidermis. Scattered chromatophores occur in the epidermis and the deeper layers of the corium. They tend to aggregate in regions which are most abundantly supplied with blood vessels. The pigment of the chromatophores undergoes remarkable changes in form under certain conditions. When the pigment is most expanded, it is widely spread out into numerous branching processes, giving the whole skin a much darker color; at other times it may be contracted into a small rounded mass. Some investigators (Pouchet, Leydig) have attributed the change in the form of the pigment to changes in the shape of chromatophores, which were supposed to send out processes and draw them in again like an Amœba. Such movements undoubtedly occur in the pigment cells of many of the lower animals, but many investigators consider that the movement of the pigment in the chromatophores of the frog takes place along preformed paths, the outline of the cell remaining approximately constant while the pigment granules flow back and forth within the processes, which are transparent, and hence invisible except when containing pigment. Virchow, Von Wittich, and Biedermann think that the changes in the chromatophores may involve both a change in the shape of the cell and a flow of the pigment within the cell.

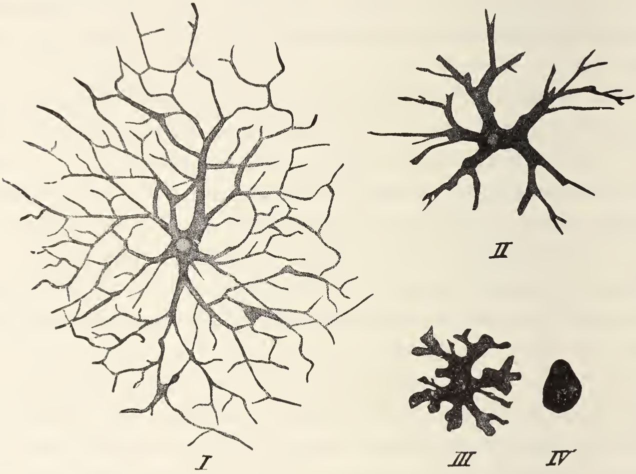

Fig. 60.—Pigment cells from the frog, in different states of extension. (From Verworn's "General Physiology.")

By teasing up bits of frog's skin in a suitable medium I have been able to isolate living pigment cells and to observe that they actually change in shape and creep about much like an Amœba. Some of the processes were often devoid of pigment, but the granules could be seen to flow in and out of them as the cell changed in form. It is probable, therefore, that pigment cells behave in much the same manner in their normal environment in the skin, and that both changes in outline and the flow of granules within the processes are involved in changes in the distribution of the black pigment.

The cells which give the skin its golden and green colors form a layer immediately beneath the epidermis. Unlike the black chromatophores they are usually rounded or polygonal in form, and they lie a little above the black cells, which constitute a sort of dark background. Their golden color is due to a fatty pigment or lipochrome, which is sometimes diffused throughout the cell and at other times aggregated into large drops (Biedermann). This pigment is soluble in alcohol, chloroform, and ether, giving a golden yellow solution which turns to a yellowish green when very dilute. The same substance, according to Kühne, produces the

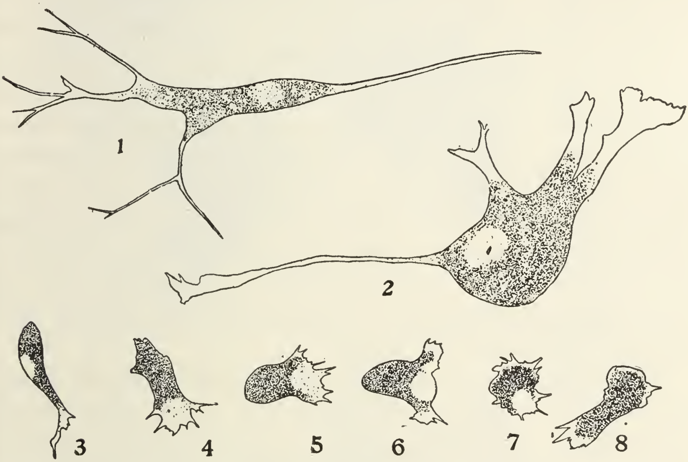

Fig. 61.—Isolated pigment cells of the skin of the frog cultivated in lymph. Figures 3-8 indicate successive changes in one cell during a half hour. All figures drawn to the same scale.

yellow color of the fat body. In frogs which have been preserved for some time in alcohol this pigment disappears, and consequently the specimens lose their golden and green coloration.

An important additional source of color in the frog is furnished by the so-called interference granules. These granules have a crystalline structure, and they show a cross striation due to the fact that they consist of a series of lamellæ. According to Ewald and Krukenberg they are composed of guanin. By transmitted light they are brown or gray, but in reflected light they are usually blue. These granules give the skin a whitish or sometimes a bluish color. Cells having these or similar granules are called leucophores. It has been held that many cells (xantholeucophores) contain both yellow pigment and guanin granules, but according to Ficalbi, von Wittich, and more recently W. J. Schmidt, the so-called xantholeucophores are really double cells, an outer one containing yellow pigment, and a deeper one containing the granules of guanin.

Red stellate pigment cells have been described in *Rana fusca* by Von Wittich and Schmidt. They occur in the corium, and were observed to undergo changes in the distribution of their pigment like those of the black chromatophores.

Nearly all of the color changes which the skin of the frog undergoes depend upon the differences in the distribution of two elements, the black and the yellow pigment. When the pigment of the black chromatophores is expanded, the skin becomes dark in color, owing to the fact that the black pigment is spread over a greater amount of surface. When the skin is light in color, the black pigment becomes contracted into small masses, thus allowing the light to be reflected from the other pigment cells. These facts may easily be demonstrated by comparing the skin of a dark

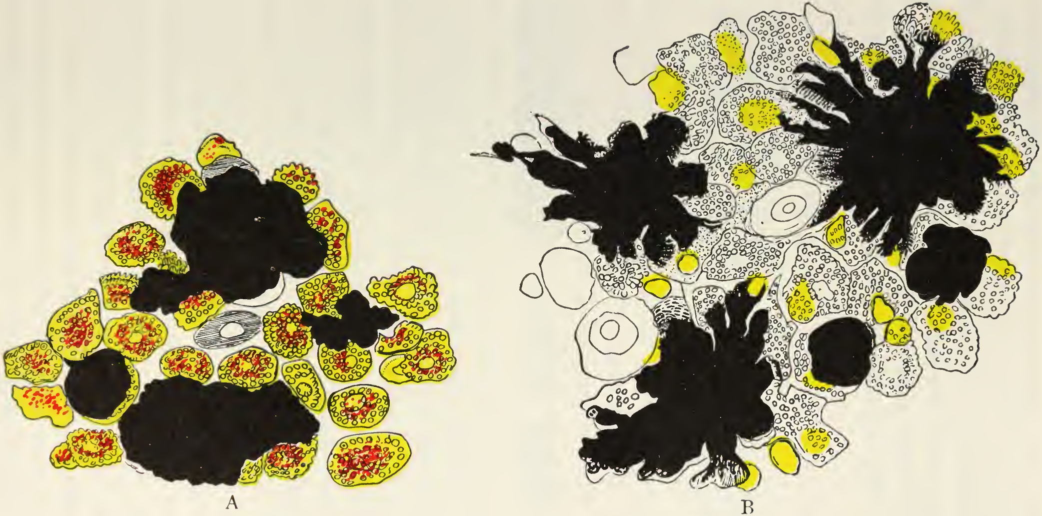

FIG. 62.—Skin of Hyla. A, skin of a golden-yellow specimen. The yellow pigment is here uniformly distributed throughout the cells. B, skin of a gray specimen. The yellow pigment is here aggregated into small masses within the cells. (From Gaupp, after Biedermann.)

frog with that of a light one, when great differences in the chromatophores will almost certainly be observed. Although the black chromatophores lie mainly below the golden cells, their branches cover the latter to a greater or less extent, and when the black pigment is fully expanded, it cuts off much of the light which would otherwise be reflected from them.

The golden color that appears in the frog's skin is due directly to the pigment in the golden cells, but the green is not produced in so simple a manner. There is no green pigment in the frog's skin, and various explanations have been offered as to how this color comes to appear. The subject has been investigated by Brücke, Harless, Von Wittich, Eberth, Biedermann, and Ehrmann, each of whom disagrees in certain particulars with the others. Brücke regarded the green color as a simple interference phenomenon caused by the granules of guanin; but that the golden pigment is necessary to the production of green was subsequently shown by the fact that when the golden pigment is dissolved out of the cells the green color disappears although the granules may remain unchanged. It is quite well established that the green is a combination effect of light reflected from the guanin granules, and the golden pigment through which the light passes. As the light reflected from the granules contains a large proportion of blue rays, we have what is practically equivalent to a blue background seen through a yellow medium, the result of which is to produce green. The yellow medium absorbs most of the colors of the spectrum, allowing yellow and a certain amount of green light to pass through. The blue background reflects only blue and green light. Since green rays are the only ones which are capable both of reflection from the blue background and of passing through the yellow medium, the background appears of a green color.

The green is produced, according to Biedermann, when the black chromatophores are expanded beneath the yellow. Then most of the light is reflected from the granules. When the black chromatophores are contracted so that the yellow cells have a lighter background, light may be reflected from other elements than the blue granules, and a yellow or golden color may predominate. The rôle of the contraction and expansion of the golden pigments is not accurately determined. It is probable that the gray or grayish blue color which is sometimes assumed may be produced by the simultaneous contraction of both the black and the golden pigments, since frogs with the black pigment spots contracted often exhibit these hues when the golden pigment has been dissolved out in alcohol. Von Wittich found in the tree

Fig. 63.—Sections through the skin of the tree frog. In A the skin appears yellow; the black pigment is concentrated, and considerable light is reflected through the yellow chromatophores from the deeper tissues. In B the color of the skin is green; the black chromatophores are in a state of moderate extension, forming a dark layer beneath the yellow cells, so that most of the light passing through the yellow cells is reflected from the bluish granules. In C the pigment from the black chromatophores has surrounded the yellow cells, giving the skin a very dark color. (From Gaupp, after Ehrmann.)

frog that a gray color was associated with the contraction of both kinds of pigment. In the ordinary color changes variations in the concentration of the golden pigment are much less important, however, than the changes in the black cells.

The color changes in the skin are produced by numerous agencies which act upon the pigment cells either directly or through the central nervous system. The chromatophores of the frog form a very delicate and responsive system which is constantly undergoing changes in response both to stimuli from the environment and the varying internal states of the animal. One of the most important of the external stimuli affecting the skin is light. It is a well-known fact that frogs exposed to a bright light become light in color, while if they are kept some time in the dark, the skin turns much darker. These changes are much more pronounced in tree frogs (Hyla) than in the species of Rana, and they bring about an adaptation of the color of the animal to that of its environment which is often very close. The question whether light affects the chromatophores directly or through the central nervous system has received considerable attention. The latter alternative was espoused by Lister, who found that a blinded frog no longer changes its color in response to changes in the intensity of light. Lister's conclusion has been only partially confirmed by subsequent investigators. Steinach found that if both the nerves and blood vessels supplying any portion of the skin were cut in two, there still remained in that part a certain capacity for color change in response to light of different intensities. When pieces of dark paper were laid over portions of the skin thus treated, or even upon portions of skin entirely removed from the body, the areas covered were found to be considerably darker than those exposed to the light. Specimens of Hyla in which certain parts were shaded while other parts were exposed to light became light colored in all except the shaded areas. This was found to occur both in normal frogs and in frogs whose spinal cord was destroyed. Color changes were found by Dutartre to take place more rapidly in normal frogs than in specimens which had been blinded, but the same reactions occurred in both cases. There is no doubt, therefore, that light brings about color changes both directly and through the central nervous system.

How the nervous system functions in the control of color changes is uncertain. There are no connections known to exist between nerve fibers and the chromatophores such as have been observed in some fishes; and the chromatophores of frogs do not show the quick response to nervous stimulation or to the cutting of nerves which the pigment cells of certain fishes exhibit. Hogben, who has recently reviewed the question, is of the opinion that "the regulation of colour response by fluctuating pituitary secretion is adequate to interpret all the accredited phenomena in adult Amphibia, without invoking a direct innervation of melanophores." As will be seen in Chapter XII, the pituitary secretion exercises a profound effect upon the pigment cells in both larval and adult frogs. The amount of this secretion in the blood would naturally vary according to different conditions of nervous stimulation, so that the nervous system might exercise an indirect control of pigmentation through the intermediary of the pituitary hormones.

Destruction of the optic thalamus of the brain has been claimed to produce a darkening of the skin (Steiner, Biedermann), but Hogben suggests that this may be due to injury to the pituitary resulting from operating on a near-by part of the brain. He finds that operations on the brain in which injury to the pituitary is carefully avoided produce no darkening of the skin color. The light color following stimulation of the medulla might be interpreted as due to an increased stimulation of the pituitary. The experiments of cutting and stimulating the nerves of the hind leg have yielded contradictory results. Hogben cut and stimulated various nerves without obtaining any consistent effect upon pigmentation.

The condition of the pigment cells is profoundly influenced by changes in the circulation. An arrest of the blood flow causes a paling of the skin. If the leg of a dark-colored frog be tightly ligatured around the knee, the part below the ligature will soon assume a much lighter color. The same result follows if the blood vessels alone are tied, and is effected more quickly if the ligature is made around an artery instead of a vein. These results are not inconsistent with the theory of control by means of internal secretions, since the arrest of the blood flow would naturally reduce the amount of the available secretion.

Raising the temperature causes the pigment of the skin to contract. Cold, on the other hand, causes the pigment to expand and the skin to assume a dark color. The dark color of winter frogs is in part at least the effect of cold, and the lighter color of summer frogs in part the result of a higher temperature. A dark-colored frog may readily be made to turn much lighter if it is placed for several minutes in water of a temperature 27° C. Changes of temperature affect the concentration of pigment even in isolated pieces of skin.

Various chemical substances affect the chromatophores, some causing a contraction, others an expansion of the pigment. Adrenalin causes the melanophores to strongly contract and the extract of the pituitary will cause them to expand even in excised pieces of the skin. Carbon dioxide produces a darkening of the skin; carbon monoxide, on the other hand, causes the skin to turn pale. Chloroform and some other anæsthetics as well as certain irritants, such as croton oil and cantharides, cause an expansion of the pigment on the parts of the skin to which they are applied. Dryness tends to cause the skin to turn pale, while immersion in water produces the reverse effect. This has been observed especially in *Rana fusca* by Biedermann and in *R. agilis* and Hyla by Werner.

Biedermann has shown that color changes are influenced in a remarkable way by contact stimuli. Specimens of Hyla placed where the skin comes in contact with rough substances become very dark in color even when surrounded with bright-colored materials. Hylas which were placed upon smooth green leaves became light colored even in the dark. While the influence of light is admitted to be an important factor, the color changes of Hyla are regarded by Biedermann as determined to a great extent by the nature of the material with which the skin comes in contact. Since in the life of the tree frog rough surfaces are generally associated with a dark environment, while smooth surfaces are usually afforded by green leaves, this method of reaction to contact stimuli conspires to bring about, in most cases, an adaptation of the color of the animal to that of its surroundings. In the species of Rana studied this mode of reaction to contact was not observed. Finally it may be observed that color changes are associated with the psychic states of the animal. Frogs, like men, may turn pale through fear, but the mechanism of the process is very different in the two cases. If frogs are held in the hand for some time, the skin turns paler; this may in part be a reaction to temperature, but the same effect is produced if the animal is pursued and caused to jump about vigorously in its attempts to escape.

Absorption and Excretion.—The power of the frog's skin to absorb water has already been described. Several investigators have endeavored to ascertain if fluids pass through the skin with equal facility in both directions. According to Reid a five per cent solution of sugar in distilled water passes through the skin more rapidly from within outward than from without inward; but if the same percentage of sugar is dissolved in a normal salt solution the fluid will pass more rapidly from without inward. Overton maintained that water would pass from without inward through the frog's skin when the osmotic pressure is the same on the two sides, but his conclusions were not supported by the experiments of Maxwell. Przylecki has shown, however, that a frog's skin containing a one per cent solution of sugar will not allow any sugar to pass through even in eight to twelve hours, whereas if the sugar solution is on the outside it will pass through with a fair degree of rapidity. After twelve hours this selective action of the skin disappears and it behaves more like a non-living membrane. Chloroform and other depressants decrease the rate of passage of fluid from without and increase its rate of passage from within.

The amount of fluid that can be forced through the skin under pressure depends also upon the direction of flow. Cima found that as much water under a pressure of 10 cm. of mercury would pass through the skin of the frog from within outward in five minutes as would pass through in the reverse direction in thirty-seven minutes.

Of the excretory function of the skin of the frog practically nothing is known.

Another function which has been attributed to the skin is, curiously enough, nutrition. According to Przylecki the skin secretes diastase and has a power of digesting carbohydrates, but the nutriment which a frog can secure in this way must, under ordinary circumstances, be quite infinitesimal. Experiments to test the ability of tadpoles to utilize nutriment absorbed through the skin have led to opposed conclusions.

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CHAPTER X

THE EXCRETORY SYSTEM

The process of excretion is an essential part of the activity of all living substance. The substances resulting from the breaking down of living matter and the various materials taken into the organism which are never built up into living substance give rise to many compounds no longer useful which must be gotten rid of if the life of the organism be maintained. Every cell of the body excretes as well as assimilates and respires. A part of the waste is eliminated in the form of carbon dioxide, which is thrown off from the body through the organs of respiration. The solid products of metabolism, however, cannot be disposed of in this way, and specialized organs are developed for their removal. In excretion, as in respiration, we must distinguish between the discharge of substances into the blood which takes place throughout all parts of the organism, and the elimination of these substances from the blood to the outside of the body. The latter function is carried on by several organs. The skin is to a certain extent an organ of excretion, although little is known of its function in this respect among the Amphibia. In higher forms in which sweat glands occur a certain amount of salts and other substances is gotten rid of by cutaneous excretion. The liver is an important excretory organ, and the walls of the intestine also subserve the same function. The most important organs of excretion, however, are the kidneys, of whose structure and function we shall give a short account.

Structure and Function of the Kidneys.—The kidneys of the frog are oval, flattened, dark red bodies lying dorsal to the peritoneum of the posterior portion of the body cavity. The duct of the kidney, or *ureter,* is joined at about the posterior third or fourth of the outer margin; it then runs for a short distance along the dorsal surface and finally becomes embedded in the substance of the kidney, running near the margin to the anterior end of that organ. The ventral surface of the kidney is flatter than the dorsal and is traversed longitudinally by the yellowish *adrenal body* (Fig. 77). The kidneys are covered by peritoneum only on the ventral surface with the exception of a very short space where this membrane is folded in over the edges.

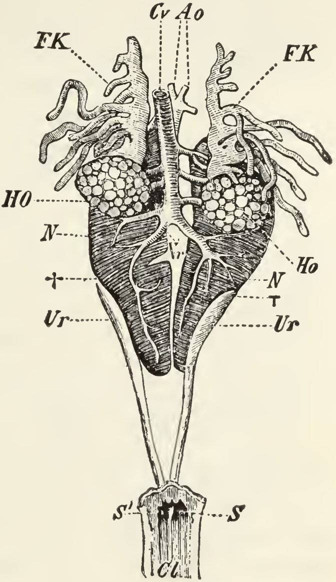

Fig. 64.—Male urinogenital organs. *Ao*, Aorta; *Cl*, cloaca; *Cv*, postcaval vein; *FK*, fat bodies; *Ho*, testes; *Ur*, ureters opening into the cloaca at *S*, *S'*; *Vr*, renal veins. (After Wiedersheim.)

The kidney may be regarded as a compound, tubular gland, made up of a large number of coiled *uriniferous tubules.* Each uriniferous tubule begins in a *Malpighian body* near the ventral surface. A Malpighian body consists of two parts, a knot of blood vessels, the *glomerulus,* and a surrounding membrane, or *Bowman's capsule.* The artery, *vas afferens,* entering the capsule breaks up into several capillaries which, after forming a few coils, emerge as the efferent blood vessel from the same opening. Bowman's capsule is an exceedingly thin membrane; there is an inner fold closely applied to the glomerulus which is continuous with the outer wall at the point where the blood vessels enter the capsule. Bowman's capsule is simply the thinned out and expanded end of a uriniferous tubule which has become pushed by the glomerulus as one might push in the end of a finger of a glove. The capsule, however, has grown around the glomerulus and closely surrounds the afferent and efferent vessels. At the dorsal side of the capsule, and usually opposite the point where the blood vessels enter, the outer wall passes into the neck of the uriniferous tubule. The very thin cells of this wall shade off gradually into cells of columnar epithelium which for a short distance carry very large cilia. Beyond the neck, which is somewhat narrower than the rest of the tubule, the cells are lined with much shorter cilia. Each tubule is lined with a single layer of cells which varies in character in the different parts. The course of each tubule is quite complicated. At first it runs dorsally, where it forms a more or less complicated coil, then it proceeds to the ventral side of the kidney, forms a second coil, and finally runs dorsally again, emptying into

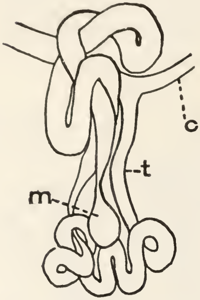

Fig. 65.—A uriniferous tubule. *c*, collecting tubule. *m*, Malpighian body; *t*, uriniferous tubule leading from the latter to the collecting tubule. (After Nussbaum.)

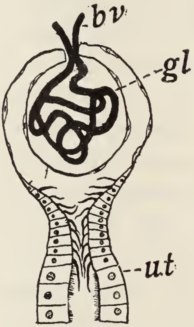

Fig. 66.—Malpighian body. *b.v.*, blood vessel; *g.l.*, glomerulus; *u.t.*, uriniferous tubule.

one of the collecting canals which extend transversely across the dorsal surface of the kidney from the inner margin to the ureter. The tubules are held together by connective tissue which forms a support also for the numerous blood vessels with which the kidney is supplied.

The ventral surface of the kidney is furnished with numerous ciliated funnels, the *nephrostomes,* whose expanded ends open into the cœlom. At their other end the nephrostomes empty into branches of the renal veins, and the cilia with which they are lined beat toward the upper end of these organs and thus create a current of lymph from the body cavity into the blood. This relation of the nephrostomes is a peculiar one and occurs only in the Anura. The lower Amphibia preserve the typical arrangement of these organs, as the nephrostomes are connected with the renal tubules. This condition, as Marshall has found, occurs also in the early stages of the life of the frog, but later the nephrostomes lose their original connection with the tubules and become united secondarily with the renal veins.

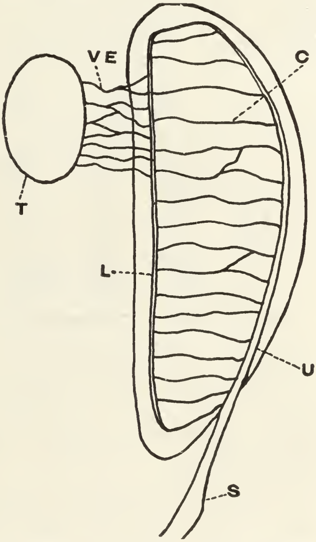

Fig. 67.—Diagram of a kidney showing the ureter and collecting tubules. *C*, collecting tubules; *L*, longitudinal canal of Bidder; *S*, seminal vesicle; *T*, testis; *U*, ureter; *VE*, vasa efferentia.

The kidney of the male frog stands in an intimate relation to the sexual organs. The *vasa efferentia,* or ducts which convey the spermatozoa from the testis, pass into the substance of the kidney, and the spermatozoa are carried through this organ to the ureter, which thus serves also as a vas deferens. The vasa efferentia are originally outgrowths of the walls of the Malpighian corpuscles which become connected with the testis. In some species (*R. esculenta*) the Malpighian bodies, which give rise to these outgrowths, still preserve their original function, and during the period of sexual activity spermatozoa may be seen in them as well as along the whole length of the renal tubules which arise from them. The vasa efferentia lead into a longitudinal canal (*Bidder's canal*) which runs near the median edge of the kidney.

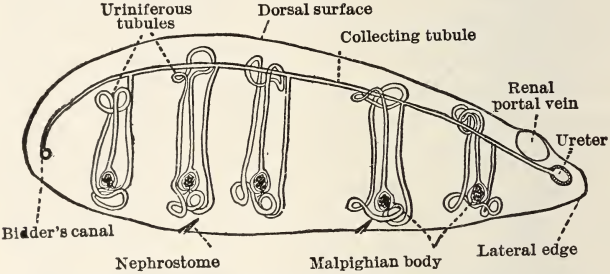

Fig. 68.—Diagram of a cross-section of the kidney of the frog.

In *Rana fusca*, according to Beissner, this canal is connected with the collecting tubules which extend across the dorsal side of the kidney to the ureter. The short tubes which connect the longitudinal canal with the collecting tubules widen out near the latter to form an ampulla. This enlargement is formed by a Malpighian body which has lost its glomerulus and consequently its original function. In *Rana fusca* there is a comparatively direct connection established between the vasa efferentia and the collecting tubules, and the spermatozoa, therefore, are not found in the Malpighian bodies and functional renal tubules. Bidder's canal occurs in the kidneys of both sexes, but its function in the female is not known.

In many of the lower vertebrates (Elasmobranchs, Amphibia) the kidney is divided into an anterior, or sexual portion, and a posterior, or excretory portion. The frog presents only the beginning of such a differentiation. The vasa efferentia are connected with the anterior part of the kidney, but the excretory function of this region is still retained. The course of the spermatozoa through the kidney varies considerably in different species of frogs, as is evinced by the fact that it is much more direct in *Rana fusca* than in *R. esculenta.* The latter presents, doubtless, the more primitive condition.

The kidney is supplied with blood from two different sources: (1) the *renal arteries,* which rise from the urinogenital arteries, or direct from the aorta, and (2) the *renal portal veins,* which convey venous blood from the posterior portion of the body. The renal arteries, of which there are usually from four to six, enter the kidney at the median edge or near the latter on the ventral surface. The divisions of the renal arteries are distributed to the renal tubules (arteriæ rectæ), and also to the glomeruli (vasa efferentia). The renal portal vein runs along the dorsal surface of the kidney very near the outer margin. From the transverse branches of this vein, which extend across the dorsal surface, small vessels are given off which penetrate the substance of the kidney and form capillary networks around the renal tubules. The vasa efferentia, which emerge from the glomeruli, together with the efferent veins arising from this capillary network, go to form the beginnings of the renal veins which convey the blood from the kidney to the posterior vena cava. The glomeruli are supplied only with arterial blood, while the renal tubules receive blood from the renal portal veins, and also, although to a less extent, from the renal arteries.

The function of the kidney is the elimination of waste matters from the blood. The renal excretion, or urine, is a fluid containing a large number of compounds in solution. Most of the nitrogen leaves the body in the form of urea, $(NH_2)_2CO$, which is a white crystalline compound, very soluble in water. Urea represents the final product of the breaking down of the nitrogenous substances of the body, and it has been shown that the formation of this substance takes place to a large extent in the liver, from which it passes into the blood. The kidney also excretes several salts such as the chlorides, sulphates, and phosphates of sodium, potassium, calcium, and magnesium, and numerous other substances in smaller proportions.

The specific rôles of the glomeruli and tubules in renal excretion have long been a matter of dispute. It is certain that water and other substances diffuse from the blood through the walls of the capillaries of the glomeruli into the renal tubules. It has been held, especially by Ludwig and his followers, that practically all of the substances excreted by the kidney pass through the glomeruli, and that the function of the tubules is to absorb the excess of water and certain other materials which pass down the lumen. By other physiologists it has been maintained that both the glomeruli and the renal tubules are secretory, but that they eliminate different products. Nussbaum's ingenious experiments on the frog seemed to offer a solution of this problem. As the glomeruli are supplied by branches of the renal arteries, Nussbaum concluded that the blood supply of these organs would be cut off if the renal arteries were tied. The opportunity was thus presented of comparing the excretion of the kidney in which the glomeruli are rendered functionless with that of the normal organ. It was found that in frogs with the renal arteries tied the secretion of urine was much diminished in amount. Solutions of sugar, peptones, and egg albumen, which when injected into the blood of normal frogs soon make their appearance in the urine, could not be detected, after injection into the blood, in the urine of frogs whose renal arteries were ligatured, even after the flow of urine was increased by the simultaneous injection of urea. Nussbaum came to the conclusion that albumen, sugar, and most salts are excreted by the glomeruli, while urea is eliminated by the cells of the uriniferous tubules. There is a source of error in such experiments, since ligating the renal arteries alone does not entirely cut off the blood supply of the glomeruli; there are anastomoses with the genital arteries by means of which these organs may receive blood in a somewhat roundabout way. Adami found that some of the glomeruli became filled by injecting the aorta of a frog in which the renal arteries were tied. This observer, in repeating Nussbaun's experiments, failed to confirm some of the latter's results and considered that the conclusions that were founded upon them were not established on a firm basis.

It seems evident that the renal tubules absorb several substances that pass through the glomeruli. Peter found that trypan blue injected into the blood was taken up first in the inner ends of the cells of the tubules. Later it passed to the outer ends and finally was absorbed into the blood. It is certain that sugar and various salts pass through the capillaries of the glomeruli. According to Clark the renal tubules absorb sugar from the urine, even when the urine contains much less sugar than the blood.

The Bladder.—The bladder is a thin-walled, bilobed sac attached to the ventral side of the cloaca, just below the openings of the ureters. It arises as an outpushing of the ventral wall of the cloaca like the allantois of the embryos of the higher vertebrates, with which it is regarded as homologous. It is surrounded by peritoneum which is continued as a median dorsal sheet attaching it to the rectum; a ventral sheet of peritoneum connects it with the ventral body wall, and a lateral peritoneal extension on either side joins the sides of the bladder to the dorso-lateral regions of the body wall.

The inner surface of the bladder is lined with a layer of epithelium about three cells thick (List), the inner layer resting upon a membrane of connective tissue. Numerous goblet cells occur among the other epithelial cells. The middle layer of the bladder consists of a network of smooth muscle fibers. The fibers are sometimes single, and sometimes united into bundles, and they extend in all directions. Outside of the muscle layer is a thin sheet of connective tissue which is covered externally by the peritoneum.

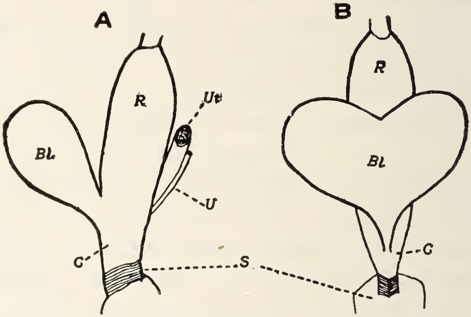

Fig. 69.—Diagram of the bladder and rectum of the frog; A, from the side; B, from below; *Bl*, bladder; *C*, cloaca; *R*, rectum; *S*, sphincter muscle; *U*, ureter; *Ut*, uterus. (Modified from Gaupp.)

The bladder is very distensible, as may readily be shown in a recently killed frog, by inflating it by means of a blowpipe introduced into the cloaca. When entirely empty, the bladder shrinks to an inconspicuous size. It was formerly doubted whether the bladder of the frog serves as a receptacle for urine, as it has no direct connection with the ducts from the kidneys. Townson, whose conclusions were followed by Dumeril in his great work on reptiles and amphibia, regarded the bladder as a sort of reservoir for water absorbed through the skin. The contents of the bladder were stated to be nearly pure water, and the urine proper was supposed to pass out and through the cloaca without entering the bladder at all. According to Dumeril,[1] "the so-called urinary bladder of frogs, tree frogs and toads, as well as that of the salamanders, is a sort of reservoir to which an almost pure aqueous humor, destined to be exhaled through the skin, appears to be carried either by the veins or by the lymph vessels." The subsequent investigations of Davy, Nussbaum, Adami and others have shown conclusively that the fluid contained in the bladder is derived from the kidneys, and that it contains urea and other substances characteristic of renal secretion.

The urine of the frog is much less concentrated than that of a human being, but it is subject to much variation according to whether the frog is kept in water or dry air. Water is absorbed by the skin and passed out through the kidneys. If urine is prevented from escaping by closing the cloaca the frog continues to absorb water only for a time (Parnas). The skin ceases to take in water after a certain concentration of the blood has been reached.

The end of the cloaca is commonly held closed by the contraction of its circular muscles, and the urine which is thus prevented from passing out collects in the bladder. The contents of the bladder are expelled suddenly by the contraction of the muscles of the body wall, which naturally subjects the bladder to a considerable pressure. The expulsion of urine often takes place when the frog leaps, and

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[1] Dumeril, "Erpétologie générale."

it is very apt to occur as a consequence of the struggles of the animal if the frog is taken in the hands, as every one who has handled frogs has doubtless discovered. The belief that the content of the bladder of the toad is poisonous is entirely without foundation.

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CHAPTER XI

THE REPRODUCTIVE ORGANS AND THE FAT BODIES

The reproductive system has the functions of producing the sex cells and transporting them outside of the body. The first function is discharged by the gonads, which are known in the female as *ovaries,* and in the male as *testes,* or *spermaries.* While the ovaries and testes are homologous organs, the sexual products are carried to the outside in the two sexes by very different methods.

Organs of the Female.—Each ovary of the frog is in the form of a sac which is more or less lobulated. Its internal cavity is divided by several partitions into chambers which are filled by fluid. Externally, the ovary is covered by peritoneum, which is continued on the dorsal side to form a double membrane, the *mesovarium,* which suspends the ovary from the dorsal body wall. The blood vessels and nerves which supply the ovary run between the two membranes of this supporting structure. The inner surface of the ovary is lined by a single layer of flattened epithelial cells, the origin of which may be traced to outgrowths from the kidney in early development. The *stratum medium,* or middle portion of the wall of the ovary, varies greatly in thickness in different parts and at different times. It is composed mainly of ova and follicle cells in various stages of development. The eggs lie within small chambers or follicles; these consist of a layer of cells (membrana granulosa) lying next to the vitelline membrane, and outside of this a very vascular network, the *theca folliculi.* After the eggs reach their full development they break through the follicle and the outer wall of the ovary, and are discharged into the body cavity. When the eggs are all extruded, the ovaries, which before had filled the greater part of the body cavity, become reduced to small wrinkled organs, containing the minute ova for the following year.

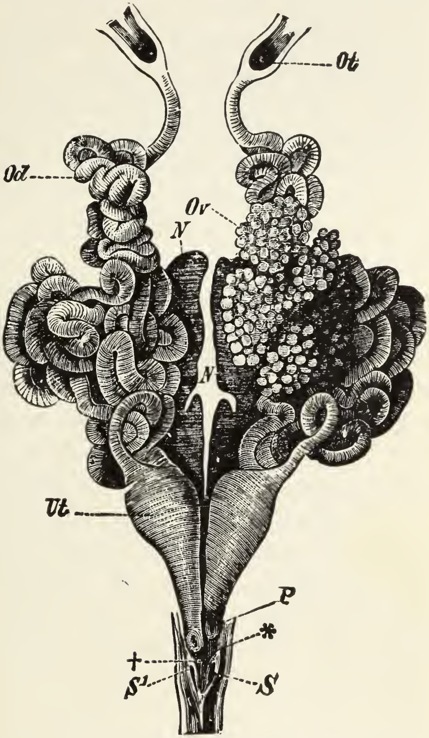

Fig. 70.—Urinogenital organs of a female frog. *N*, kidneys; *Od*, oviduct; *Ot*, its opening into the cœlom; *Ov*, ovary; *P*, opening of the oviduct into the cloaca; *S*, *S′*, openings of the ureters; *Ut*, uterine dilatation of the oviduct. (After Wiedersheim.)

The *oviducts* are a pair of convoluted tubes extending the length of the body cavity on either side of the middle line. They are surrounded by peritoneum which is continued dorsally to form a supporting membrane which extends to the dorsal body wall outside of the mesovaria. Anteriorly, each oviduct opens by a wide mouth, or ostium, into the body cavity near the base of the lung. At the posterior end it enlarges to form the thin-walled, very distensible *uterus;* the openings of the two uteri lie close together on the dorsal wall of the cloaca. With the exception of the uterus, and a short space at the anterior end, the oviducts possess a thick glandular wall. The inner surface of the oviduct is thrown into longitudinal ridges, which are covered with ciliated epithelium. The grooves between the ridges receive the openings of the numerous glands which secrete the gelatinous coats of the eggs. These glands are mostly of the simple tubular type; they are lined by a single layer of cylindrical secreting cells which become very much enlarged during the breeding season. When the secretion is discharged, the outer membrane of the cells is burst (Lebrun), and the contents, which formed a greater part of the bulk of the cell, flow into the lumen of the gland. After the discharge of the secretion the glands become very much reduced in size, and the whole oviduct much thinner, and of a yellowish color from the accumulation of fat. As Boettcher has shown, the oviducts in the breeding period possess a remarkable capacity for the absorption of water. A pair of oviducts, which when just taken out of the body weighed 9.6 g., were found to weigh 1084 g. after they had lain some time in water; *i.e.* they had increased in weight 113 times. After the breeding season this power of absorbing water is very much reduced. The eggs, as they are discharged from the ovaries, are taken into the mouths of the oviducts by means of ciliary action. They are then carried down the oviducts by means of the cilia on the ridges of the inner walls. During this passage they receive their coats of jelly, after which they collect in the uteri, whose walls they greatly distend. Here they may remain for several days, the length of time depending upon the presence or absence of the male (see p. 54).

The males of several species of Rana possess a curious homologue of the oviduct of the female. In *Rana pipiens* it is very well developed, and contains an enlargement at its posterior end representing a uterus. It lies just external to the ureter, and extends as a fine tube some distance in front of the kidney. Its function, if it has any, is unknown. Cases are not uncommon in which organs characteristic of one sex are found in a rudimentary form in the other, and it is not improbable that the oviduct of the male frog is simply a useless, although rather large, rudiment of this kind. In the bullfrog (*Rana catesbiana*) this duct is absent.

Organs of the Male.—The *testes* are rounded or ovoid organs lying ventral to the kidneys. Like the ovaries, they are surrounded by peritoneum, which is extended dorsally as a double membrane, the *mesorchium,* to the dorsal side of the body cavity, where it becomes continuous with the general cœlomic lining. The *vasa efferentia,* or ducts of the testes, consist of a variable number of slender tubes, which extend within the mesorchium to the inner margin of the kidney, where they connect with Bidder's canal. The vasa efferentia often branch and anastomose more or less, in a way which varies greatly in different individuals.

The testis is made up essentially of a mass of tubules, together with blood vessels and nerves, and a small amount of connective tissue binding the tubules together. The whole is surrounded by a connective tissue membrane, the *tunica albuginea,* outside of which is the peritoneum. Toward the outer portion of the testis the tubules extend radially, and end blindly next to the tunica albuginea. Near the point where the vasa efferentia enter they become coiled irregularly. The vasa efferentia form a network within the testis, into which the tubules open at their inner ends. Each tubule possesses an outer *membrana propria* and an inner lining of cells, some of which (*spermatogonia, spermatocytes,* and *spermatids*) represent stages in the formation of spermatozoa; others form the so-called "follicle-cells," and the flattened cells described by Bertacchini, which lie next to the outer membrane. The follicle cells form a sort of wall around groups of cells from which the spermatozoa take their origin.

The spermatozoa of the frog pass through the substance of the kidney into the ureter. In many species of frogs the free portion of the ureter is dilated to form a seminal receptacle in which the spermatozoa are stored against the time of their discharge from the body. The seminal receptacle is poorly developed in *Rana pipiens* and *R. catesbiana*. In the European species *R. fusca* it becomes very large and divided into a number of compartments.

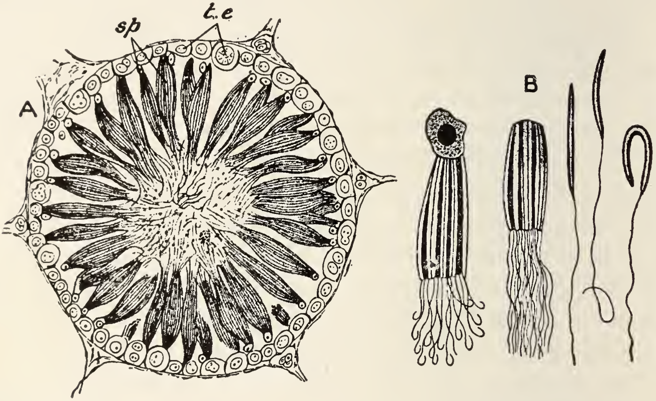

FIG. 71.—A, cross section of one of the tubules of the testis; *sp*, bundles of spermatozoa; *t.e*, epithelial lining of the tubule. B, stages in the development of spermatozoa. (After Parker and Parker.)

Corresponding to the various stages in the development of the spermatozoa the testes of the frog assume a different appearance in different times of the year. In *Rana fusca*, according to Nussbaum and Ploetz, the testes are smallest in May, after they have discharged their spermatozoa. Then they gradually increase in size until August, when they attain their maximum, after which they decrease in size during the fall and less rapidly during the winter. In *Rana esculenta,* according to Ploetz, the testes vary little in size in different months. This is, perhaps, due to the fact that during most of the year all stages of spermatogenesis may be met with in some of the tubules. The interstitial substance between the tubules increases in *Rana fusca* from March to September. There is a storage of fat and pigment during this period which later disappears (Ploetz, Friedmann). In *Rana esculenta* there is most interstitial substance around those tubules in which the process of sperm production is most rapidly going on.

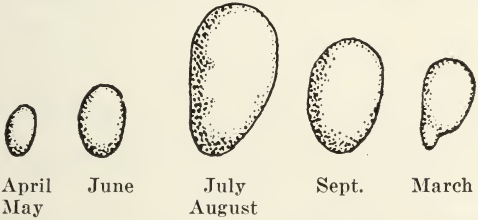

FIG. 72.—Seasonal changes in the size of the testes of *Rana temporaria.* Natural size. (After Witschi.)

The Fat Bodies (*Corpora Adiposa*).—The fat body is a yellowish organ lying just in front of the gonads. It is furnished with a number of finger-like processes whose number varies not only in different individuals but also in the same individual at different times. In the male the fat body is broadly and closely attached to the anterior end of the testis. In the female it is less closely attached to the gonad than in the male.

The fat bodies serve as a sort of storehouse of nutriment. They undergo great changes in size during different seasons of the year, as has been described in a previous chapter. The histological phenomena which accompany these changes have been studied by Toldt, Neumann, and Giglio-Tos. In the spring nearly all of the fat disappears from the cells (Toldt), and as there are usually two or more nuclei in each cell at this time, it is probable that cell division takes place. After the feeding period begins there is a rapid storage of a yellowish fat in the cells, which become greatly increased in size.

The development of the fat body is closely connected with that of the gonads. Both, in fact, arise from the differentiation of the genital ridge, the anterior portion of which forms the fat body, the posterior portion the ovary or testis.

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CHAPTER XII

INTERNAL SECRETION AND THE ENDOCRINE GLANDS

Most secreted substances with which we are familiar are formed in glands and discharged through a duct. There are several organs, however, whose products instead of being carried off by a duct are diffused into the blood or lymph. The latter process is known as internal secretion. The term internal secretion was first employed by Claude Bernard in connection with his classical investigation on the glycogenic function of the liver. While the liver secretes bile which is carried to the intestine through the bile duct, the dextrose which is derived from the stored glycogen passes into the blood. Urea is also formed in the liver and is likewise passed into the blood stream. But quite regardless of the original use of the term, the production of sugar and urea are no longer considered as typical examples of internal secretion. Whether warranted or not, the term internal secretion is commonly employed in a more restricted sense to designate the production of a class of compounds called *hormones* which have an important influence in stimulating the activity of other parts of the body.

Organs which produce hormones are spoken of as *endocrine glands.* Several so-called ductless glands belong in this category, but the presence or absence of a duct has no necessary relation to the production of hormones. The pancreas and the testes have ducts for the discharge of some of their products, nevertheless they elaborate important hormones which pass into the blood.

In recent years the study of internal secretions has become one of the most important and fruitful fields of physiological research. It has not only thrown much light on the coordination of physiological functions, but it has yielded results of great value in the practice of medicine. A few of these endocrine glands were considered by some investigators as mere rudiments of organs useful once, but now functionless. It is now known that some of these organs, far from being useless rudiments, are absolutely essential for the maintenance of life. Just how they act is still an unsettled problem, but their secretions appear to afford stimuli which are necessary to evoke the normal functioning of other organs of the body.

The Pancreas.—In addition to the pancreatic juice which performs so many important digestive functions, the pancreas secretes a hormone which is of even greater importance in the vital economy of the body. Removal of the entire pancreas from one of the higher vertebrates causes the onset of diabetes which soon leads to death. In diabetes there is an abnormal amount of sugar in the blood. From the blood it is eliminated by the kidneys and hence appears in the urine. Under ordinary circumstances the undue production of sugar is prevented through the agency of the internal secretion which is given off from the pancreas into the general circulation. If the duct of the pancreas is tied so as to prevent the discharge of the external secretion of this organ, there is no abnormal production of sugar and the animal may live for a long time. A large part of the pancreas may be removed, or the whole organ may be removed and grafted into some other part of the body without producing fatal results. So long as the body receives the sugar-regulating hormone secreted by the pancreas it may be kept alive, but without this precious substance, fatal effects soon follow.

The part of the pancreas concerned in the elaboration of this hormone is considered to be the groups of cells known as the islands of Langerhans which lie between the tubules which secrete the pancreatic juice. This conclusion is strengthened by the fact that if the pancreatic duct is tied the cells of the tubules atrophy and only the islands of Langerhans persist. It is also supported by the fact that in many cases of diabetes the cells of the islands of Langerhans show a pathological condition.

Efforts to extract the sugar-regulating hormone of the pancreas proved unavailing until a few years ago when Dr. Banting succeeded in obtaining a substance called *insulin* which when injected into the blood of animals suffering from diabetes had a most remarkable effect in checking the abnormal production of sugar. This striking triumph of patient and ingenious experimentation has proven a means of saving many human lives from a malady with which the medical profession had long struggled in vain.

Most of our knowledge of the functions of the pancreas has resulted from experiments on mammals. Islands of Langerhans occur in the pancreas of the frog and are formed quite early in development (Aron and Alfonsi). Experiments on injecting insulin into the blood of the frog were found by Schwartz and Bricka to reduce the sugar content of the blood, although the glycogen reserve of the liver was little affected. Gayda has found that the removal of the pancreas from the frog resulted in the appearance of abnormal quantities of sugar in the urine. It is probable, therefore, that the pancreas of the frog functions in essentially the same manner as it does in higher animals.

The Spleen.—The *spleen* of the frog is a rounded, reddish body lying dorsal to the anterior end of the cloaca, where it is attached to the supporting mesentery. It receives blood from a branch of the anterior mesenteric artery, and gives off the splenic vein, which forms a branch of the hepatic portal system; both blood vessels enter at a common point called the *hilus*. The spleen is surrounded by a fibrous membrane outside of which the greater part of the surface is coated with peritoneum. The inner framework of the spleen consists of a network of areolar tissue which contains the essential part of the organ, the *spleen pulp*. The latter is composed of several kinds of cells, many of which represent stages in the development of leucocytes, of which the spleen contains a large number. There are numbers of large cells containing an abundance of pigment, both yellow and black. The pigmented cells have the property of absorbing pigment granules with which they come in contact; if coloring matters are injected into the blood, they are taken up by these cells in large quantities (Ponfick, Siebel). The spleen also contains large cells in which red blood corpuscles are frequently found in all stages of degeneration.

The spleen is an organ having various functions. It is a place where red blood corpuscles are destroyed, probably when they have reached a moribund condition. Pigment and other foreign matters in the blood are taken up by certain cells of the pulp. Leucocytes are in all probability formed in the spleen, as various stages in their production have been observed, and it has been found that there is a greater number of these cells in the blood of the splenic vein than in that of the splenic artery. Red blood corpuscles and spindle cells are produced in the spleen according to H. E. Jordan who regards the spleen as the chief organ for renewing all kinds of blood corpuscles.

The Thyroid Glands.—The thyroid glands of the frog are completely separated from each other, being situated on either side of the hyoid apparatus in a small space between its posterior lateral and thyro-hyoid processes. Gaupp has described some thyroid tissue (accessory thyroid) on the ventral side of the hyoglossus muscle, and I have been able to confirm this observation in *Rana pipiens.* The tissue of the thyroid shows a unique structure, being composed of a mass of rounded follicles united by a small amount of connective tissue in which there is a rich supply of blood vessels. Each follicle is a perfectly closed sac lined by a single layer of cubical epithelial cells. In the center of each follicle is a colloidal mass of transparent substance which probably represents the secretion of the epithelial lining.

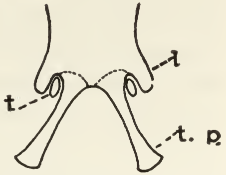

FIG. 73.—Diagram showing the position of the thyroid glands, *t; l*, lateral process of hyoid cartilage; *t.p*, thyro-hyoid process of hyoid.

What knowledge we have of the functions of the thyroid in the frog indicates that they are much the same as in man and other mammals. The removal of the thyroid in the higher vertebrates commonly produces fatal results unless there are accessory organs, such as the parathyroids, which in some of the mammals are able to maintain life in the absence of the thyroid. Removal of a part of the gland creates, as a rule, but little disturbance. Life may be maintained for a considerable period after complete removal of the thyroid by giving injections

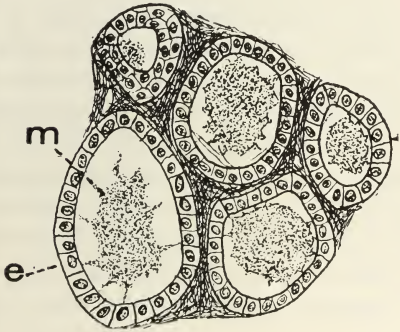

FIG. 74.—Part of a cross section of the thyroid of *Rana pipiens. e*, epithelial layer of vesicles; *m*, colloidal substance in vesicle.

of extracts of the gland into the blood. In man the disease called myxœdema, or, cretinism, caused by atrophy or functional insufficiency of the thyroid, is often much helped, or even cured by the administration of thyroid extract. The substance to which the thyroid owes its important function is a crystalline compound known as thyroxin which contains a comparatively large amount of iodine. Treupel found that frogs from which both thyroids were removed lived only two or three days, but he was not entirely certain that the result was not due to the effects of the operation rather than to the loss of the parts in question.

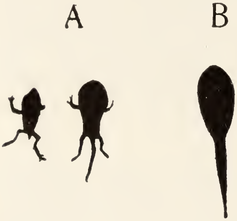

Fig. 75.—*A*, Tadpoles fed on thyroid; *B*, tadpole of the same age not given thyroid. Both natural size. (After Gudernatsch.)

Most of the experimental investigations on the functions of thyroid in the Amphibia have been performed upon the larvæ. This work was initiated by the spectacular results obtained by Gudernatsch in feeding tadpoles on the thyroid glands obtained from mammals. Thyroid feeding caused a marked inhibition of growth combined with a very early metamorphosis, so that the tadpoles began to transform into frogs long before they had reached their usual size. Some of the frogs thus obtained were diminutive creatures not much larger than house flies. The thyroid feeding, therefore, hastened differentiation while it checked growth.

The experiments of Gudernatsch led Dr. B. M. Allen to ascertain the effect of removing the thyroids in very young tadpoles. The loss of the thyroids produces little effect on development until the stage at which the hind legs begin to grow, when further differentiation ceases and the tadpoles fail to undergo metamorphosis. The larvæ, however, continue to grow, but while the differentiation of most organs is inhibited, the sex organs continue to develop even more rapidly than in normal tadpoles. The male larvæ may produce mature spermatozoa, and the female larvæ may show a considerable growth of the egg cells in the ovary.

If larvæ having no thyroids are fed upon the thyroid they may undergo metamorphosis. Swingle has shown that various compounds of iodine, or food impregnated with iodine, may cause metamorphosis in thyroidectomized tadpoles, and that iodine and its compounds check growth and accelerate differentiation much as is done in thyroid feeding. He concludes that iodine *per se* is the essential substance involved in causing metamorphosis. However, iodine and most of its compounds are unable to compensate for thyroid deficiency in the mammals, and they do not cause the other physiological effects produced by thyroxin. The physiological influence of thyroxin on the mammals and its effect upon the development of frogs and toads depend apparently on different mechanisms. Both involve the influence of iodine, but in the mammals this element must form a part of a particular compound, whereas this is unnecessary for its effect upon the metamorphosis of amphibians.

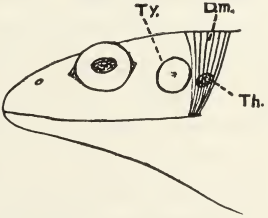

FIG. 76.—Diagram showing position of the thymus, *Th. Dm*, depressor mandibulæ muscle; *Ty*, tympanum.

The Thymus.—The *thymus* is a small, oval organ, somewhat reddish in color, situated behind the tympanic membrane under the depressor madibulæ muscle. As in most higher forms, the thymus diminishes in size with age. Maurer found that in *Rana esculenta* the thymus attained its maximum size in specimens of two or three centimeters in length. In old frogs (7 to 8 cm.) the organ is much smaller and shows marks of degeneration in structure.

The thymus has essentially the structure of a lymphoid gland. In its fine network of adenoid tissue lie numerous small, rounded cells. There are also several large cells of concentric structure concerning whose origin and significance there has been much discussion, but of whose function nothing positive is known.

It is probable that blood corpuscles are produced to a certain extent in the thymus (Mayer). According to Abelous and Billard, if both thymus glands of the frog are removed, the animal soon dies, after a period of great muscular weakness, ulceration of the skin, and a variety of other pathological symptoms. Hammar, however, failed to confirm these results. He found that both thymus glands may be removed from the frog without injury, and concludes that the results obtained by Abelous and Billard were the effects of accidental infection.

According to Adler, when the thymus is removed from young frog tadpoles, the gonads increase in size much beyond those of normal larvæ. This conclusion is contradicted by B. M. Allen who finds in a larger series of tadpoles than Adler worked with that removal of the thymus has no appreciable effect upon the gonads. Allen holds that the thymus exerts no marked influence upon either growth or metamorphosis, nor does it have any effect upon the development of the thyroid. On the other hand, the removal of the thyroid, according to Rogers, checks the usual degeneration of the thymus which follows metamorphosis, and prevents it from migrating to its definitive position. This result is probably just an incident of the general effect of the removal of the thyroid in checking differentiation.

It was claimed by Gudernatsch that frog larvæ fed upon thymus grow well, but metamorphose little, if at all. Thymus feeding was held to produce effects the reverse of those obtained by feeding thyroid. Repetition of Gudernatsch's experiments under varied circumstances have not entirely confirmed his findings and doubt has been cast on his interpretation of his results.

The Pseudothyroid and the Epithelial Bodies.—The *pseudothyroid* and the *epithelial bodies* are organs of similar structure and origin. They are derived from the modification of the epithelium of the gill slits of the larva and are therefore products of the entoderm. The two pseudothyroids are the largest of these. They are rounded reddish bodies, lying on either side of the posterior portion of the hyoid cartilage. They were formerly mistaken for the thyroids, but they possess a very different internal structure, which is essentially that of a lymphoid gland.

The *epithelial bodies* are small, rounded structures usually more than two in number on each side and somewhat variable in position, but generally situated near the pseudothyroids. As an organ probably belonging in the same category as the preceding may be mentioned the propericardial body, which is a transverse oval organ lying ventral to the hyoglossus muscle between the thyroids. It possesses a lymphoid structure and is larger in young than in old frogs (Gaupp). From its mode of development Maurer classes the carotid gland also among the epithelial bodies, but its structure in the adult shows no resemblance to that of the organs described above.

Another epithelial derivative, but one having a quite different structure from the rest, is the *post branchial body,* a paired organ lying beneath the mucus membrane of the pharynx on either side of the glottis. Each organ, according to Maurer, consists of a group of four to six small follicles, lined by cylindrical epithelium, which sometimes bears cilia. Its structure resembles that of the thyroid glands, but the follicles contain a thin fluid instead of a colloidal substance (Maurer).

A small lymphoid organ, the *procoracoidal body,* has been discovered by Gaupp between the coracoid and procoracoid portions of the pectoral girdle. Its mode of origin has not been traced, but it is found in young larvæ with external gills. It probably does not belong in the category of epithelial bodies, although it bears a certain resemblance to them in internal structure.

Little is known concerning the functions of any of these bodies. B. M. Allen has shown that after the removal of the thyroids of toad larvæ the bodies he designates as parathyroids increase greatly in size. They do not take on the peculiar structure of thyroid tissue although their growth suggests that they may compensate in a measure for the loss of thyroid function. Schulze has fed frog tadpoles on the parathyroids of cattle and reports that there followed an inhibition of growth and an acceleration of metamorphosis similar to that which follows thyroid feeding.

The Adrenal Bodies.—The *adrenal bodies* are thin bands of a golden yellow color extending along the middle of the ventral surface of the kidneys. They consist essentially of small solid groups of cells which lie close to the branches of the renal veins. Among the ordinary epithelial cells composing the main bulk of the organs are scattered cells of larger size and often of brownish color. The former, according to Stilling, correspond to the peripheral or cortical cells of the adrenals of mammals, and the latter to the central cells. A third type of cell, which is characterized by its granular contents, and its taking an intense red color when stained in eosin, was found by Stilling to occur only during the summer months. On the other hand, the ventral portion of the adrenals was found to contain numerous lymphoid cells only in the winter and spring. The "cortical cells" are derived from the peritoneum, while the "central cells" are generally regarded as modifications of the cells of the sympathetic ganglia. In the higher vertebrates the central cells form a single mass which is surrounded by a definite cortex, but in the frog they are scattered through the cortical cells in an irregular manner.

Abelous and Langlois found that if both adrenals of the frog were destroyed, the operation was soon followed by fatal effects; but if only one adrenal was destroyed, the animal would continue to live. If after the destruction of both adrenals portions of one of the bodies were transplanted in the dorsal lymph space, life was maintained for a considerably longer period than would otherwise have been possible. Fatal results following the removal of both adrenals have recently been reported by Gayda who finds that frogs succumb after increasing muscular weakness and lack of heat production in eight to twelve days. It is well known that the adrenals produce an internal secretion upon which the life of the organism is dependent. This material (adrenalin, epinephrin) may be extracted from the bodies and its physiological action tested. It has been much experimented with among higher animals, and is now used to a considerable extent in medicine and surgery. It has the property of greatly increasing blood pressure by causing a

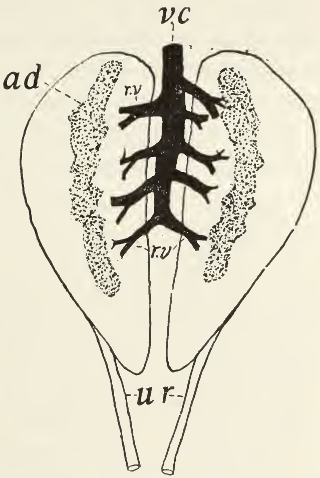

Fig. 77.—Kidneys and adrenal bodies. *ad*, adrenals; *r.v.*, renal veins; *ur*, ureters; *v.c.*, vena cava.

strong contraction of the smooth muscle fibers of the blood vessels.

Experiments on the effects of the extract of the adrenals of the frog show that this substance has much the same properties as among mammals. When injected into the blood of a mammal, it produces a marked rise in blood pressure; and, on the other hand, injection of the extract from the mammalian gland into the frog produces very marked results, which may be fatal if the dose is large. Moore and Vincent found that "after injection of a glycerin extract equivalent to about .5 g. of the fresh gland into the dorsal lymph sac, paralysis immediately comes on. . . . With larger doses there are spasms of fibrillary twitchings in various parts." With smaller doses (.3 g. of the fresh gland) Oliver and Schäfer found a similar paralysis, but it came on more slowly. After half an hour the animal appeared to be "nearly, if not quite, in a normal condition."

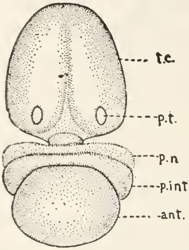

FIG. 78.—Hypophysis of *Rana catesbiana*, ventral side. *ant.*, anterior lobe; *p.int.*, pars intermedia; *p.n.* pars nervosa; *p.t.*, pars tuberalis; *t.c.*, tuber cinereum (infundibulum). (After Swingle.)

The Hypophysis, or Pituitary Body.—The hypophysis, or pituitary body is an organ consisting of two chief parts having a quite different origin. The so-called pars anterior, or anterior lobe, arises from the ectoderm of the dorsal side of the mouth cavity. The pars posterior, or posterior lobe, first appears as an outgrowth from the floor of the third ventricle of the brain. In the higher vertebrates the two parts become very intimately united. They are less closely associated in the frog, and the so-called pars anterior comes to lie posterior to the true posterior lobe. In addition to the anterior and posterior lobes there is a pars intermedia between the two, and a pars tuberalis, both of which arise from the original outgrowth from the roof of the mouth.

In the higher vertebrates complete removal of the pituitary speedily results in death. The two parts of the gland secrete distinct hormones having very different functions. According to Robertson, the anterior lobe produces a substance, tethelin, which has a marked stimulating effect upon growth, a fact correlated with the circumstance that overgrowth of the pituitary may lead to gigantism and a relatively large size of the hands, feet and head. From the posterior lobe a substance, pituitrin, has been extracted which exerts a strong stimulating influence on unstriated muscle and on the functions of several glands.

The pituitary is an organ of several functions also in the Amphibia. The fatal effects reported as resulting from the removal of the pituitary of the frog do not necessarily follow. Hogben found that frogs could be kept alive for a considerable period even after the removal of both lobes. A few hours after the operation the animals exhibited a remarkable and persistent pallor. The melanophores were strongly contracted, and the xantholeucophores, on the other hand, were in a state of extension. Ordinary influences, such as cold or darkness, which cause frogs to become dark had no appreciable effect on the operated animals. The injection of extracts of the pituitary of the frog or the commercial preparation from the posterior lobe of the ox was found to cause the skin to resume its dark color.

In the frogs from which only the anterior lobe of the pituitary was removed these effects were not produced. It has been clearly established that the hypophysis produces some substance which has a powerful influence upon the pigment cells as has been illustrated in the chapter on the skin. The results of these investigations are quite in harmony with those obtained previously by extirpating the hypophysis of tadpoles. Adler removed the hypophysis from frog larvæ and found that metamorphosis was delayed. Soon afterward B. M. Allen and P. E. Smith, working independently, removed the hypophysis from young tadpoles and observed a reduction of growth, an inhibition of metamorphosis and a remarkable paling of the skin, so that the tadpoles appeared whitish in color. There was also a reduced development of the thyroid glands. The pale color of the larvæ is due in part to the reduction of black pigment, but chiefly to the contraction of the melanophores and the expansion of the more superficial xantholeucophores. There seems to be little effect on the development of the sex glands. If the stunted larvæ with no hypophysis are fed with anterior lobe substance from cattle, or if an anterior lobe is engrafted from another larva, growth to normal size may be resumed.

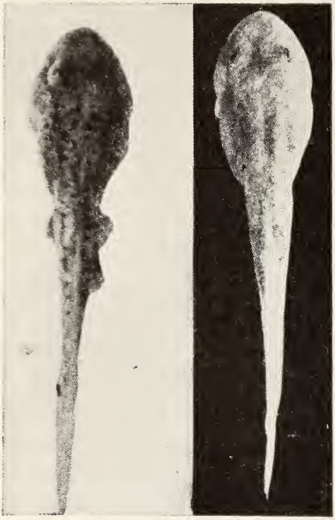

Fig. 79.—Normal tadpole to the left. To the right a tadpole after removal of the hypophysis. (After P. E. Smith.)

According to Allen it is the secretion of the intermediate lobe which is responsible for the distribution of pigment as is indicated by the fact that extracts of beef in intermediate lobe will produce normal pigmentation in the operated larvæ. Grafting the intermediate lobe, or the intermediate and posterior lobes of the frog into larvæ without a hypophysis produces a similar effect, but transplanting the posterior lobe alone does not cause a restoration of the dark color. The experiments of Hogben with adult frogs, however, indicate that the posterior lobe has the greatest influence upon the chromatophores. Whether these different conclusions are due to experimentation at different ages is at present uncertain.

The Sex Hormones.—Among the organs of internal secretion must be ranked the gonads which, while not essential for the maintenance of the life of the individual, exercise, as in higher vertebrates, a considerable influence upon the physiological state of the body. As we have already seen in Chapter II, the reproductive organs are subject to marked seasonal changes, and along with these, there are corresponding modifications in other organs. The clasping propensities of the male are evoked in the spring at a time when the testes are much enlarged. Nussbaum, Meisenheimer and Harms have shown that if the testes are removed some months before the breeding season, the clasping reflex is largely inhibited. If the operation is performed during the breeding season the clasping may continue much as usual. The removal of the gonads requires a considerable time to produce its full effect.

If a testis is grafted into the body of a castrated frog the clasping reflex will return. Injection of the extract of the testes, or even the ovary, will cause a recurrence of the clasping propensity, but the effect lasts only for a few days. Extracts of most other organs failed to elicit the same response, but Steinach found that extracts of the brain of male frogs in the breeding season would evoke the clasping reflex in castrated males. If the extract was made from the brain of a male that had been castrated it failed to produce the same result. The conclusion drawn was that the testicular hormone is taken up by the substance of the brain and thereby checks the usual inhibitory action of that organ over the clasping reflex which, as experiments have shown, can be elicited any time of year by cutting the spinal cord in two near the medulla.

The development of the thumb of the male is also associated with the sex cycle and, according to Nussbaum, if male frogs are castrated early the enlargement of the thumb is prevented. Nussbaum and Meisenheimer find that if parts of the testis are grafted into the body of a castrated frog the enlargement of the thumb will again occur in the breeding period. Similar results were obtained by injecting extracts from the testis into castrated frogs. These conclusions have been challenged by G. Smith who finds that frogs "completely castrated Dec., 1911, after acquiring perfectly smooth thumbs, without a trace of papillæ on them in the summer and autumn of 1912, grew papillæ again in January, 1913, without any experimental treatment at all," and he concludes that "no evidence exists sufficient to prove that injection of testes or ovarian extracts, or implantation of testes or ovaries can call forth the growth of papillæ on the thumb of a castrated frog." According to Harms the thumb of male frogs tends to undergo its usual seasonal changes even after castration, but these changes are less marked than in normal individuals. While it seems clearly established that the testis produces an internal secretion which is responsible for the appearance of the clasping reflex, it is not proven that the same hormone affects the development of the thumb and seminal vesicles, even if the changes in these organs may be stimulated by a testicular secretion. The seminal vesicles, which are much more fully developed in the breeding season, are much less developed, according to Nussbaum, in castrated frogs. Other investigators are not convinced that the observed changes are caused by castration, and hold that the changes described would have occurred in normal animals. Despite the several studies on the relation of sex hormones to secondary sexual characters in the frog, the subject is still in a state of considerable confusion.

The Pineal Gland.—We have already briefly described the pineal gland in Chapters III and V. Observations and experiments on higher vertebrates indicate that this structure is an organ of internal secretion. Pineal tumors are frequently associated with rapid growth and a precocious development of the sex organs, and the extirpation of the pineal gland has been followed by increased growth and a more rapid development of the testes. The functions of the pineal gland are still very imperfectly understood. Little is known of its function in the frog except that feeding tadpoles on pineal extract causes a paling of the skin, due to a strong contraction of the melanophores. The effect is temporary and apparently does not occur in adult frogs (M'Cord and Allen[1]).

Internal Secretions as a Means of Functional Correlation.—From what has been said it is evident that internal secretions play an important rôle in securing the coördination of functions of the various organs of the body. They act as regulative agents, making possible the partial control of one organ by another independently of the central nervous system. Organs through their internal secretions may act and react upon each other, and in this way bring about the harmonious functioning of the different parts which is essential to the life of the whole.

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[1] M'Cord and Allen, *Jour. Exp. Zool.*, Vol. 23, p. 207, 1917.

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CHAPTER XIII

THE SKELETON

In the skeleton, or bony framework, of the frog we commonly distinguish two main divisions, the *axial,* consisting of the skull and vertebræ, and the *appendicular,* composed of the limbs and their girdles or supports. We shall begin our description with the skull.

Bones of the Cranium.—In the skull we may distinguish the *cranium,* or part inclosing the brain and principal sense organs, and the *visceral skeleton,* which forms the jaws and hyoid arch. The cranial portion of the skull is relatively small, and is narrowest in the central part, between the very large spaces, or orbits, which lodge the eyes. At the posterior end is a large aperture, the *foramen magnum,* through which the spinal cord passes. On either side of this opening are the *exoccipital bones,* which are separated from each other above and below by a small piece of cartilage. At the sides of the foramen magnum these bones bear a pair of rounded prominences, the *occipital condyles,* which articulate with the *atlas,* or first vertebra. Just external to each condyle is a small aperture for the exit of the vagus nerve.

At the sides and in front of the exoccipitals lie the *proötic* bones, each of which forms a ring-like lateral projection on each side of the skull, which incloses the inner ear. Anteriorly each proötic is perforated by a large aperture, through which pass the 5th, 6th, and 7th cranial nerves. On the outer side there is an opening, the *foramen ovale,*

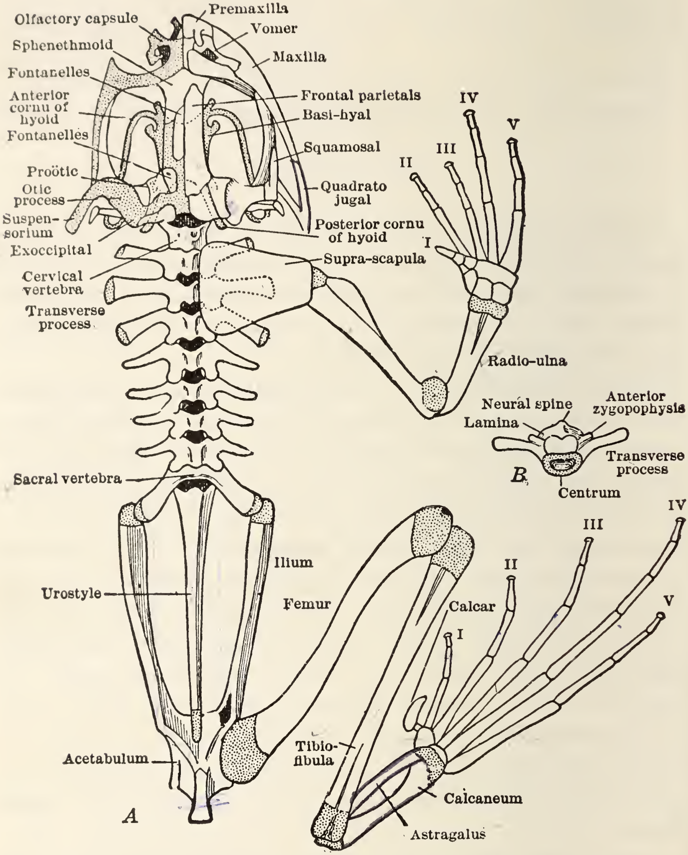

FIG. 80.—*A*, skeleton of *Rana temporaria*. The left limbs, left shoulder girdle and membrane bones of the left side of the skull are removed. Cartilaginous parts dotted. *I—V*, digits. *B*, the fourth vertebra seen from in front. (From Hegner, slightly altered from Howes.)

which is plugged with cartilage against which abuts the inner end of the columella of the ear.

In the ventral side of the skull is a large bone, the *parabasal,* or *parasphenoid,* which is in the shape of a dagger without any handle; the lateral portions underlie the two proötics.

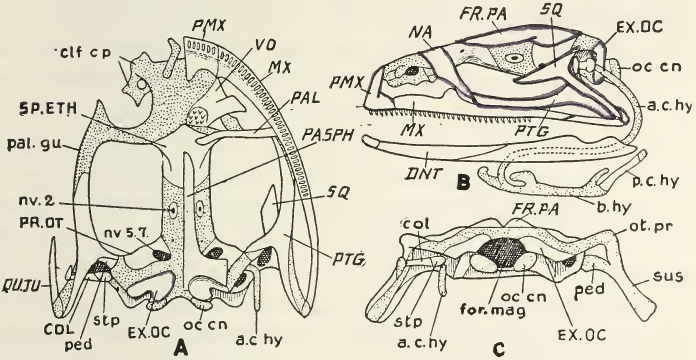

Fig. 81.—Skull of *Rana temporaria.* A, from beneath, with the membrane bones removed from the right side (left of figure); B, from the left side, showing the lower jaw and hyoid; C, from behind Names of cartilage bones in thick; those of membrane bones in italic capitals. *a.c.hy*, anterior cornu of hyoid; *b.hy*, body of hyoid; COL, columella; *DNT*, dentary; EX.OC, exoccipital; *for.mag*, foramen magnum; *FR.PA*, fronto-parietal; M.MCK, mento-meckelian bones; *MX*, maxilla; *NA*, nasal; *nv. 2*, optic foramen; *nv. 5, 7*, foramen for the fifth and seventh nerves; *oc.cn*, occipital condyle; *olf.cp*, olfactory capsule; *ot.pr*, otic process; *PAL*, palatine; *pal.qu*, palatoquadrate; *PA.SPH*, parasphenoid; *p.c.hy*, posterior cornu of hyoid; *ped*, pedicle; *PMX*, premaxilla; PR.OT, proötic; *PTG*, pterygoid; *QU.JU*, quadrato-jugal; SP.ETH, sphenethmoid; *SQ*, squamosal; *stp*, stapes; *VO*, vomer. (From Newman, slightly altered from Howes.)

The *fronto-parietal* bones form most of the roof of the skull. Along the middle line they are united by the *sagittal suture.* Each represents two bones, a frontal and a parietal, and in the early stages of the development of the skull these elements are separate, but subsequently they fuse into a single bone.

The anterior end of the cranium is surrounded by a bony ring, the *ethmoid* (or *sphenethmoid*) bone. This is overlapped by the fronto-parietals above and the parabasal below, and is separated from the proötics behind by quite a long interval of unossified cartilage. The anterior part of the ethmoid is widened out and divided into two chambers by a median vertical partition. The expanded portion forms the posterior wall of the nasal cavity; the latter may be seen to communicate with the cranial cavity by a pair of small openings through which the olfactory nerves pass. The rest of the nasal capsules are formed mainly by cartilage.

The *nasals* are two narrowly triangular bones, lying above the nasal capsules; their bases, which lie near each other in the middle line, are separated from the fronto-parietals by a small part of the roof of the ethmoid.

The *vomers* lie ventral to the nasal capsules; each has three outer processes, between the two posterior of which occur the internal nares; the ventral surface bears the *vomerine teeth.*

Suspensorium and Jaws.—The jaws are attached to the cranium by means of an intermediate suspensory apparatus in which the following separate bones are to be distinguished:—

(1) The *tympanic* (*squamosal*), a T-shaped bone, the main limb of which extends outward and backward to the angle of the jaws; the posterior end of the cross piece articulates with the proötic, while the anterior end extends obliquely downward in front. Below the tympanic lies (2) the *pterygoid,* a triradiate bone, the inner limb of which attaches to the outer side of the proötic, while the two outer limbs diverge, the one running beneath the long stem

of the tympanic to connect with the posterior end of the upper jaw, the other extending forward and joining the upper jaw near its middle. The tympanic and pterygoid are separated from each other by a strand of hyaline cartilage.

(3) The *palatines* are slender, rodlike bones on the lower side of the cranium, which extend from the anterior end of the ethmoid to the upper jaw.

The upper jaw, or *maxillary arch,* is composed of three pairs of bones. The posterior portion of the arch is formed by the *quadrato-jugals.* These are short bones, devoid of teeth, articulating behind with the pterygoid and tympanic, and joining the maxillary in front by an oblique suture. The *maxillaries* are the largest bones of the upper jaw; they connect with the *premaxillaries* in front, and quadrato-jugals behind; they are furnished with teeth throughout their length. On the upper side each bears a frontal process which is overlapped by the nasal. The *intermaxillaries* or *premaxillaries* are the two small bones which form the apex of the maxillary arch; they are furnished with teeth and are produced backward on the upper side into the facial processes which are instrumental in closing the nares in respiration.

The *lower jaw,* or *mandibular arch,* is composed of a central core, called *Meckel's cartilage,* which is partly surrounded by two membrane bones. The bone at the proximal end is called the *angulare,* or *angulo-splenial.* Meckel's cartilage runs in a groove along the outer side of this bone and widens out at the posterior end, where it forms the facet for articulation with the suspensorium above. A short distance in front of the articulation the angulare bears a prominence, the *coronoid process,* which gives attachment to the muscles for closing the jaw.

The *dentale* lies on the outer side of the distal end of the angulare, overlapping Meckel's cartilage, which there runs between these two bones. The apical portion of the mandibular arch consists of two short movable elements, the *mento-meckelian* bones, which result from the ossification of the distal portions of Meckel's cartilage. They underlie the premaxillaries, and when they are raised, cause a corresponding elevation of the latter bones.

The Hyoid.—The branchial skeleton of the frog is composed of the *hyoid cartilage* and its processes. The body of the hyoid is a large flat plate of hyaline cartilage, more or less quadrate in general outline, lying in the floor of the buccal cavity. Its anterior margin, where the base of the tongue is inserted, is strongly concave. At the anterior end of the body arise the *anterior cornua,* which are long, slender rods of cartilage, which pass backward and upward on either side of the throat and join to the proötic bones of the skull.

On the inner side of the base of each cornu is a short anterior process. The *alary processes,* flattened, distally expanded plates of cartilage, arise just behind the anterior cornua. The postero-lateral angles of the body are produced to form the *postero-lateral processes.* The *thyroid processes* diverge from the middle part of the posterior margin of the body and lie on either side of the larynx, which they help to support. They are the only parts of the hyoid apparatus to become ossified.

The Cartilaginous Cranium. The skull of the frog is composed of cartilage to a much greater extent than in the higher vertebrates. Only here and there does its original cartilaginous basis become converted into bone. The various bones which constitute the skull may be divided as regards their origin into *cartilage bones,* which result from the ossification of cartilage, and *membrane bones,* which are

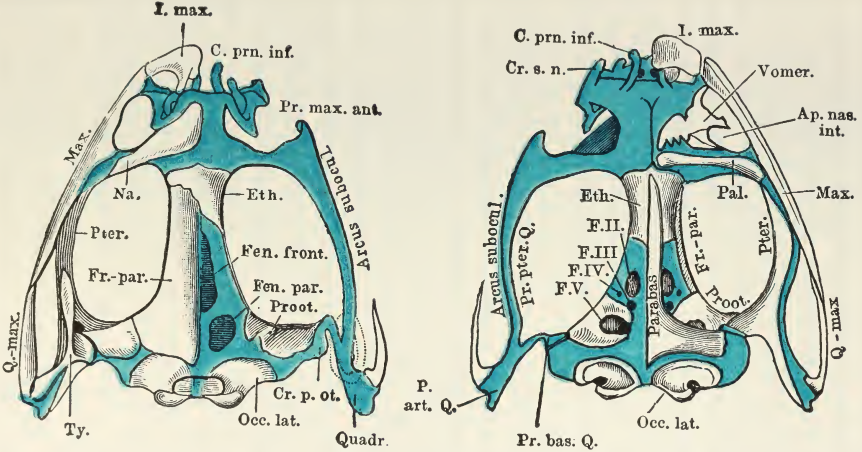

FIG. 82.—Skull of *Rana esculenta*, after removal of the membrane bones of the right side; in the left figure from above, in the right from below. The cartilage is shown in blue. *Ap. nas.int*, anterior nasal aperture; ***arcus subocul***, subocular arc; *c.prn.inf*, inferior prenasal cartilage; *Cr.p.ot*, crista parotica; *Eth*, ethmoid, or sphenethmoid; F.II-IV, foramina for the second to fourth nerves respectively; F.V, foramen for the fifth, sixth, and seventh nerves; *Fen.front*, fenestra frontalis; *Fen.par*, fenestra parietalis; *Fr.par*, fronto-parietal; *I.max*, intermaxillary, or premaxillary; *Max*, maxillary; *Na*, nasal; *Occ.lat*, exoccipital; *P.art.Q*, pars articularis of the quadrate; *Pal*, palatine; *Parabas*, parabasal, or parasphenoid; *Pr.bas.Q*, bāsal process of quadrate; *Pr.pter.Q*, pterygoid process of quadrate; *Proot*, proötic; *Pter*, pterygoid; *Q.max*, quadrato-maxillare or quadrato-jugal; *Quad*, quadrate; *Ty*, tympanic, or squamosal. (After Gaupp.)

developed from membranes. The latter are more superficial in position and may be stripped off from the rest of the skull leaving a sort of cartilaginous box with ossifications here and there which represent the so-called cartilage bones. In the cranium only the exoccipitals, the proötics, and the ethmoid are cartilage bones, the fronto-parietal, parabasal, nasals, and palatines are developed from membranes, and may readily be separated from the underlying cartilage. The cartilaginous cranium forms an almost complete case for the brain; the roof, however, is incomplete, there being a large oblong opening, or *fontanelle,* the *fenestra frontalis,* near the middle, and a pair of smaller openings, *fenestræ parietales,* farther back.

The *suspensorium* and *jaws* also have a cartilaginous basis which is continuous with that of the cranium proper. The bones of these parts, with the exception of the quadrato-jugal and the mento-meckelian bones, are developed from membrane. A cartilaginous bar runs between the pterygoid and tympanic to the angle of the upper jaw, whence it is continued forward beneath the maxillary as far as the palatine bone, where a transverse process joins the posterior end of the nasal capsule. The exposed cartilage on the side of the cranium is perforated by a large foramen for the optic nerve and by smaller openings for the third and fourth nerves. The angulare and dentary of the lower jaw are membrane bones applied to the cartilaginous core, or Meckel's cartilage. The thyroid processes of the hyoid are developed from cartilage.

The frog's skull represents a type between the skulls of the lower fishes and those of the higher vertebrates. In such forms as sharks and skates the cranium and its various appendages are entirely composed of cartilage. Higher up in the scale we meet with fishes, such as some of the ganoids, in which ossifications of membranes, or dermal bones, become applied to the cartilaginous cranium, while the latter remains in great part unossified. In the birds and mammals ossification of the original cartilaginous basis of the cranium has become almost complete, and the bones that are developed from membrane enter into more intimate relations with the cartilage bones than they do in the frog, the whole forming a structure which is very firm and compact.

The Vertebral Column.—The vertebral column of the frog consists of ten bones of which the first nine are vertebræ proper, the tenth, or *urostyle,* being a long rodlike bone extending from the ninth vertebra to the apex of the pelvic girdle. A typical vertebra of which we may take the third as an example consists of the following parts:—

(1) The *centrum,* a basal portion, which is oval in cross section and concave in front for the reception of the centrum of the preceding vertebra and convex posteriorly.

(2) The *neural arch,* which incloses the neural canal, in which is lodged the spinal cord. The neural arch is produced in the mid-dorsal line into a projection called the *neural spine,* and at the sides it bears a pair of elongated *transverse processes* which extend almost at right angles to the body; the tips of these processes are furnished with cartilaginous epiphyses. Both the posterior and anterior margins of the neural arch bear a pair of short *articulating processes* or *zygapophyses,* by means of which the successive vertebræ are joined together; the articular faces of the anterior articulating processes look upward and inward, and are covered by the posterior zygapophyses of the preceding vertebra, the articulating faces of which look downward and outward. The opposed faces of the adjoining zygapophyses are smooth and allow a limited gliding movement when the spinal column is bent from side to side.

The first vertebra, or *atlas,* differs from the others in having no transverse processes, in the absence of the anterior zygapophyses, and in having in front a pair of oval, concave facets for articulating with the occipital condyles of the skull. The ninth vertebra has the transverse processes very strong and directed obliquely backward; it has no posterior zygapophyses, and the posterior surface of the centrum bears a pair of prominences for articulation with the urostyle.

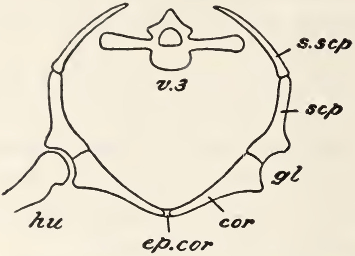

Fig. 83.—Transverse section of shoulder girdle. *cor*, coracoid; *ep.cor*, epicoracoid; *gl*, glenoid cavity; *hu*, humerus; *scp*, scapula; *s.scp*, suprascapula; *v.3*, third vertebra. (After Parker and Parker.)

The *urostyle* is elevated on the dorsal side into a prominent keel which extends nearly to the posterior end. The anterior surface possesses a pair of cavities for articulation with the ninth vertebra. The vertebral canal is small and triangular in outline. There is a pair of small openings through the sides of the urostyle near the anterior end for the exit of the last pair of spinal nerves.

The centra of the vertebræ are joined together by means of pads of hyaline cartilage; connecting ligaments extend along both the ventral and the dorsal surfaces of the centra; and the arches and neural spines are joined by ligaments. The spinal nerves make their exit through the *intervertebral foramina,* between the sides of the neural arches.

The Pectoral Girdle and Sternum.—The pectoral girdle is a bony arch which gives support to the fore limbs. The upper end of the girdle is formed by a flat, distally expanded portion, the *suprascapula,* which is composed of cartilage which is more or less calcified at the base. The suprascapula articulates below with the long *scapula,* which is oblong and constricted in the middle; the posterior side of the lower end forms part of the *glenoid fossa,* which receives the head of the *humerus.* A notch occurs at the glenoid fossa, dividing the lower end of the scapula into dorsal or *glenoid* part from a ventral *acromial* portion.

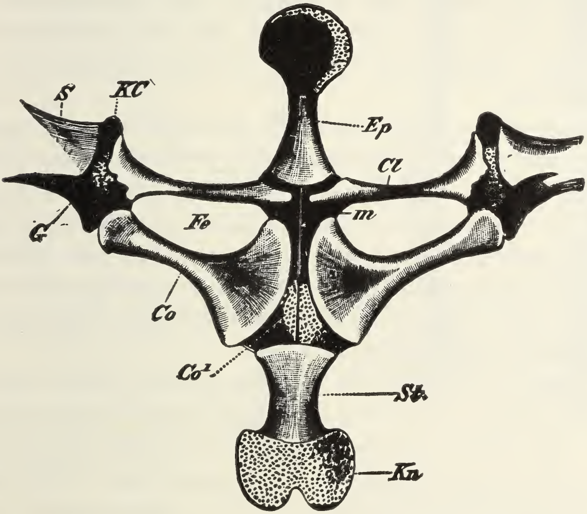

Fig. 84.—Middle part of the shoulder girdle of the frog from below. *Co,* coracoid; *Co′,* epicoracoid; *Cl,* clavicle; *Ep,* episternum; *G,* glenoid cavity; *Fe,* fenestra; *KC,* cartilage between scapula and clavicle; *Kn,* xiphisternum; *m,* junction of epicoracoids; *S,* scapula; *St,* sternum. (After Wiedersheim.)

From the lower end of the scapula two bars extend toward the middle line. The anterior of these consists of a bar of hyaline cartilage, the *procoracoid,* in front of, and partly inclosing which is a membrane bone, the *clavicle.* At its outer end the clavicle is bent forward, and applied to a forward projection of cartilage, the *acromion,* at the lower end of the scapula. The posterior bar, the *coracoid,* is a stout bone constricted in the middle, and broadly expanded at its inner end; at its outer extremity it forms a portion of the glenoid fossa. Between the two ends of the coracoid, and extending forward between the clavicles, are the two *epicoracoid cartilages,* which are usually more or less calcified along the ventral side of their line of junction.

The *episternum* lies in front of the epicoracoids and consists of a basal piece of bone and a terminal piece of cartilage, which has an almost circular expansion at the anterior end.

The *sternum* proper resembles the episternum in general shape, and in being composed of a proximal piece of bone (mesosternum), and a distal expanded piece of cartilage. The latter has a notch in the middle of its posterior margin, which receives the anterior abdominal vein just before it leaves the body wall. Both the sternum and the episternum are capable of a limited vertical movement, especially at the flexible cartilaginous ends.

In addition to forming a place of attachment for the muscles which move the fore limbs, the pectoral arch protects the various internal organs, such as the lungs, heart, etc., and serves to maintain the general form of the body. It also gives attachment to the ventral muscles which draw back the hyoid, and depress the floor of the mouth, and for these purposes the distal ends of the sternum and episternum are flattened and expanded, their cartilaginous consistency enabling them to accommodate themselves to the changes produced in the body wall.

The Fore Limbs.—The upper bone of the fore limbs is the *humerus;* its proximal end, or head articulates with the glenoid cavity of the pectoral girdle; the distal, or lower extremity has a rounded articular prominence in the middle, on either side of which is a small projection, or condyle. A large crest, the *deltoid ridge,* extends from the head of the humerus to about the middle of the ventral side. At the distal end of the humerus there is a ridge above each of the two condyles; the inner ridge is much larger in the male than in the female.

The skeleton of the forearm consists of the *radio-ulna,* which arises from the fusion of two originally distinct bones, the radius and ulna, the line of union between which is very marked, especially at the distal end. The postaxial or ulnar part is produced backward at its upper end to form the olecranon, which fits over the rounded end of the humerus at the joint of the elbow. The distal end of the radio-ulna is widened, and ends in two epiphyses, one for each of the component bones.

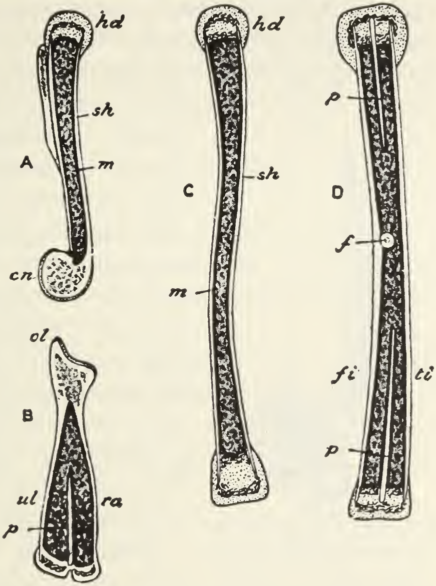

Fig. 85.—Longitudinal sections of the larger bones of the limbs. A, humerus; B, radio-ulna; C, femur; D, tibio-fibula. *cn,* condyle; *f,* foramen for artery; *fi,* fibula; *hd,* head; *m,* marrow; *ol,* olecranon; *p,* bony partition; *ra,* radius; *sh,* shaft; *ti,* tibia; *ul,* ulna. (After Parker and Parker.)

The *carpus,* or wrist of the frog, contains six bones arranged in two rows. In the proximal row the *ulnare* and *radiale* are situated at the ends of the ulna and radius, respectively, and at the inner or preaxial side of the radiale is the *centrale.* In the distal row the first *carpal* occurs just behind the rudimentary thumb; the second carpal, a very small bone, lies behind the second digit; the outer carpal is of relatively large size, and is formed by the fusion of three originally distinct bones one for each of the three outer digits of the hand. Beyond the wrist are the five *metacarpals,* which form the skeleton of the proximal part of the hand. The first metacarpal is rudimentary and usually cartilaginous in the female, but in the male it is larger, and becomes calcified or even ossified. The other metacarpals are elongated cylindrical bones, somewhat expanded at the two ends; the inner one of the four is stouter in the male than in the female, and bears a prominent crest on the inner margin. The metacarpals, except the first, are succeeded by the *phalanges,* of which each of the two outer digits have three, while the two inner ones have but two.

Fig. 86.—Pelvic girdle of the frog from the right side. *G,* acetabulum; *Il,* ilium, *Is,* ischium; *P,* pubis. (After Parker and Parker.)

The Pelvic Girdle.—The *pelvic girdle* which supports the hind limbs is a V-shaped mass of bone, the apex of which lies at the posterior end of the skeleton, and receives the tip of the urostyle; the two anterior ends are united to the large, transverse processes of the ninth or sacral vertebra. Each half of the pelvic girdle is composed of three elements, the *ilium,* the *ischium,* and the *pubis.* The first named is a long bone, attached to the ninth vertebra in front, and meeting its fellow behind; on the dorsal side is a high thin crest, at the anterior end of the ventral side of the junction of the two ilia is a prominence called the anterior spine of the pelvis. The ilium forms the anterior part of the cup, or acetabulum, which receives the head of the femur.

The pubis is a triangular mass of hyaline, or in older frogs calcified, cartilage on the ventral side of the pelvic girdle; it forms a part of the lower side of the acetabulum.

The posterior portion of the pelvic girdle is represented by the ischium; it forms the posterior part of the acetabulum, and extends forward dorsally as far as the top of a prominence, the posterior spine of the pelvis, which is situated above, and a little behind the acetabulum; here it is fused with the ilium; the suture between these bones can best be seen in young frogs. The lines of union of the pubic and ischial bones of opposite sides are known respectively as the *pubic* and *ischial symphyses.*

The pelvic girdle of the frog is remarkable on account of the elongation of the ilia, the reduction of the pubis and ischium, and the intimate fusion of the two latter with the posterior expanded part of the ilium to form an almost circular mass.

The Hind Limbs.—The skeleton of the hind limb of the frog is constructed on essentially the same plan as that of the fore limb. It consists of an upper bone, the *femur,* corresponding to the humerus of the fore limb. Below this is the *tibio-fibula,* corresponding to the radio-ulna; and following the tibio-fibula the *tarsus* and *foot,* corresponding to the carpus, and hand. The femur is an elongated, cylindrical, very slightly sigmoid bone; it articulates by its expanded and rounded head with the acetabulum above, forming the hip joint.

The tibio-fibula is an elongated, very slightly bent bone somewhat expanded and flattened at either end, where it is marked on both sides by a groove which indicates its formation from two bones, the tibia and the fibula, which were originally separate. The tibia is preaxial in position and corresponds to the radius of the forearm; the fibula is postaxial and corresponds to the ulna. Near the middle the tibio-fibula is perforated by a foramen for the anterior tibial artery.

The *tarsus* of the frog is peculiarly modified in that the proximal portion is much elongated and consists of but two bones; the preaxial bone next to the tibia is called the *tibiale,* the postaxial one next to the fibula, the *fibulare;* the two bones are united at their ends, inclosing a narrowly oval space between them. The centrale is represented by a small bone on the preaxial side of the distal end of the tibiale; at its distal end it supports the prehallux. The *tarsalia* (which correspond to the carpalia of the hand) are much reduced both in size and number. There is a small first tarsal behind the base of the first metatarsal bone. Behind the second and third metatarsals is a small bone which represents the fused second and third tarsalia. The fourth and fifth tarsalia are absent. There are five metatarsal bones, all of which are elongated and cylindrical. Of the phalanges the first and second toes contain two each, the third and fifth toes three each, and the fourth toe four. The small *prehallux* is composed usually of two pieces.

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CHAPTER XIV

THE MUSCULAR SYSTEM

The function of muscle is the production of movement through contraction. The muscles of the frog retain their vitality for a long time after they have been removed from the body, and they are consequently well adapted for physiological experiments. The large *gastrocnemius,* or calf muscle, of the frog is so favorable a one for investigation that much of what is known of the general physiology of muscular activity is derived from a study of this object. When a muscle contracts, it increases in thickness as it decreases in length. Contraction may be brought about, as is readily demonstrated with a fresh muscle, by a variety of causes, since it follows upon the application of nervous, thermal, mechanical, chemical, or electrical stimuli. The response to stimulation in voluntary muscle takes place very quickly but in involuntary muscle the response is much slower.

Most of the muscles are attached by one or both ends to bones. The attachment in some cases is direct, in others it is by means of a *tendon,* which is a band of very tough, inelastic connective tissue. The outer surface of a muscle is covered by a connective tissue membrane, or *fascia,* which is more or less elastic. The tendons of many muscles are formed by a continuation of the fascia, which becomes thicker toward the end of the muscle, where it graduates into a dense fibrous band. The end of a muscle which is fastened to a relatively immovable part is called the origin;

the more movable end is the insertion. The contraction of a muscle has the effect of drawing the origin and insertion nearer together. The *gastrocnemius* muscle, which may be taken as an illustration, has its origin by two heads, one from a tendinous band extending from the lower end of the femur to the tibio-fibula, the other by a narrow tendon which joins the tendon of the triceps on the anterior side of the thigh. At its lower extremity the muscle is inserted by means of a strong tendon which passes over the ankle joint and spreads out over the lower or plantar surface of the foot. When the muscle contracts, it may produce two movements. It may straighten out, or extend the foot, and hence is spoken of as an *extensor* of that member. It may also bend the leg upon the thigh at the knee, a movement which is called *flexion.* The gastrocnemius is designated, therefore, as an *extensor* of the foot and a *flexor* of the leg. A muscle which draws the limb posteriorly toward the long axis of the body is called an *adductor,* one which pulls it in the opposite direction an *abductor.* Then there are *rotators,* which cause a limb to rotate about its long axis; *levators,* which raise a part, such as the muscles which raise the lower jaw; and *depressors,* which produce the opposite movement, such as the *depressor mandibulæ,* which lowers the jaw. The kind of movements a limb may make is dependent on the nature of its joints and the number and attachments of its muscles; and the actions which the frog as a whole is capable of performing are dependent in a similar manner upon the organization of its skeletal and muscular systems, although the order and combinations of the movements are directed by impulses from the central nervous system.

The action of muscles may be well illustrated by a study of some of the muscles of the hind leg. If the skin be stripped off from the leg and the frog laid on its back, the following muscles may be seen on the ventral side of the thigh:—

The *sartorius,* a narrow muscle having its origin on the ilium, just in front of the pubis. It crosses the thigh obliquely and is inserted by a tendon a short distance below the head of the tibia. When it contracts, it flexes the leg on the thigh and pulls the whole limb forward and ventrally.

The *adductor magnus,* a large thick muscle lying behind the sartorius, which it crosses at its lower end. Its origin is from the pubis and ischium, and it receives a small slip which originates on the tendon of one of the heads of the *semitendinosus.* It is inserted into the distal end of the femur. Its action is to bend the thigh ventrally and to pull it anteriorly or posteriorly according to the position of the limb. When the thigh is pulled forward so that a line connecting the centers of the origin and insertion of the muscle lies in front of the head of the femur, the contraction of the adductor magnus has the effect of moving the limb still farther forward while pulling it ventrally. When the thigh is bent back so that the head of the femur lies in front of a line connecting the centers of the origin and insertion, the contraction of the muscle has the opposite effect. The *adductor magnus* thus acts as an adductor or an abductor according to circumstances.

The *adductor longus,* a narrow muscle arising from the ventral part of the ilium just dorsal to the head of the sartorius; distally it joins the *adductor magnus.* It is partly covered by the sartorius, but a small portion of it is exposed along the preaxial side of that muscle. It pulls the thigh forward and ventrally.

The *triceps femoris,* a very large muscle covering the whole front of the thigh. It arises by three heads. The anterior head (*caput anticum* or *cruralis*) arises from the anterior border of the acetabulum at the junction of the

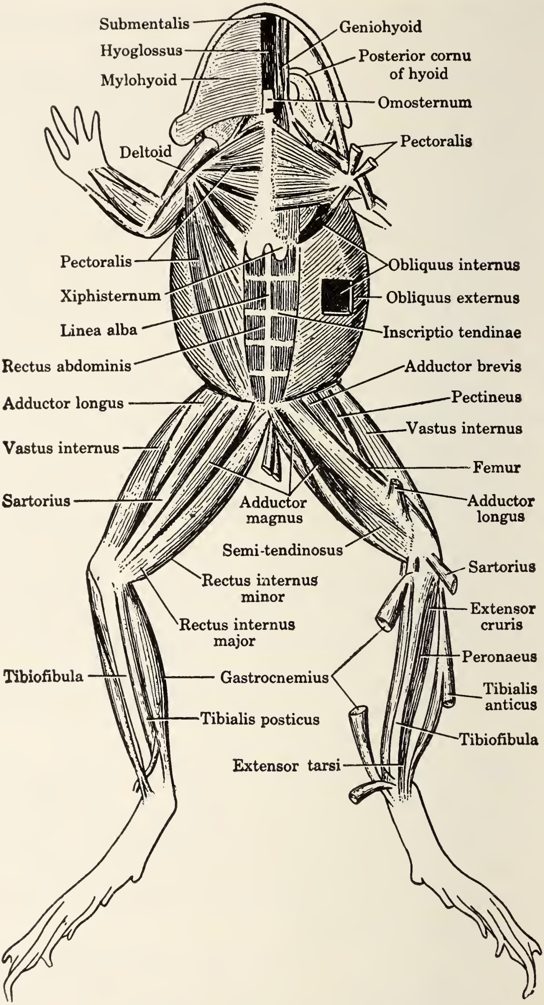

Fig. 87.—Muscles of the frog, ventral view. On the left side (right of figure) some of the muscles have been partly removed. (From Hegner after Parker and Haswell.)

ilium and pubis. The middle head (*caput medium*) is a short, flat muscle which arises from the ventral side of the ilium near the middle and joins the fascia of the rest of the muscle at about the proximal third of the anterior margin of the thigh. The posterior head (*caput posticum, vastus externus, gluteus magnus*) arises from the posterior end of the crest of the ilium; distally its fibers join those of the *cruralis* or anterior head. The whole muscle is inserted by a very strong tendon which passes over the knee and joins the upper end of the tibio-fibula. A tendinous connection passes also to one head of the *gastrocnemius*. The action of the whole muscle is to extend the crus and draw the whole leg forward.

The *gracilis major*, a large muscle lying along the posterior side of the ventral surface of the thigh. It arises by a small tendon from the posterior margin of the ischium. Its distal tendon divides into two parts, the one passing beneath the tendon of the *sartorius* to be inserted into the preaxial side of the proximal end of the tibia, the other passing dorsal to the tendinous insertion of the *semitendinosus* and joining the posterior side of the head of the tibio-fibula. Near the middle the muscle is crossed by an oblique tendinous inscription. The *gracilis major* pulls the femur backward and either flexes or extends the crus according to the position of the latter in relation to the femur. If the crus is flexed so that it makes an angle of less than 90° with the femur, the action of the gracilis is to flex it still more. If, however, the crus is partly extended so that it makes a considerably greater angle than 90° with the femur, the contraction of the *gracilis* still further extends it. The difference of the action of the muscle under these different conditions depends upon the change in the fulcrum which is brought about by the bending of the leg.

The *gracilis minor* is a slender muscle which arises from a tendon behind the ischiac symphysis. Distally it joins the tendon of insertion of the *gracilis major.* The muscle is also attached to the skin of the posterior side of the thigh. Its action is similar to that of the *gracilis major.*

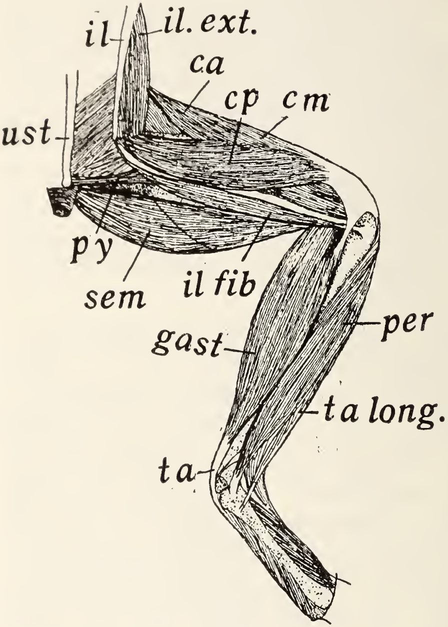

FIG. 88.—Muscles of the hind leg of the frog seen from the dorsal side. *c.a., c.m., c.p.,* caput anticum, caput medium, and caput posticum of the triceps extensor femoris; *gast,* gastrocnemius; *il,* ilium; *il. ext.,* iliacus externus; *il. fib.,* ilio-fibularis; *per,* peroneus; *py,* pyriformis; *sem,* semimembranosus; *t, a,* tendo Achillis: *t. a. long.* tibialis anticus longus; *ust,* urostyle.

The two following muscles appear on the dorsal side of the thigh: the *semimembranous,* a large muscle lying on the posterior side of the dorsal surface of the thigh just above the gracilis major. It arises by a broad fleshy attachment from the dorsal half of the posterior margin of the ischium. It is inserted by a short tendon which passes beneath the tendon of origin of the *gastrocnemius* into the proximal end of the tibio-fibula behind the knee. There is an oblique tendinous inscription running across this muscle as in the *gracilis major.* The *semimembranosus* adducts the thigh, or pulls it backward, and, like the *graci-*

lis, flexes or extends the leg according to whether it is in a flexed or an extended position.

The *ilio-fibularis,* a slender muscle lying between the *semimembranosus* and the posterior head of the *triceps femoris.* It arises from the ilium, just behind the posterior end of the dorsal crest, and it is inserted into the proximal end of the fibula. It draws the thigh dorsally and flexes the leg.

The *semitendinosus,* a slender muscle which is covered by the *gracilis major.* It arises by two tendinous heads from the ischium. The ventral head passes between the dorsal and ventral heads of the *adductor magnus* and affords a point of attachment for the small third head of the latter muscle. The two heads unite near the middle of the thigh; the muscle is inserted by a narrow tendon into the preaxial side of the proximal end of the tibia. It adducts the femur and flexes the leg.

The *pyriformis,* a short, slender muscle extending from the tip of the urostyle to a short distance beyond the head of the femur. It lies between the *semimembranosus* and the posterior head of the *triceps.* It pulls the urostyle to one side and draws the femur dorsally.

The *iliacus externus* arises on the outer side of the dorsal crest of the ilium from the anterior third to within a short distance from the posterior end. It extends backward, passing between the middle and posterior heads of the *triceps* to be inserted on the posterior side of the head of the femur. It rotates the femur forward.

The *iliacus internus* arises from the ventral border of the ilium, a little in front of the anterior spine. In the anterior position of its broad origin its fibers run below the lower margin of the ilium to be attached to the median surface. Its insertion extends from the hip joint to about the middle of the femur. This muscle is broad and flat, and extends between the middle and anterior heads of the *triceps* ventral to the *iliacus externus.* It draws the thigh forward.

There are several smaller muscles around the head of the femur; viz. the *pectineus, obturator externus, obturator internus, ilio-femoralis, quadratus femoris,* and *gemellus,* for a description of which the student is referred to Ecker's "Anatomy of the Frog." The muscles of the leg, or crus, are as follows:—

The *gastrocnemius* which has been mentioned above is the largest muscle of the leg. It arises by two heads, the larger one from a tendinous arch which extends from the posterior side of the distal end of the femur to the head of the tibio-fibula; the other head joins the tendon of the *triceps.* The muscle tapers distally where it is inserted by a very strong tendon, which passes over the ankle joint and spreads over the plantar surface of the foot. It acts as a flexor of the leg and an extensor of the foot.

The *tibialis posticus* lies on the posterior side of the leg beneath the *gastrocnemius.* It arises from the greater portion of the length of the tibio-fibula and ends in a tendon, which, running in a groove on the inner side of the distal end of the tibia, passes between the ends of the tibio-fibula and the bones of the ankle to be inserted into the anterior side of the proximal end of the tibiale. When the foot is flexed, it acts as an extensor and pronator, and when the foot is fully extended, it flexes it to within about 45° of a continuation of the long axis of the crus.

The *tibialis anticus longus* is a narrow muscle on the front of the crus. It arises by a long, narrow tendon from the distal end of the femur. Distally it divides into two parts which are inserted into the proximal ends of the tibiale and fibulare. It acts as an extensor of the leg and a flexor of the foot.

The *peroneus* lies on the postaxial side of the preceding muscle, partly covered by *gastrocnemius.* It arises by a narrow tendon from the distal end of the femur. One part of the muscle is inserted into the distal end of the fibula, the other passes over the ankle joint and joins the outer angle of the head of the fibulare. The muscle acts to extend the leg; when the foot is partially extended, it acts to extend it still farther, and pronates it, *i.e.* turns its plantar surface downward; when the foot is strongly flexed, it acts as a flexor, bringing it up close to the crus; it also pulls the ankle postaxially.

The *extensor cruris* is a slender muscle lying on the anterior side of the leg, partly covered by the *tibialis anticus longus.* It arises by a slender tendon, from the distal end of the femur. It is inserted directly upon the bone, along the anterior side of the tibio-fibula. It extends the leg.

The *tibialis anticus brevis* is a short muscle lying close alongside of the extensor cruris. It arises from the distal third of the tibio-fibula where it is attached directly to the bone. Distally it ends in a tendon which is inserted in the proximal end of the tibiale. It flexes the foot.

There are numerous smaller muscles for moving the different parts of the foot, whose description we shall omit.

When a muscle works in company with others, its action is often quite different from that produced when it acts alone. This fact has been well illustrated by Dr. Lombard,[1] who has worked out the double action of the muscles of the frog's leg in a very thorough manner. The *triceps femoris,* for instance, when working alone acts as an extensor of the leg; but since it pulls the thigh forward at the same time, it causes the flexor muscles on the back of the thigh to become tense, and thereby indirectly brings about a flexion

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[1] "Contributions to Medical Research, dedicated to V. C. Vaughan," p. 260, 1903.

of the leg. The muscles of the frog's leg are so arranged that any force which pulls the leg forward causes the crus to flex against the thigh and the foot to flex against the crus, and any force which pulls the leg backward extends the crus and foot. The movements of the frog's leg in jumping and swimming consist mainly in alternately bringing the leg up against the side of the body, folding the various parts together, and pulling it backward and extending or unfolding its different parts. Any muscle, such as the *iliacus internus,* which pulls the femur backward, brings about a flexion of the crus through the tension produced on the flexors of the back of the thigh. A flexion of the crus stretches the *tibialis anticus longus* on the anterior side of the crus and thereby brings about a flexion of the foot. If a muscle pulls the femur backward, the *triceps femoris* is put on the stretch: this tends to straighten the leg, the tendency becoming stronger the farther back the thigh is pulled. Extending the leg causes the *gastrocnemius* to be put on a strain, and the tension is increased through the pull on the tendon this muscle receives from the lower end of the *triceps.* Through the pull on the *gastrocnemius* the foot is extended. Other muscles are of course brought into play in this process, but what has been said will illustrate the principle on which coördination of movements employed in jumping or swimming is effected. The relative intensity of the nervous impulses distributed to the various muscles is an important factor in determining the kind of movement the limb will make, but the basis for the unity of action of the parts in the ordinary movements of the limb lies in the structural arrangement of the bones and muscles.

As an extended treatment of the remaining portions of the muscular system lies beyond the scope of this work, only a few of the more noteworthy muscles will be described.

On the ventral side of the body the large *rectus abdominis* extends from the pubis, to which its fibers converge behind, to the sternum in front. Its two halves are separated in the middle line by the *linea alba,* and there are five connective tissue septa (*inscriptiones tendinæ*) which cross it transversely and divide it into segments.

The *obliquus externus* is a large muscle covering most of the sides of the body. It originates on the sides of the ilium and dorsal fasciæ above, and is inserted into the sides of the rectus abdominis. Its fibers extend obliquely upward and forward.

The *transversus* is a broad muscle lying beneath the external oblique and forming the innermost muscular layer of the body wall. Its fibers run for the most part transversely. Anteriorly some of its fibers are inserted into the esophagus and closely overlie the pericardium; other fibers attach to the coracoid and xiphisternum; the posterior portion of the muscle is inserted into a flat tendon which extends dorsally to the *rectus abdominis* to the mid-ventral line. All of these muscles have the general effect of contracting the body cavity.

The *cutaneous pectoris,* a paired muscle lying on the ventral side of the anterior part of the body. Posteriorly it is attached to the body wall, and it is inserted anteriorly into the skin between the fore legs.

The *pectoralis major,* a large muscle on either side of the anterior part of the body. It is composed of three parts, an abdominal portion arising from the sides of the anterior half of the rectus abdominis, a middle portion arising from the sternum and xiphisternum, and an anterior portion arising from the coracoid and epicoracoids. All three parts are inserted near together on the ventral crest of the humerus.

The *submaxillary* muscle extends transversely across the floor of the buccal cavity, between the two rami of the lower jaw. It raises the floor of the buccal cavity in respiration.

The *submentalis* is a small muscle lying in the anterior angle of the lower jaw. Its fibers run transversely, and by their contraction raise the tip of the jaw and thereby bring about the closure of the nares in respiration.

The *subhyoid,* a small muscle arising from the anterior corner of the hyoid near the skull and joining ventrally the posterior margin of the *submaxillary.* It raises the hyoid.

The following muscles are attached to the hyoid and take part in the movements of respiration: The *geniohyoid,* extending from near the anterior angle of the jaw to the thyroid and posterior lateral processes of the hyoid. It draws the hyoid forward and upward. In connection with *sternohyoid* it lowers the jaw.

The *sternohyoid,* attached posteriorly to the dorsal surface of the sternum and coracoids, where it joins the *rectus abdominis,* of which it may be regarded as an extension. Anteriorly it is inserted into the lower surface of the hyoid and its thyroid processes. It draws the hyoid backward and lowers it, thus enlarging the buccal cavity.

The *omohyoid,* extending from the scapula to the lateral portion of the ventral surface of the hyoid. It draws the hyoid backward.

The *petrohyoids,* a series of four slender muscles arising from the outer portion of the proötic bone and inserted into the hyoid. The anterior muscle is the largest, and is attached ventrally to the lateral margin or the body of the hyoid near the middle. The three posterior petrohyoids diverge ventrally to be inserted upon the thyroid process of the hyoid. The petrohyoids raise the hyoid apparatus and pull it forward.

The *hyoglossus* arises from the thyroid processes and ventral surface of the body of the hyoid. The two halves of this muscle converge toward the middle line as they pass forward. Anteriorly the single muscle thus formed bends backward around the concave anterior margin of the tongue, where it breaks up into numerous branches.

CHAPTER XV

THE CIRCULATORY SYSTEM

THE principal functions of the circulatory system are to carry food material and oxygen to all parts of the body, and to remove the carbon dioxide and other waste products of tissue metabolism to the organs where they are eliminated. These functions are discharged by means of two fluids, the blood and the lymph. We shall describe the blood first.

The Blood.—The blood of the frog consists of a fluid, the *plasma*, in which there occur numerous free cells, or *corpuscles*. The corpuscles are of three kinds: *red corpuscles* (*erythrocytes*), *white corpuscles* (*leucocytes*), and *spindle cells* (*thrombocytes*). The red corpuscles are elliptical in outline and have an oval nucleus in the center. When seen on edge they appear flattened and slightly bulging in the center where the nucleus lies. The nearly transparent cytoplasm of the cell contains a large percentage of hemoglobin, which gives it a yellowish color. Blood appears red only when a layer of considerable thickness is seen.

The white corpuscles, unlike the red ones, vary exceedingly both in size and form. The outline of the white corpuscle undergoes changes much like those of an Amœba. The changes are slow, but they may easily be shown by making outline sketches of the corpuscle at intervals of one or more minutes. The cytoplasm of the white corpuscles is nearly colorless, but it often contains granules of various sizes and staining reactions. The form of the nucleus varies greatly in different cells. In some cases, especially in the smaller leucocytes, it is nearly spherical. In other cells it is very irregular in outline and may be deeply constricted in several places, and not infrequently it may be divided into two or more distinct nuclei. In the smallest leucocytes the amount of cytoplasm is relatively small and forms a narrow, irregular envelope around the spherical nucleus. The cytoplasm of the larger corpuscles is relatively much greater in amount.

By virtue of their amœboid movements the white corpuscles have the power of independent locomotion and they even pass through the delicate walls of the capillaries into the spaces between the other cells of the body. They are not confined, therefore, to the blood vessels like the red cells, but may be found in almost every part of the organism. And they often pass out of what are, strictly speaking, the limits of the body into the mouth and alimentary canal.

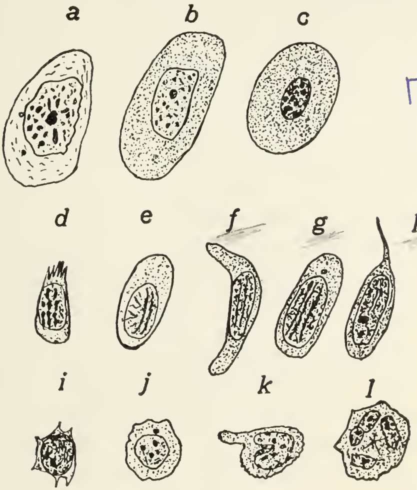

Fig. 89.—Blood corpuscles of the frog. *a*, *b*, *c*, red blood corpuscles; *a* and *b*, young stages; *c*, mature corpuscle; *d–h*, spindle cells in different stages; *d*, early stage; *e*, a somewhat later stage; *f*, *g*, *h*, typical spindle cells; *i–l*, forms of leucocytes; *i*, very early stage; *j*, an older stage; *k*, cell with lobed nucleus; *l*, cell with four nuclei. (After Dekhuyzen.)

red

spin

whi

One important property of the white cells is their power of ingulfing small bodies, which are taken in much as an Amœba takes in its food. Bacteria are devoured in this way, and the leucocytes thus afford the body a measure of protection against these organisms, which are constantly being introduced into the system in one way or another, and might, if unchecked, be productive of serious if not fatal effects. An irritation set up in any region causes leucocytes to be attracted to the spot in large numbers. The introduction of bacteria into any part of the body is followed by the invasion of that part by leucocytes, and it frequently happens that the bacteria are devoured by these cells before they gain a strong foothold. It is very probable that one important factor which causes the movements of the leucocytes in such cases is the presence of substances given off by the bacteria which exercise a chemotactic effect upon these wandering cells, causing them to congregate about the center of diffusion. The chemotactic influence of such substances is shown by the following experiments first performed by Massart. If a fine capillary tube sealed at one end be filled with a culture fluid containing the bacterium *Staphylococcus pyogenes albus,* and introduced into one of the large lymphs spaces under the skin, it will be found in the course of ten or twelve hours that a swarm of leucocytes have made their entrance into the open end of the tube. If a similar tube filled only with the culture medium be introduced, no leucocytes will be found to enter it. The substances produced by the bacteria are apparently the cause of the invasion of the tube by the wandering cells.

Besides protecting the body against the germs of disease, the white cells take part in the removal of tissue which has become broken down and no longer of service to the organism. In the degeneration of the tail of the tadpole the removal of skeletal and muscular tissues is effected in large part through the agency of the white corpuscles.

The spindle cells (thrombocytes), as their name implies, are spindle shaped, but their general outline is subject to considerable variation. They are from one-half to two-thirds the length, and from one-third to one-half the breadth of the red cells. They possess a certain power of amœboid movement, especially in the young state. The spindle cells, according to Neumann, are developed from the small leucocytes. They are normal constituents of the blood at all times of year and are usually colorless. Soon after the blood is shed they run together into masses and disappear.

The plasma, or fluid portion of the blood, is of very complex constitution; it contains fats, sugar, and numerous proteins in solution, vitamines, hormones, a considerable number of salts, various products arising from the breaking down of tissues throughout the body, several gases, chiefly oxygen, nitrogen, and carbon dioxide, and many other substances not included in any of the above classes. While all but a small part of the oxygen is carried by the hemoglobin of the red blood corpuscles, the other materials of the blood are contained in a state of solution in the plasma. Under certain conditions the plasma coagulates, or gives rise to a solid substance called *fibrin*, which, with the corpuscles which become entangled in it, forms the clot. The remaining portion of the plasma is called the serum. Clotting of blood is brought about by means of contact with foreign bodies. Powdered substances, filter paper, or any objects which bring a large amount of surface in contact with the fluid greatly facilitate the precipitation of fibrin. On the other hand, if blood be drawn into a vessel whose sides are smeared with oil, it may be kept from clotting for a comparatively long time. Cold greatly checks clotting, the process being delayed almost indefinitely if blood is kept near the point of freezing. If blood be heated to near 100° C., its power of clotting is destroyed. The formation of clot is dependent in some way upon the presence of calcium salts in the plasma; for if these are precipitated out, clotting may be prevented. The process of clotting is due to the formation of fibrin from a substance called fibrinogen which exists in a state of solution in the plasma. The change is due, like the formation of cheese in milk, to a ferment which transforms the soluble compound into an insoluble form. The formation of clot has the function of preventing indefinite bleeding after an injury has been received, the contact with foreign bodies causing the clot to form and thereby checking further loss of blood.

According to several observers the spindle cells play an important part in clotting the blood. The spindle cells quickly disintegrate when brought into contact with glass or most other substances, but Tait and Green have shown that if blood is kept in contact with paraffin after it is drawn the spindle cells retain their normal form. If they are removed the blood does not coagulate even in contact with glass. "Spontaneous coagulation of centrifuged frog's plasm is due wholly to disintegration of the contained thrombocytes." Contact, according to this interpretation, produces coagulation of the blood by causing the destruction of the spindle cells which liberate a substance which acts on some of the dissolved proteins of the plasma.

The Lymph.—The lymph is a colorless fluid, devoid of red corpuscles, but furnished with numerous leucocytes. Its plasma coagulates, but not quite so readily as that of blood.

The Production of New Corpuscles.—The corpuscles of the blood, after functioning for a certain time, die and are replaced by new cells. The process of regeneration of new corpuscles does not take place uniformly throughout the year as in higher animals, but is most active in the spring and early summer. During the late fall, winter, and early spring there is a period of inactivity in the production of new cells. Only after the breeding period, when the frog begins to take food, and store up nutriment in the body is there a rapid regeneration of the blood. The process reaches its maximum in one or two weeks, after which the production of new corpuscles suffers a gradual diminution until fall.

As Bizzozero and Torre have shown an important seat of the formation of new corpuscles is in the marrow of the bones. Marquis found that the marrow undergoes periodic changes corresponding to the changes in the blood. In the late spring and early summer, during the period of most active renewal of blood cells, the marrow assumes a lymphoid character; during the summer it gradually accumulates fat, and retains a fatty character during the fall and winter. During the spring, the fat is more or less completely resorbed, and the lymphoid cells, which are concerned in the formation of new corpuscles, undergo rapid multiplication.

After hibernation the chief seat of the formation of new corpuscles, according to Jordan and Speidel, is the spleen. Red, white, and spindle cells are produced in this organ, and certain large cells (macrophages) in the spleen engulf and destroy the old blood corpuscles. In the tadpole blood corpuscles, according to Jordan and Speidel, are produced chiefly in the kidneys.

The mature red corpuscles do not divide. Most observers hold that the red, white and spindle cells are all derived from the small leucocytes (lymphocytes) since various gradations occur between the latter and the different kinds of mature corpuscles.

While most of the corpuscles, both red and white, arise in the marrow of the bones and in the spleen, it is certain that both kinds of cells are also produced by the division of preëxisting cells in the circulating blood. This is notably the case in the white corpuscles; and divisions of the young stages of the red corpuscles have been witnessed by a number of observers. The spindle cells undergo indirect division, even after they have acquired hemoglobin. In their young stages, the red cells have a more or less circular but irregular form, comparatively little hemoglobin, and a relatively large irregular nucleus. However different the various forms of corpuscles may be in their adult condition, they arise from cells of a very similar, if not identical, structure.

The Structure of the Heart.—The heart of the frog is situated in the anterior part of the body cavity, ventral to the liver. It lies within a sac, the *pericardium,* whose cavity is completely cut off from the cœlom, although originally continuous with it in early development. The pericardium is composed of two layers, the *parietal,* forming the outer wall of the sac, and the *visceral,* which closely invests the heart. The two layers are continuous, passing into each other in the region of the truncus arteriosus below and the anterior venæ cavæ above. The relation is such as would be produced if the heart were pushed into the hollow pericardial sac from in front, although as a matter of fact it is not brought about in this way.

When the pericardium is opened on the ventral side, the following parts come into view; (1) The conical *ventricle,* with its apex pointing backward; this part of the heart has very thick muscular walls and appears paler than the rest. (2) The *auricles* lie immediately in front of the ventricle. The auricles are thin-walled and are separated from each other internally by a septum, but from the outside they present only a faint indication of this division; they are clearly separated from the ventricles by the coronary sulcus. (3) The *bulbus cordis,* lying in front of the right side of the ventricle; it is a thickened muscular tube, extending obliquely across the right auricle; anteriorly it is continued into the thinner-walled *truncus arteriosus* from which it is demarcated by a sulcus. (4) The *truncus arteriosus* is somewhat narrower than the bulbus; it soon divides into two diverging trunks, which give rise to three arteries, the *common carotid,* the *aorta,* and the *pulmo-cutaneous.*

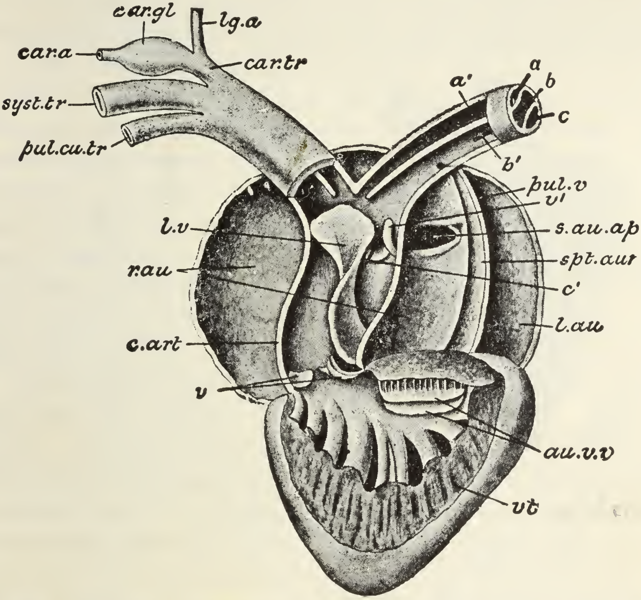

FIG. 90.—The heart of a frog cut open and seen from the ventral side. *a*, *a′*, bristle passed into the left carotid trunk; *au.v.v*, auriculo-ventricular valves; *b*, *b′*, bristle passed into the left systemic trunk; *c*, *c′*, bristle in left pulmo-cutaneous trunk; *car.a*, carotid artery; *car.gl*, carotid gland; *c.art*, bulbus cordis (conus arteriosus of some authors); *car.tr*, carotid trunk; *l.au*, left auricle; *lg.a*, lingual artery; *l.v*, longitudinal or spiral valve; *pul.cu.tr*, pulmo-cutaneous trunk; *pul.v*, opening of pulmonary veins; *r.au*, right auricle; *s.au.ap*, sinu-auricular aperture; *spt.aur*, inter-auricular septum; *v*, *v′*, valves; *vt*, ventricle. (From Parker and Haswell's Zoölogy.)

On the dorsal side of the heart is the triangular, thin-walled *sinus venosus;* at the two anterior angles of the sinus the *precaval veins,* or *anterior venæ cavæ,* enter; the posterior apex receives the large *postcaval* vein, or *posterior vena cava.* In front of the anterior margin of the sinus is the *pulmonary vein,* which empties into the left auricle.

The internal structure of the heart presents a complicated and beautifully adapted mechanism for propelling the blood always in one direction and keeping the pure and impure blood separated. By removing the ventral wall of the auricles, ventricles, and bulbus, most of the features of the internal structure may be exposed to view. The *interauricular septum* is so situated that the right auricle is much larger than the left. In the right auricle, close to the septum, is the large *sinu-auricular aperture,* through which blood enters from the sinus venosus. It is a transverse oval opening guarded by valvular lips on the anterior and posterior sides, which prevent the blood that has entered from the sinus from being forced back again when the auricles contract. The left auricle receives blood from the pulmonary vein through a small opening near the septum slightly anterior to the sinu-auricular aperture; there is no valve at this point, but since the vein perforates the wall obliquely, the pressure caused by the contraction of the auricle serves to close the opening and thus prevents the backward flow of the blood. Both auricles empty into

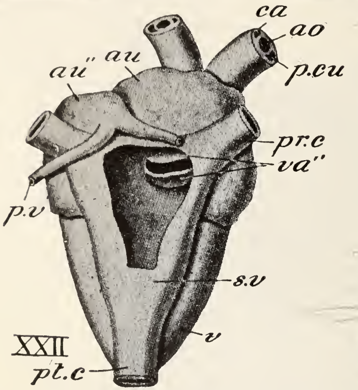

Fig. 91.—Heart seen from the dorsal side with the sinus venosus opened up. *ao*, aortic trunk; *au*, right auricle; *au″*, left auricle; *ca*, carotid trunk; *p.cu*, pulmocutaneous trunk; *pr.c*, precaval vein; *pt.c*, postcaval vein; *p.v*, pulmonary vein; *s.v*, sinus venosus; *v*, ventricle; *va″*, sinu-auricular valves. (After Howes.)

the ventricle by a large opening, the *auriculo-ventricular aperture,* which is divided by the interauricular septum. This opening is guarded by four valves, two large ones on the dorsal and ventral edges, and a small valve at either end; small fibers extend from the ventricular wall to be inserted into the free edges of the valves; they prevent the edges of the valves from being turned back into the auricles when the ventricle contracts, and thus keep the blood from flowing from the ventricle into the auricles. The ventricle possesses in addition to the central cavity at its base a number of fissure-like chambers in the thick muscular wall; these chambers are separated from each other by muscular partitions and extend outwardly nearly to the periphery of the ventricle; they receive a large part of the blood that passes through the heart, and have the important function, as will be seen later, of preventing the mixing of the blood that comes in from the two auricles.

The opening from the ventricle into the bulbus cordis is guarded by three *semilunar valves.* They are in the form of pockets, open anteriorly, whose walls may be pressed down when blood is passing out of the ventricle, but when blood tends to pass the other way, they fill and prevent its return. In front of these valves is a peculiar and important structure known as the *spiral valve.* It consists of a longitudinal fold attached along the dorsal wall of the bulbus, its ventral edge lying free. At its posterior end it is attached to the left side of the bulbus, near the opening into the ventricle. It passes obliquely across the bulbus, and widens out at its anterior end into a cup-like valve. Two smaller valves occur at the same level. In front of these valves is the unpaired portion of the truncus, which is partly divided by a ridge extending from the point of union of the two branches to the middle of the anterior enlargement of the spiral valve. Each of the two branches of the truncus is divided by two septa into three compartments. The anterior compartments, which lead to the common carotid arteries, both enter the unpaired division of the truncus to the right of the septum. The middle compartments, which lead to the aorta, open into the unpaired portion of the truncus on either side of the septum.

The posterior compartments, which are continued into the pulmo-cutaneous arches, join each other and open by a common aperture into the bulbus cordis behind the valves at its anterior end.

The Arteries.—The *arteries,* or vessels which carry blood away from the heart, have thicker walls than the veins, and after death are usually almost devoid of blood. The ultimate ramifications of the arteries lead to a system of minute *capillaries,* through the very thin walls of which there is an exchange of products between the blood and the tissues. From the capillaries the blood flows into the *veins,* by which it is returned to the heart. All of the blood vessels with the exception of the capillaries are provided with coats of unstriated muscle, by the contraction and relaxation of which their caliber may be diminished or increased.

The arterial system begins in the truncus arteriosus, which, after its bifurcation, splits up into three pairs of arteries which are symmetrically disposed on either side of the middle line. The anterior of these three arteries, the *common carotid,* soon divides into the *lingual,* or *external carotid,* and the larger *internal carotid.* The lingual runs forward, giving branches to the thyroid, pseudo-thyroid, various muscles of the hyoid apparatus, and tongue. At the junction of the internal and external carotid, but principally upon the former, there is an oval enlargement known as the *carotid gland.* Internally the carotid gland contains a spongy network which serves as an impediment to the flow of the blood. As this organ becomes somewhat distended after each pulsation of the heart and then slowly contracts (Hyrtl, Sabatier), it also serves to equalize the blood flow, especially in the internal carotid. The carotid gland is developed in the larva through the anastomoses of vessels connecting the afferent and efferent arteries of the first gill arch; between the blood vessels are cells derived from the epithelium of the gill slits (Maurer).

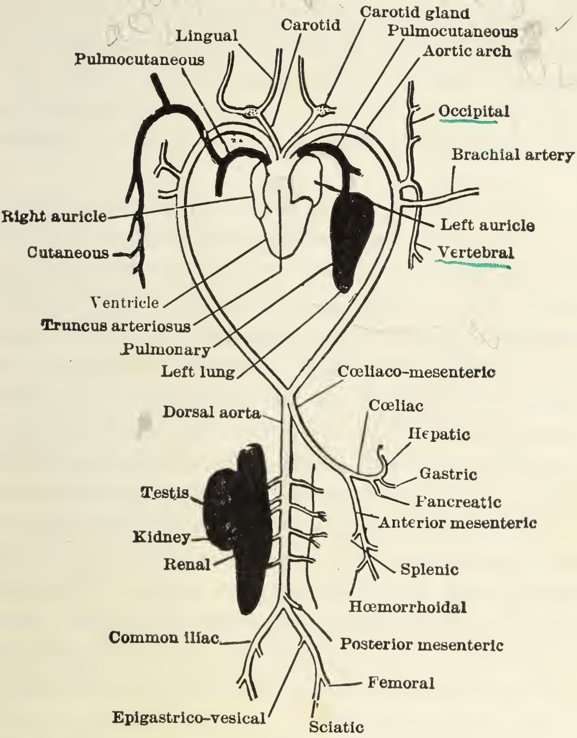

FIG. 92.—Diagram of the arterial system of the frog, ventral view. (After Howes.)

The internal carotid proceeds outward and dorsally from the carotid gland, and then forward and somewhat toward the middle line to the base of the skull. In front of the lateral process of the parasphenoid bone it gives off the *palatine artery,* which courses forward along the roof of the mouth, a little farther forward the *cerebral carotid* arises, entering the skull in the region of the orbit and supplying the brain. The third branch, the *ophthalmic,* passes forward and supplies the eye and some of the neighboring parts.

The second branch of the truncus arteriosus, or *systemic arch, passes* outward and then dorsally around the alimentary canal, meeting its fellow of the opposite side to form the *dorsal aorta.* Near its origin each systemic arch gives off a small *laryngeal* artery, which supplies the larynx and certain muscles of the hyoid. The small *esophageal* arteries are given off at about the level of the second vertebra; they are distributed to the dorsal side of the esophagus. The *occipito-vertebral* artery arises slightly beyond, or sometimes in common with, the last and passes forward across the transverse process of the second vertebra; it then divides into two branches which run above the transverse processes of the vertebræ near the centra. The posterior branch, or *vertebral* artery, extends backward along the spinal column. The anterior branch, or *occipital* artery, runs forward to the head, giving branches to the upper and lower jaw, orbit, and nose.

The large *subclavian* artery arises immediately behind the occipito-vertebral, and passes laterally, giving branches to the shoulder and body wall, and then, as the brachial artery, supplying the arm.

The two systemic arches unite at about the level of the sixth vertebra to form the *dorsal aorta,* which proceeds backward beneath the vertebral column. At the point of meeting of the two systemic trunks, but usually more on the left than on the right, the large *cœliaco-mesenteric* artery is given off which supplies the alimentary canal and its appendages. It divides into an anterior branch, or *cœliac* artery, and a posterior branch, the *anterior mesenteric* artery. The former, after giving off the *left gastric* artery, which goes to the left side of the stomach, divides into the *right gastric* artery, supplying the right side of the stomach and pancreas, and the *hepatic,* which, after giving a branch to the anterior lobe of the pancreas, is distributed to the liver. The *anterior mesenteric* artery supplies the small intestine, spleen, cloaca, and anterior portion of the rectum.

The *urinogenital* arteries are four to six small arteries which arise from the ventral side of the aorta, and are distributed to the reproductive organs, fat bodies, and kidneys. They vary greatly in their mode of origin, but typically they arise by very short median trunks which divide into right and left branches.

The *lumbar* arteries are small vessels, one to four in number on either side, which arise from the dorsal side of the aorta and are distributed to the body wall.

The *posterior mesenteric* artery is a small vessel given off from near the posterior end of the aorta. It supplies the posterior portion of the rectum and, in the female, the median dorsal wall of the uterus.

At its posterior end the dorsal aorta divides into two large *iliac* arteries, which are distributed mainly to the hind limbs. A short distance behind the bifurcation each iliac artery gives off a branch which divides into an *epigastric* artery, supplying the ventral body wall, and a *recto-vesical* artery to the rectum and bladder. A small artery arising from the iliac close to the above supplies the seminal vesicles in the male, and the lateral part of the uterus in the female.

A short distance beyond the foregoing the *femoral* artery is given off to the skin and muscles of the anterior part of the thigh. Distal to the origin of the femoral artery the iliac artery is continued as the *sciatic,* which passes out of the body cavity, along with the sciatic nerve, just behind the posterior end of the crest of the ilium, and supplies the hind limbs.

The third branch of the truncus, the *pulmo-cutaneous* artery, passes outward and dorsally, and gives off posteriorly the *pulmonary* artery to the lungs; it is then continued as the *great cutaneous* artery, which passes upward and forward, dividing behind the tympanic membrane into three branches: (1) the *auricularis,* which supplies the tympanum and gives branches to the thymus, lower jaw, pharynx, and hyoid, and anastomoses with branches of the occipital and internal carotid; (2) the *dorsalis,* which is mainly distributed to the skin of the back; and (3) the *lateralis,* which passes outward and is extensively distributed to the skin of the side of the body. With the exception of a few minor branches the distribution of the pulmo-cutaneous artery is such as to bring the blood into regions where it may undergo oxygenation. The blood which does not go to the lungs passes into the great cutaneous artery, the largest branches of which are distributed to the skin, where much of the respiration of the frog takes place; the buccal cavity and pharynx, which are also respiratory organs, receive blood from the same source.

The Veins.—With the exception of the blood coming from the lungs, all of the blood is returned to the heart through the three large venous trunks which enter the sinus venosus. The two anterior venæ cavæ, which enter the anterior angles of the sinus, are each formed through the junction of three branches, the *external jugular,* the *innominate,* and the *subclavian.* The most anterior of these, the external jugular, passes forward, where it receives branches from

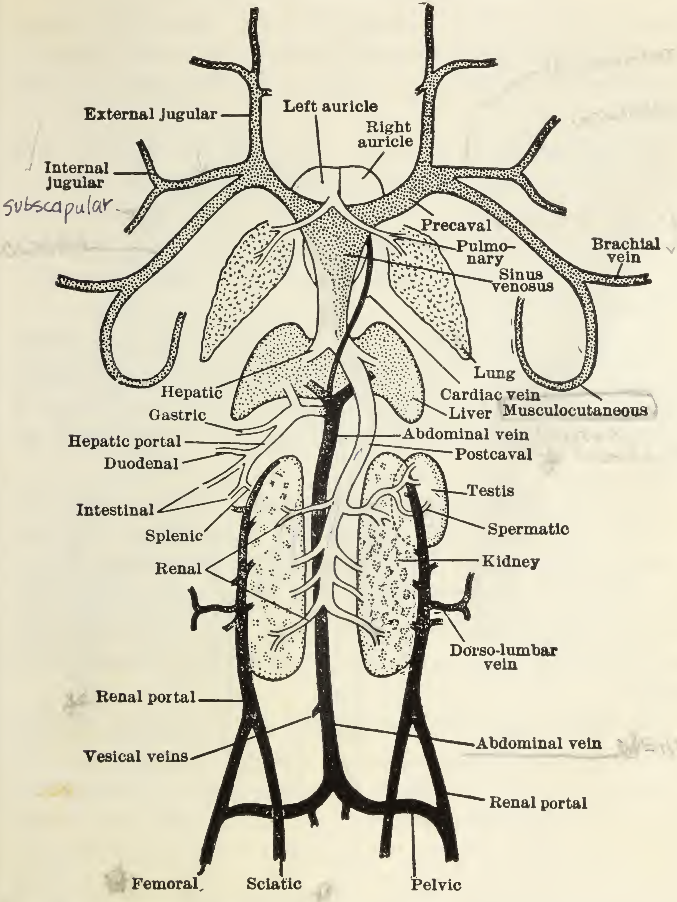

FIG. 93.—Venous system of the frog seen from the dorsal side. (From Hegner, slightly altered from Parker and Haswell's Zoölogy.)

the tongue, hyoid, thyroid, and pseudothyroid glands and floor of the mouth.

The *innominate vein,* or second branch of the anterior vena cava, passes laterally and divides into the *internal* *jugular,* which receives blood from the brain and various parts of the head, and the *subscapular,* which runs along the outer side of the fore limb and receives branches from the shoulder.

The *subclavian,* or posterior branch of the anterior vena cava, is formed by the confluence of the *brachial,* which is distributed to the fore limb, and the large *cutaneous* vein, which is extensively distributed over the side of the body and head. The latter returns most of the blood carried by the cutaneous artery.

The large *posterior vena cava* arises between the kidneys, and runs forward ventral to the dorsal aorta to the tapering posterior end of the sinus venosus. Near the latter it receives the large but very short *hepatic* veins from the liver.

The *renal* veins, four to six in number on each side, lead from the kidneys into the posterior vena cava; the veins from the reproductive organs (*spermatic* or *ovarian,* according to the sex of the animal) lead either directly into the vena cava or first into the renal veins. The vena cava also receives one or two branches on either side from the fat bodies.

The blood from the hind limbs does not empty directly into the posterior vena cava as in the higher vertebrates, but it is forced to pass through a second system of capillaries before reaching that vessel. Two large veins convey the blood from the hind legs, the *sciatic,* which runs along the post-axial side of the thigh, and the *femoral,* which courses along the dorsal and anterior side of the thigh and passes under the iliac bone into the body cavity. These two veins are connected close to the hip joint by the *transverse iliac* vein, which passes dorsally to the femur and enters the body cavity behind the crest of the ilium. The femoral vein branches in front of the base of the thigh into two parts, one

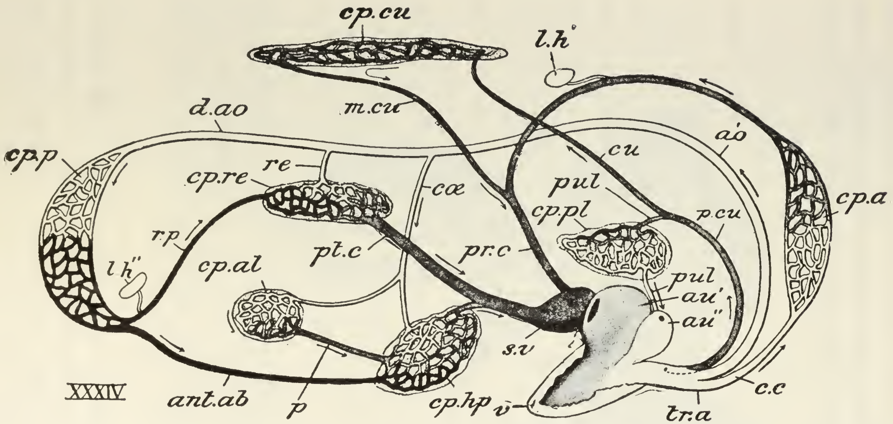

FIG. 94.—Diagram representing the general course of blood in the frog and the principal sets of capillaries (*cp.*) through which the blood flows. The vessels through which impure blood goes are dark, while those carrying pure blood are left unshaded. The arrows indicate the direction of blood flow. *ant.ab*, anterior abdominal vein; *ao'*, aorta; *au'*, right auricle; *au''*, left auricle; *c.c.*, common carotid artery; *cœ*, cœliaco-mesenteric artery; *cp.a*, anterior systemic center; *cp.al*, alimentary center; *cp.cu*, cutaneous center; *cp.hp*, hepatic center; *cp.p*, posterior systemic center; *cp.pl*, pulmonary center; *cp.re*, renal center; *cu*, great cutaneous artery; *d.ao*, dorsal aorta; *l.h'*, anterior lymph heart; *l.h''*, posterior lymph heart; *m.cu*, musculo-cutaneous vein; *p*, hepatic portal vein; *p.cu*, pulmo-cutaneous vein; *pr.c*, precaval vein; *pt.c*, postcaval vein; *pul*, pulmonary vein; *re*, renal artery; *rp*, renal portal vein; *s.v*, sinus venosus; *tr.a*, truncus arteriosus; *v*, ventricle. (After Howes.)

of which passes ventrally and joins its fellow of the opposite side to form the *anterior abdominal* vein, which runs forward in the middle of the ventral body wall; the other branch, the *external iliac,* passes forward, and dorsally, and joins the sciatic vein to form the *common iliac* or *renal portal* vein, which runs forward along the outer margin of the kidneys, into the substance of which it sends its branches. The renal portal receives the *dorso-lumbar* vein, from the body wall, and in the female several branches from the oviducts. The system of veins which lead blood to the kidney is known as the *renal portal system.* There is also a *hepatic portal system* which carries venous blood to the

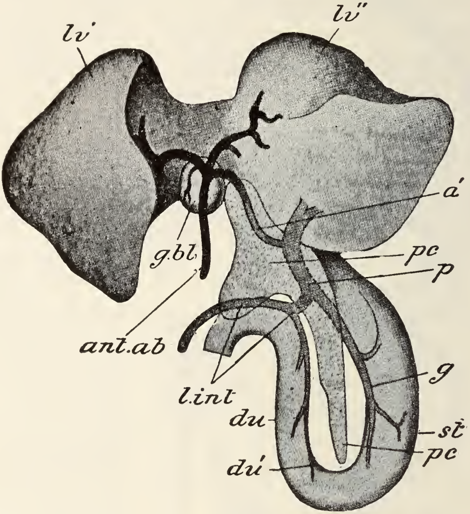

Fig. 95.—The hepatic portal system, showing its relations to the stomach, intestine, pancreas, and liver. *a'*, branch from the anterior abdominal to the portal vein; *ant.ab*, anterior abdominal vein; *du*, duodenum; *du'* artery to same; *g*, gastric vein; *g.bl*, gall bladder; *lv'*, *lv''*, right and left lobes of the liver respectively; *p*, portal vein; *pc*, pancreas; *st*, stomach. (After Howes.)

liver. The latter consists of (1) the *anterior abdominal vein*, which receives blood from the femoral veins, bladder, and ventral body wall, and (2) the *portal vein*, which carries blood from the stomach, intestine, spleen, and pancreas, the terminal portion passing through the latter organ to empty into the left lobe of the liver. The abdominal vein, just before it enters the liver, receives a small branch, the *vena bulbi cordis*, from the bulbus cordis; the other parts of the heart are devoid of special blood vessels.

The Action of the Heart.—In the beating of the heart, which may readily be observed in a frog that has recently been killed, the contraction first occurs in the sinus venosus; and this is followed by successive contractions of the auricles, ventricle, and bulbus. As we have seen, the arrangement of the valves of the heart is such as to keep the blood flowing through these parts in the order named. Although the frog does not possess a complete double circulation, such as occurs in birds and mammals, in which the systemic and the pulmonary circulations are entirely separated, the impure and the oxygenated blood are, nevertheless, not allowed to completely mix, but are kept more or less apart and sent out to different parts of the body. It was formerly held that the blood from the two auricles was completely mingled in the ventricle, but Mayer showed in 1835 that if the tip of the ventricle be cut off, two blood streams, a dark and a red, issue from the cut end. Later (1851) the noted physiologist Brücke studied the structure and action of the frog's heart in detail and explained the mechanism by which the two kinds of blood were kept separate. Brücke's observations were extended and in most points confirmed by Sabatier in 1873. The interpretation of the latter author has been followed by Gaupp in his recent revision of Ecker's "Anatomie des Frosches."

When the auricles contract, the blood from the left auricle, which has come in from the pulmonary vein and is therefore oxygenated, is forced into the left side of the ventricle, while the impure blood from the right auricle, which comes through the sinus venosus, pours into the right side and middle portion of the ventricle. The blood from these different sources is prevented from becoming mixed by being received into the slit-like chambers in the ventricular wall. During the contraction of the ventricle the impure blood lying near the opening of the bulbus naturally passes out first, while the pure pulmonary blood from the left side is forced out only toward the close of the ventricular contraction. When the ventricle first contracts, the wall of the bulbus cordis is relaxed, and the impure blood flows freely over the edge of the spiral valve into the left compartment, whence it is free to issue into the pulmo-cutaneous arches through their common opening. Now the blood is under less pressure in the pulmo-cutaneous arches than in the others, because its route is shorter and there are no impediments to its flow. In the carotid arches the blood meets with a partial obstruction in the carotid gland, and at the outer ends of the systemic arches there is a small valve (valvula paradoxica), which also tends to retard its flow. The blood first issuing from the heart takes the line of least resistance, namely, the pulmo-cutaneous arches, and is forced through the first two pairs of arches only when it has no easier avenue of escape. Toward the close of the contraction of the ventricle, when the pure blood is passing out, there is a contraction of the bulbus cordis. This brings the wall of the bulbus against the free edge of the spiral valve and prevents the blood from flowing over into the left or pulmonary side of this division of the heart. The blood is prevented from access to this side anteriorly by valves, so there is now no course open to it but through the carotid and systemic arches. Since the common opening of the pulmo-cutaneous arches lies behind the valves at the anterior end of the bulbus, it can receive no blood when the communication between the two sides of the bulbus is cut off. In this way the impure blood first sent out of the heart goes mainly to the lungs and skin, where it is purified, while the purer blood passing out toward the close of the contraction of the heart is sent to the various other parts of the body.

The heart of the frog may beat for hours, or, under favorable conditions, even for days, after it has been removed from the body. Even isolated parts of the heart, such as the sinus venosus, auricles, or ventricle, may continue beating, although not with the same rhythm. If the heart is removed so as to leave the sinus venosus within the body, the auricles and ventricle beat with a rate less than the normal, but the sinus continues to beat with nearly the same rhythm as before. If the sinus is removed with the rest of the heart, the beating of the whole heart is more rapid than that of the auricles and ventricle when removed alone. It is apparently the sinus venosus which sets the rhythm for the beating of the other parts of the heart. After the heart has ceased to beat spontaneously it may be caused to resume its activity by the application of a stimulus.

Circulation in the Web of the Foot.—The web of the frog's foot affords a classical object for the study of the capillary circulation. It may easily be prepared for observation with the microscope by tying the frog down to a small piece of board, and spreading its toes apart so that the web is stretched across a notch or hole through which light may be passed from below. The toes may be held in position by small pieces of thread tied to the tips and fastened by their other ends to the board.

In a web thus prepared the blood may be seen flowing rapidly in the small veins and arteries, and more slowly in the capillaries. The red corpuscles will be found to become elongated and narrowed as they thread their way slowly through the small capillaries. The leucocytes often creep slowly along the walls of the vessels, and may be seen to stop frequently, and sometimes to migrate through the capillary walls. In the arteries a pulsation due to the beating of the heart may be observed; the caliber of the arteries often changes, owing to the contraction of the muscle fibers of their walls.

The capillary circulation may also be easily studied in the tail of the tadpole.

The Lymphatic System.—The lymphatic system of the frog is remarkable on account of the abundance and large size of the lymph spaces in various parts of the body. There are no well-defined lymphatic vessels such as occur in the mammals; the lymph flows in irregular spaces between and within the different organs; the larger spaces are lined by flattened endothelial cells, but are entirely devoid of a muscular coat, and usually, also, of a lining of connective tissue.

The subcutaneous lymph spaces are especially well developed; they are separated from each other only by the narrow septa of connective tissue by which the skin is here and there attached to the underlying muscles. One of the largest of the lymph spaces within the body is the subvertebral lymph sinus, or *cisterna magna,* which extends above most of the dorsal side of the body cavity.

The lymph spaces of the body stand in communication so that there is a flow of lymph from the one to the other, but of the course of the flow, if there be a constant one, little is known. There is a flow of lymph into the blood through the four *lymph hearts* and also through the ciliated nephrostomes on the ventral surface of the kidney which lead from the cœlom into the renal veins. The anterior lymph hearts are situated just behind the transverse processes of the third vertebra, and empty into the vertebral vein, which flows into the internal jugular. The posterior lymph hearts lie on either side of the tip of the urostyle, and empty into the transverse iliac vein. All of the lymph hearts pulsate regularly, and pump the lymph from the lymph spaces with which they communicate into the blood. At their openings into the veins there is a pair of semilunar valves which prevent the blood from passing into the lymph heart when it becomes relaxed. At the opposite end there are ostia (but apparently no valves) through which the lymph enters the heart from the lymph sacs. The lymph hearts are furnished with a muscular coat composed of a network of bundles of striated muscle fibers.

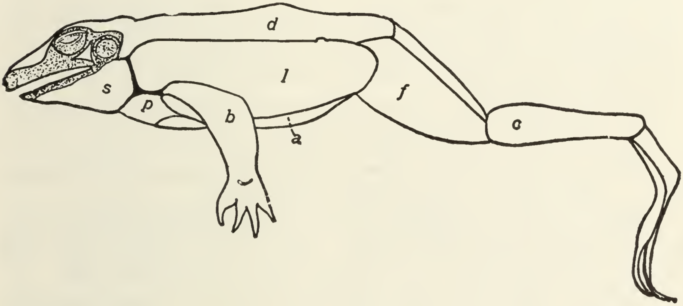

Fig. 96.—Lymph sacs of *Rana*. The dark lines indicate where the septa extend between the skin and the body. *a*, abdominal lymph sac; *b*, lateral brachial lymph sac; *c*, crural lymph sac; *d*, dorsal lymph sac; *f*, femoral lymph sac; *l*, lateral lymph sac; *p*, pectoral lymph sac; *s*, submaxillary lymph sac. (Modified from Gaupp.)

The beating of the lymph hearts may readily be observed in a recently killed frog. Often the pulsations of the posterior lymph hearts may be seen beneath the skin, but they are easily demonstrable in a very satisfactory manner by removing the integument on each side of the end of the urostyle. Their pulsations have no relation to those of the heart, nor is there unison between the beats of the lymph hearts on the two sides of the body.

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CHAPTER XVI

THE NERVOUS SYSTEM

The frog has the power not only of performing a large number of complicated movements, but of adapting its actions to the various elements of its environment. The initiation and control of these movements are dependent upon the reception of stimuli either from within or without the organism and the transfer of the impulses thus arising to the muscles which by their contraction bring about the required actions. When the frog withdraws its foot when it is irritated, or snaps at a moving insect, it is performing an act of an adaptive nature in response to an external stimulus. It is evident that the actions of the frog in relation to external stimuli and the coördination of activities going on in different parts of the organism necessitate some highly specialized means for the transfer and direction of impulses, and it is with these functions that the nervous system is especially and primarily concerned. But the nervous system has another important function, inasmuch as it affords the means for the accumulation of the effects of experiences whereby the animal is enabled to profit by its former behavior and modify its conduct to suit new situations. This latter power forms the basis of intelligence, a faculty rather feebly developed in the frog, it is true, but, as we shall see later, a not unimportant element in the life of the animal.

The nervous system has often been compared to a system of telegraph wires by means of which any one part of a country may be put into communication with any other part. The nerves correspond to the wires, and the ganglia to the central stations where messages may be transferred from one line to another. All parts of the body are supplied with nerves which are connected with the central nervous system; and through this channel connections may be established between any two or more parts of the organism. In this way there is rendered possible the coördination of movements in different parts of the body, and the ability of the organism to act as a whole in relation to external objects.

The nervous system is composed of three rather closely associated divisions: the *cerebro-spinal,* consisting of the spinal cord and brain; the *peripheral,* consisting of the spinal and cranial nerves; and the *sympathetic.*

The Spinal Cord.—The spinal cord of the frog is short and somewhat flattened. It presents two enlargements, one in the brachial region, where the large nerves to the fore limbs are given off, and one farther back, where the large nerves originate which supply the hind legs. Behind the posterior enlargement the cord tapers to a narrow thread, the *filum terminale,* which extends into the urostyle. At its anterior end the cord widens gradually into the *medulla oblongata,* the posterior division of the brain. Both the dorsal and the ventral sides of the cord are divided by a median fissure. At the sides of the cord the roots of the *spinal nerves* are given off; each nerve arises from a dorsal and a ventral root which combine just after they emerge from the vertebral canal through the intervertebral foramina. The roots of the posterior spinal nerves are much elongated, inasmuch as the shortening of the cord brings their origin far in front of the vertebræ to which they correspond; the bundle of roots thus formed, together with the *filum terminale,* is known as the *cauda equina.*

Both the cord and the brain are surrounded by membranes which are designated by Gaupp as follows: Externally is the dura mater, consisting of two layers separated by a lymph space (*interdural space*); the outer layer of this is pigmented and closely applied to the inner surface of the cranium and neural canal; the inner layer is devoid of pigment and lies close to the brain and cord. Within the dura mater is a thin vascular layer corresponding to the *pia mater* and *arachnoid* of the higher vertebrates; only here and there does it present a division into two lamellæ. This layer is very closely applied to the central nervous system, and is continued into various fissures of the brain, and the ventral fissure of the spinal cord.

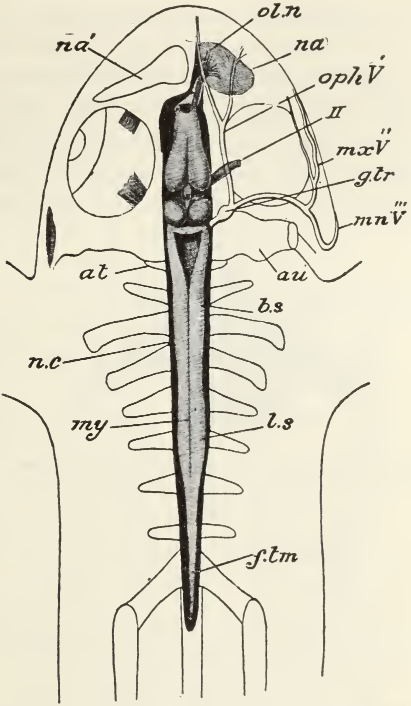

Fig. 97.—The central nervous system of the frog. The roof of the skull and vertebral column removed to show the brain and spinal cord. *at*, atlas, or first vertebra; *au*, auditory capsule; *b.s*, brachial enlargement of the cord; *f.tm*, filium terminale; *g.tr*, proötic ganglion (trigeminus, or Gasserian ganglion of many authors); *l.s*, lumbar enlargement of cord; *mn* (V'''), mandibular branch of fifth nerve; *mx* (V''), maxillary branch of trigeminus nerve; *my*, myelon, or spinal cord; *na*, right nasal sac; *na'*, left nasal bone; *n.c*, neural canal; *ol.n*, olfactory nerve; *oph* (V'), ophthalmic branch of fifth nerve; *II*, optic nerve. (After Howes.)

A cross section of the cord shows it to

be composed mainly of ganglion cells and nerve fibers. The central part of the cord is formed of gray matter which consists chiefly of ganglion cells and non-medullated nerves. Near the center of the gray mass is a small canal, the *canalis centralis,* lined by a single layer of epithelial cells. This canal is the remnant of the lumen formed by the closing over of the edges of the medullary groove during development; at its anterior end it widens out into the ventricles of the brain.

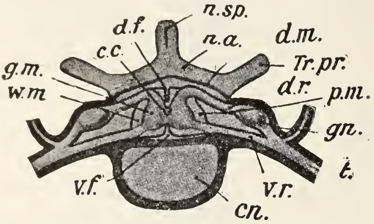

Fig. 98.—Cross section through the vertebral column, and spinal cord showing the origin of the spinal nerves. *c.c,* central canal; *cn,* centrum; *d.f,* dorsal fissure; *d.m,* dura mater; *d.r,* dorsal root of nerve; *g.m,* gray matter: *gn,* ganglion of dorsal root; *n.a,* neural arch; *n.sp,* neural spine; *p.m,* pia mater (the reference line should stop at the margin of the cord); *t,* nerve trunk; *Tr.pr,* transverse process; *v.f,* ventral fissure; *w.m,* white matter. (After Howes.)

At the sides the gray matter is produced both dorsally and ventrally into the dorsal and ventral *cornua* or *horns.* The gray matter on the two sides of the cord is connected both above and below the central canal by means of the *dorsal* and *ventral gray commissures,* which consist chiefly of non-medullated nerve fibers. Just below the ventral gray commissure is a conspicuous oblique crossing of medullated fibers in the white matter, the *ventral white commissure.* Below the white commissure is the *ventral fissure,* which separates the right and left columns of white matter. From the shallow *dorsal fissure* there extends a narrow septum as far as the dorsal gray commissure. The nervous elements of the cord are bound together by stellate neuroglia cells and by processes which arise from the tapering outer ends of the cells lining the central canal; these processes branch repeatedly, and some of them extend to the periphery of the cord.

The white matter of the cord is composed mainly of medullated fibers. Most of these run longitudinally. Isolated ganglion cells appear, but there seems to be no regularity in their distribution. Strands of gray matter, largely ependyma fibers, radiate from the central part of the cord to the outer surface.

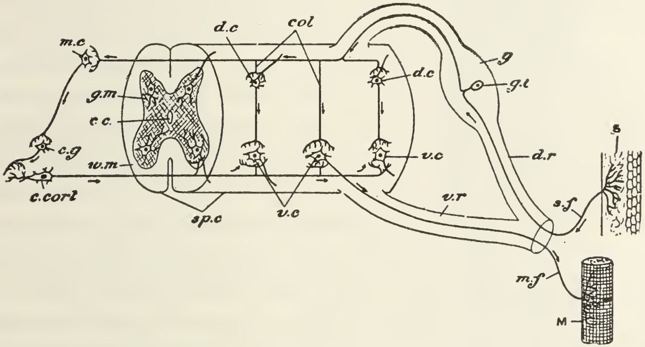

Fig. 99.—Diagram of the spinal cord showing the paths taken by nervous impulses. The direction of the impulses is indicated by arrows. *c.c*, central canal; *col*, collateral fibers; *c.cort*, cell in the cerebral cortex; *c.g*, smaller cerebral cell; *d.c*, cells in dorsal horn of gray matter; *d.r*, dorsal root; *g*, ganglion of dorsal root; *g.c*, ganglion cell in dorsal ganglion; *g.m*, gray matter; *M*, muscle; *m.c*, cell in medulla oblongata; *m.f*, motor fiber; *S*, skin; *s.f*, sensory fiber; *sp.c*, spinal cord; *v.c*, cells in ventral horn of gray matter; *v.r*, ventral root of nerve; *w.m*, white matter. (After Parker and Parker.)

The cells of the gray matter give off processes by means of which connections become established between different parts of the cord. In the broad ventral cornua there are several ganglion cells of unusual size from which processes arise which form the axis cylinders of the fibers of the ventral roots of the spinal nerves; other processes from these cells cross to the opposite side of the cord in the ventral white commissure, and still other processes branch irregularly in both the gray and white matter of the same side. Scattered about through most of the gray substance are the commissural cells which give off axis cylinder processes which cross to the opposite side of the cord in the ventral gray commissure and then give off branches which run in the white matter both anteriorly and posteriorly; protoplasmic processes are also given off which connect with similar processes from other cells in the gray matter in the same side. Other cells give off axis cylinder processes, which run in both directions in the white matter of the same side of the cord. Still other cells occur whose axis cylinder processes divide, the one branch going into the white matter of the same side of the cord, the other crossing through the ventral gray commissure to the white matter of the opposite side. Finally there are numerous cells whose processes do not enter the white matter, but branch and connect with cells in the gray matter of the same or the opposite side.

A cross section through a region where the spinal nerves are given off shows the fibers of the dorsal root passing through the dorso-lateral portion of the white matter to enter the gray substance in a narrow bundle. Most of the fibers of the dorsal roots are processes of cells lying in the spinal ganglion. Each fiber as it enters the cord gives off branches which run in opposite directions. Connections are made with processes of the large cells which supply the ventral or motor roots of the nerves as well as with the cells of the gray matter on both sides of the cord. The ventral roots of the spinal nerves are broader and consist of several isolated strands.

The Spinal Nerves.—The frog possesses but ten pairs of spinal nerves. The tadpole has a much larger number (twenty-two in *R. fusca*), but the posterior ones disappear with the degeneration of the tail. There is also a pair of nerves which appears in the embryo in front of what is the first pair of spinal nerves of the adult, but we shall continue to speak of the latter as the first pair. Each spinal nerve arises from the cord by a *dorsal* and a *ventral* root which unite just outside the inter-vertebral foramina through which they emerge. Near its junction with the ventral root each dorsal root bears a *ganglion* whose cells give rise to most of the fibers of which that root is composed as well as the sensory fibers of the peripheral portion of the nerve. At the outer end of the ganglion each nerve divides into a *dorsal* and a *ventral* branch. Each of these contains both sensory and motor fibers. The dorsal branches divide into several nerves which supply the skin and muscles of the dorsal side of the body; the ventral

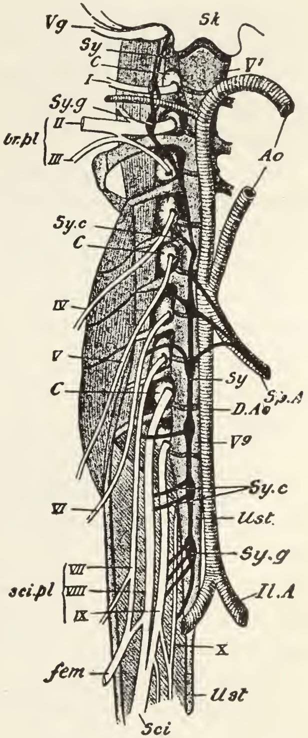

Fig. 100.—Spinal nerves and sympathetic system of the frog, the right side seen from below. Only the ventral branches of the spinal nerves shown. Sympathetic system in black. *I*—*X*, spinal nerves; *Ao*, systemic arch of aorta; *br.pl*, brachial plexus; *C*, calcareous bodies, around the spinal ganglia; *D.Ao*, dorsal aorta; *fem.* femoral nerve; *Il.A*, iliac artery; *sc*, sciatic nerve; *sci.pl*, sciatic plexus; *Sk*, skull; *Sp.A*, splanchnic, or cœliaco-mesenteric artery; *Sy*, sympathetic cord; *Sy.c*, commissures between sympathetic and spinal nerves; *Sy.g*, sympathetic ganglia; *Ust*, urostyle; V^1–V^6, centra of vertebræ; *Vg*, vagus nerve. (From Parker and Parker.)

branches supply the ventral musculature and limbs; a short communicating nerve connects each ventral branch with the trunk of the sympathetic system. The distribution of the spinal nerves, exclusive of their dorsal rami, is as follows:—

The *first* nerve emerges between the first and second vertebræ, its principal branch, the hypoglossal, innervates the tongue and several of the muscles attached to the hyoid; a short communicating branch joins the second nerve.

The *second pair* of nerves emerges between the second and third vertebræ. This pair, which is of large size, forms with branches received from the first and third pairs the *brachial plexus,* from which the nerves arise which are distributed to the fore limb and muscles of the shoulder.

The *third* pair of nerves, after giving a branch to the brachial plexus, supplies the anterior part of the external oblique and transversus muscles and gives some twigs to the skin.

The *fourth, fifth,* and *sixth* nerves are small and are distributed mainly to the skin and muscles of the wall of the abdomen.

The *seventh, eighth,* and *ninth* nerves pass almost directly backward and anastomose with each other to form the *lumbo-sacral,* or *sciatic plexus.* The seventh nerve, before it enters the plexus, gives off the *ilio-hypogastric* nerve which is distributed to the muscles of the abdomen. The *cruralis* nerve is given off from the plexus ventral to the posterior portion of the ilium; it is distributed to the muscles of the abdomen and skin of the anterior part of the thigh. The largest nerve coming from the plexus is the *sciatic,* which emerges from the body cavity just behind the posterior end of the crest of the ilium, passing between the pyriformis and posterior head of the triceps extensor muscle and extending down the back of the thigh; a short distance

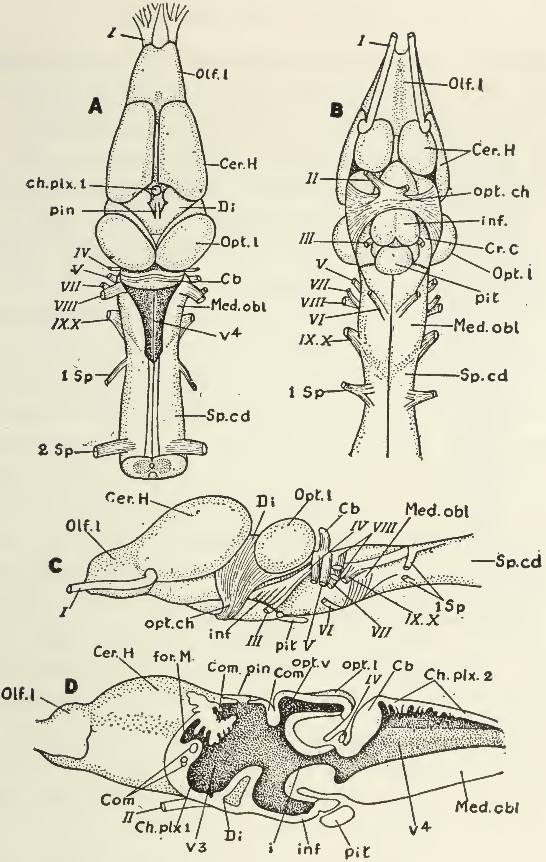

FIG. 101.—Brain of frog. A, dorsal side; B, ventral side; C, left side; D, in vertical longitudinal section through the middle. *Cb*, cerebellum; *Cer.H*, cerebral hemispheres; *ch.plx*^{1} anterior, and *ch.plx*^{2} posterior, choroid plexus; *com*, commissures connecting the right and left halves of the brain; *Cr.C*, crura cerebri; *Di*, diencephalon, or thalamencephalon; *for.M*, foramen of Monro; *i*, iter, or aqueduct of Sylvius; *inf*, infundibulum; *Med.obl*, medulla oblongata; *Olf.l*, olfactory lobe; *Opt.l*, optic lobe; *opt.v*, optic vesicle; *pin*, pineal body; *pit*, pituitary body; *Sp.ed*, spinal cord; v^3, third ventricle; v^4, fourth ventricle; *I–X*, cranial nerves; *1 Sp*, *2 Sp*, first and second spinal nerves. (From Newman, slightly modified from Parker and Parker's Zoölogy.)

proximal to the knee it divides into the *tibialis* nerve and the *peroneus.* The former extends along the posterior or flexor side of the leg, and innervates the gastrocnemius, tibialis posticus, and numerous muscles of the plantar surface of the foot. The peroneus runs under the tendon of the triceps and extends along the extensor surface of the crus, giving branches to the peroneus muscle, the tibialis anticus, and the muscles on the extensor surface of the foot.

The *tenth* nerve with a branch from the *ninth* forms the *ischio-coccygeal plexus,* from which branches are given off to the bladder, cloaca, oviducts, and posterior lymph hearts. The tenth nerves are of small size and emerge from small foramina in the sides of the urostyle near the anterior end. An eleventh spinal nerve sometimes occurs. When present it emerges from the urostyle behind the opening for the tenth and joins the ilio-coccygeal plexus. All of the plexuses are subject to considerable variation in different individuals.

The Brain.—The brain is composed of the following parts taken in order from behind forward: the *medulla oblongata,* or *hind-brain;* the *cerebellum;* the *mid-brain;* the *thalamencephalon;* and the *fore-brain,* which consists of the *cerebral hemispheres* and *olfactory lobes.*

The medulla oblongata is formed by a widening of the anterior end of the spinal cord. On its dorsal side is situated the wide, more or less triangular *fourth ventricle,* which communicates by its tapering posterior end with the central canal of the cord. Its roof is thin and thrown into folds bearing the *posterior choroid plexus* of blood vessels. At the sides the medulla gives rise to several pairs of cranial nerves. Its lower surface is divided by a median fissure which is continuous with the ventral fissure of the cord.

The *cerebellum* consists of a small transverse fold at the anterior margin of the fourth ventricle. In most other vertebrates the cerebellum is an organ of considerable size, but in the frog it is almost rudimentary.

The *optic lobes,* which form the dorsal part of the *mid-brain,* are large rounded bodies lying just in front of the cerebellum. Their cavities, the *optic ventricles,* communicate with each other and also with the channel between the third and fourth ventricles. Below the optic lobes are the *crura cerebri,* which extend from the medulla to the cerebral hemispheres and form the floor of the mid-brain.

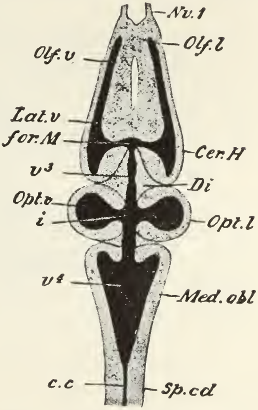

Fig. 102.—Diagram of a horizontal section of a frog's brain. *c.c*, central canal; *Cer.H*, cerebral hemisphere; *Di*, diencephalon, or thalamencephalon; *for.M*, foramen of Monro; *i*, iter; *Lat.v*, lateral ventricle; *Med.obl*, medulla oblongata; *Nv.1*, first, or olfactory nerve; *Olf.l*, olfactory lobe; *Olf.v*, olfactory ventricle; *Opt.l*, optic lobe; *Opt.v*, optic ventricle; *Sp.cd*, spinal cord; v^3, third ventricle; v^4, fourth ventricle. (After Ecker and Wiedersheim.)

The *thalamencephalon* is in the region between the optic lobes behind and the cerebral hemispheres in front. Its roof is thin and lined with a vascular membrane, the *anterior choroid plexus;* it bears two outgrowths in the mid-dorsal line, the paraphysis, a vascular outpocketing of the epithelium of the roof, and a short distance behind the latter, the *epiphysis,* a hollow, thin-walled canal which terminates blindly at its anterior end. A small *parietal nerve* runs along the dorsal surface of the epiphysis and extends forward over the paraphysis and then passes through the sagittal suture of the skull to end in the brow spot. The epiphysis, which originally was continuous with the brow spot, becomes constricted off from it in early larval life. On the ventral side of the thalamencephalon is the *optic chiasma,* or crossing of the nerves which go to the eyes. In the frog all of the fibers cross to the opposite side.

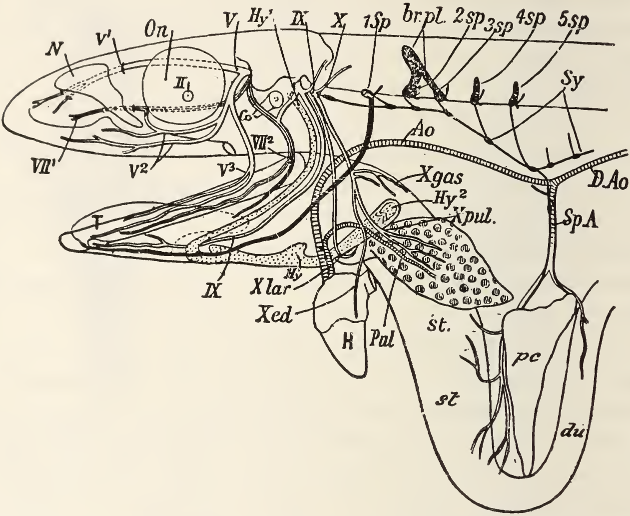

FIG. 103.—Diagram of the distribution of the fifth, seventh, ninth, and tenth cranial nerves, the first spinal nerve, and the anterior part of the sympathetic. *Ao,* systemic arch of aorta; *br.pl,* brachial plexus; *D.Ao,* dorsal aorta; *du,* duodenum; *H,* heart; *Hy,* hyoid with *hy*¹ anterior and *hy*² posterior horns; *L,* lung; *N,* nasal bone; *On,* orbit; *Pul,* pulmonary artery; *Sp.A,* splanchnic, or cœliaco-mesenteric artery; *St,* stomach; *Sy,* sympathetic; *II,* cut end of optic nerve; *V*¹, ophthalmic, *V*², maxillary, and *V*³, mandibular branch of fifth, or trigeminus nerve; *VII*¹, palatine, and *VII*², hyomandibular branch of facial; *IX,* glossopharyngeal nerve; *X,* vagus with *Xcd,* cardiac, *Xgas,* gastric, *Xlar,* laryngeal, and *Xpul,* pulmonary branches; *1 Sp,* first spinal nerve, or hypoglossal; *2 sp–5 sp,* second to fifth spinal nerves. (From Parker and Parker's Zoölogy, slightly modified from Howes.)

Just behind the optic chiasma is the *infundibular lobe,* a flattened bilobed structure, emarginate posteriorly and divided by a median longitudinal groove. It is formed of nervous tissue and contains a cavity which is continuous with the third ventricle.

The *hypophysis cerebri* lies behind and partly covered by the infundibular lobe. It is composed of an anterior and posterior part; the former is divided into a median and two lateral portions, the posterior part is flattened and more or less quadrate in outline. Genetically the true anterior part of the hypophysis has no connection with the brain, but arises as an outgrowth from the roof of the stomodeum.

The *cerebral hemispheres* are elongated bodies lying in front of the thalamencephalon; they taper somewhat anteriorly and are separated from each other by the *sagittal fissure.* Their cavities, the *lateral ventricles,* communicate with the third ventricle by the *foramen of Monro;* anteriorly the lateral ventricles extend into the olfactory lobes.

The *olfactory lobes* lie just in front of the cerebral hemispheres, of which they are but the continuation. They are separated from the latter by a shallow lateral sulcus. Unlike the cerebral hemispheres, they are closely fused together in the middle line; on the ventral side, however, they show a well-marked median fissure. Anteriorly they give off the olfactory nerves.

The Cranial Nerves.—There are ten pairs of nerves in the frog which arise from the brain and are known consequently as cranial nerves.

The first nerves, counting from before backward, are the *olfactory.* They arise from the olfactory lobes by two roots, the anterior one emerging from the front end, the posterior running along the ventral side of the lobe nearly to its posterior end. The olfactory nerves pass through small foramina in the ethmoid bone and are distributed to the walls of the nasal chambers.

The *optic,* or second pair of cranial nerves, arise from the thalamencephalon, and, after crossing in the chiasma, emerge from the skull through foramina in the sides of the chondrocranium, and are distributed to the eyes. Both the olfactory and the optic nerves are purely sensory.

The third nerve, *oculo-motor,* is small and arises from the ventral surface of the crura cerebri. It emerges from the skull through a small foramen near the opening for the optic nerve, and innervates four of the muscles of the eyeball, the rectus superior, rectus inferior, rectus medialis, and obliquus inferior. After giving off a branch to the rectus superior, the third nerve becomes connected with the ciliary ganglion; this ganglion also receives a branch from the ophthalmic division of the fifth nerve, and gives off the small ciliary nerves to the retractor bulbi muscle and the tunics of the eye.

The fourth nerve, the *trochlearis,* is very small; it arises from the dorsal side of the brain, between the optic lobes and the cerebellum. It leaves the skull through a special foramen a little above the optic nerve and is distributed to the superior oblique muscle of the eye. Both the third and the fourth nerves are exclusively motor.

The fifth nerve, the *trigeminus* or *trifacial,* is one of the largest of the cranial nerves. It arises from the sides of the anterior end of the medulla by a pair of roots which unite in a large *proötic* ganglion before leaving the skull. This ganglion, which corresponds in part to the Gasserian ganglion of higher forms, is connected with the sixth and seventh nerves and also the sympathetic. Two branches of the trigeminus, the *ophthalmic* and the *maxillo-mandibular,* emerge from the ganglion, and leave the skull by a foramen in the anterior part of the proötic bone. The former runs along the dorsal side of the orbit, passes through a foramen in the posterior wall of the nasal capsule, and divides into branches, most of which emerge from the nasal capsule again, and are distributed to the skin of the anterior part of the head. The *maxillo-mandibular* nerve runs outward behind the eye; it soon divides into the *maxillaris superior* and the *maxillaris inferior,* or *mandibular.* The former runs forward and outward below the eye and supplies the upper lip and adjacent structures. The latter supplies the principal muscles for moving the lower jaw, the lower lips, and skin of the lower side of the mouth. The trigeminus is a mixed nerve, partly sensory and partly motor.

The sixth nerve, the *abducens,* arises from the ventral side of the medulla. It joins the proötic ganglion and emerges through the same opening as the fifth nerve, to be distributed to the lateral or external rectus and retractor bulbi muscles of the eye.

The seventh, or *facial,* nerve arises from the medulla, closely behind the fifth, in company with which it leaves the skull after emerging from the proötic ganglion. It soon divides into two branches; the first, the *palatine,* courses along the ventral side of the orbit, just above the mucous membrane of the mouth. At the anterior end of the orbit it gives off a branch which extends laterally and joins the maxillary branch of the fifth nerve. The main nerve passes forward to the nasal chambers and anterior portion of the roof of the mouth. The second branch, the *hyomandibular,* runs outward and then backward, around the auditory capsule, passing over the columella, and, after receiving a branch from the glossopharyngeal, runs outward, gives some twigs to the ear and muscles of the lower jaw, and then divides near the angle of the jaw into the *mandibularis internus,* which runs forward close to the mandible, and the *hyoideus,* which innervates the subhyoideus muscle and the skin in the region of the throat. The seventh nerve, like the fifth, contains both sensory and motor fibers.

The eighth, or *auditory,* nerve is distributed entirely to the inner ear.

The ninth, or *glossopharyngeal,* nerve arises from the sides of the medulla from a group of roots in common with the vagus; these roots emerge from the skull through a foramen in the exoccipital external to the condyle and enter the large *jugular ganglion.* Shortly after its emergence from this ganglion the trunk of the glossopharyngeal bears a small ganglionic swelling and then soon divides, the one branch passing forward to join the hyomandibular division of the facial, the other running forward in a sinuous course along the floor of the mouth and innervating the mucous membrane of the tongue and pharynx.

The tenth (*vagus* or *pneumogastric*) nerve emerges from the jugular ganglion generally by two trunks; the small anterior trunk, the *ramus auricularis,* is distributed to the region of the tympanum; the main nerve passes backward, and, after giving off some small branches to the muscles of the shoulder, becomes distributed to the larynx, esophagus, stomach, lungs, and heart. Both the glossopharyngeal and vagus contain sensory and motor fibers. The *accessorius,* which is a small branch supplying the cucullaris muscle, becomes in the higher vertebrates an independent cranial nerve.

The Sympathetic System.—The main trunks of the sympathetic system consist of a nervous strand on either side of the spinal column. Anteriorly each trunk begins in the proötic ganglion, from which it extends backward within the cranial cavity, leaving the skull by the jugular foramen in common with the vagus. It receives a branch from the jugular ganglion, which enters the first ganglionic enlargement of the main trunk. Each trunk receives a branch (*ramus communicans*) from each of the spinal nerves, and where the two join there is a ganglionic enlargement. The eighth spinal nerve, however, is connected with the sympathetic by two communicating branches, and the ninth nerve by three and sometimes four. The last ganglion of the sympathetic chain consists of the ninth and tenth ganglia fused into one; it receives, besides the branches from the ninth spinal nerve, a single small branch from the tenth.

A part of the fibers from the sympathetic trunks enter the spinal nerves by way of the communicating rami; other fibers form independent sympathetic nerves. From the anterior portion of the trunks branches are given off to the subclavian and occipito-vertebral arteries and anterior ends of the oviducts. Farther back (from third to sixth ganglion) several nerves are given off which unite to form the *cœliac or solar plexus,* in which several ganglionic masses occur. From this plexus nerves are distributed to the stomach, intestine, liver, pancreas, spleen, ovaries, oviducts, and kidneys. Farther back several branches anastomose to form the *urogenital plexus,* which supplies the kidneys, ovaries, oviducts, and testes. The ganglion cells of the sympathetic system are often situated very far from their point of origin. They are found embedded along the course of certain nerves such as the vagus and facial; in the walls of the intestine (*Auerbach's* and *Meissner's plexuses*); in the heart (*Remak's, Bidder's, Dogiel's ganglia* and several smaller groups of cells); in the walls of the bladder; and in the skin.

Reflex Action.—The reflex actions of the spinal cord of the frog may be illustrated by the following experiment: Cut the spinal cord of a frog across just behind the medulla and, after destroying the brain, suspend the animal upon a hook passed through the upper jaw. Now pinch one of the toes; the hind foot will be drawn up to the body. If a piece of blotting paper saturated with dilute acetic acid be placed on one side of the body, the hind leg of that side will be brought forward and the acid wiped away with the foot. If the acid is placed near the middle of the body, both hind feet may be employed to remove it. The vigor of the response depends upon the strength of the stimulus, a weak stimulus producing only a slight movement, while a very strong stimulus will throw the animal into violent contortions. Similar responses may be evoked from the fore limbs, and if acid be placed on the side of the body some distance in front of the hind legs, both fore and hind limbs may be employed to remove the irritant. These actions are of a very definite and mechanical type, and, if the frog is in good condition, follow inevitably upon the application of the stimulus. They are termed reflex actions on account of a certain analogy with the reflection of light which may be thrown back upon its original source by a mirror. The spinal cord nerves contain two kinds of fibers, the afferent or sensory, which conduct impulses from the periphery to the cord, and efferent (usually motor fibers), by means of which impulses are carried outward to other organs. What happens during a simple reflex action of the cord, then, is this: Impulses set up by a stimulation of the sensory nerve endings of the skin travel along the sensory fibers of a spinal nerve to the cord, entering it through a dorsal root. The afferent fibers as they enter the cord divide and run for a distance both anteriorly and posteriorly, and then give off collaterals, which branch in the gray matter. Some of these form connections with the cells of the ventral roots of the spinal nerves of the same side of the cord. In the simplest case impulses reaching these cells through the collaterals are transmitted to the axis cylinders of the motor nerves arising from them and pass out through the ventral root and down the same spinal nerve to the muscles of the leg, causing them to contract. The spinal cord here serves as a medium of communication between sensory and motor nerves. If a dorsal root be cut, stimulation of a sensory nerve produces no effect. If, however, the distal end of the part in connection with the cord is irritated, muscular contractions will be produced. If the ventral or motor root of the nerve be cut, reflex action in the part supplied by that nerve is destroyed. If the cut end of the nerve is irritated, the muscles to which it is distributed will contract, but stimulation of the end connected with the spinal cord will have no effect.

The impulses passing through the cord are not limited to a single path, but they may take any one or more of several routes. They may cross by way of the gray commissures to the opposite side of the cord and become transferred through the branches of the gray commissural fibers to the ventral roots of that side, or they may pass across by means of the white commissures. They may also pass backward or forward along the cord either in the gray matter or in the white. In this way a stimulus applied to any part of the body may give rise to movements not only on the two sides, but also in regions in front of and behind the point stimulated. The stronger the stimulus, the greater is the part of the body involved in the response. A weak stimulus applied to the foot produces movement only in the member stimulated, while a much stronger stimulus may cause a movement of the opposite leg as well as other parts of the body. If acid be placed on one side of the body and the leg of that side held, the leg on the opposite side is sometimes brought around to wipe the acid away. This apparently intelligent act is obviously dependent upon the passage of impulses from one side of the cord to the other. And it requires a stronger stimulus to bring it about than is necessary to produce a simple unilateral reflex.

These reflex actions of the spinal cord are of a purposive nature; they bring the limbs away from injurious stimuli and remove irritating substances from the body. They are dependent upon the organization of the animal, the neuromuscular mechanism being such that a stimulus to any part of the body brings about the appropriate actions for removing or escaping from the source of injury.

The reflex actions of a frog may be checked or modified by impulses from the brain. A frog with its brain in connection with the cord will not respond to stimulation in the same regular and unvaried manner as a brainless individual. Its actions are much less mechanical and more spontaneous and uncertain of prediction. The influence of the brain is rendered possible by means of nerve trunks which pass from the brain down the spinal cord and form connections with the neurones of the spinal nerves. If the anterior end of the spinal cord is strongly stimulated at the same time a stimulus is applied to the foot, the withdrawal of the latter may be entirely prevented. In this way the ordinary reflex actions of the cord are continually checked and modified by impulses from the higher nervous centers.

The Croaking Reflex.—If the side of a frog be stroked with the finger, the animal often responds by croaking. The same reaction frequently occurs when the frog is picked up in the hand. It takes place more often in the male frog than in the female, especially during the breeding period, when the croaking mechanism is very readily put into activity. A frog that is seized may continue to croak vigorously for some time, and when it has ceased to croak it may be induced to continue by rubbing its side with the finger. The croaking reaction, however, is very variable, and in certain individuals it may not be performed at all. And the same individual reacts quite differently at different times, according to what seems its own caprice.

It is quite otherwise with frogs from which the cerebral hemispheres have been removed. It was found by Goltz that animals thus operated on croak with mechanical regularity whenever one strokes their side or back. They never croak when the hind legs or ventral side of the body is stroked, and they croak only once after each stroke on the back or side. The experiment succeeds well with both sexes, but the croak of the male is naturally much louder than that of the female. "I know of scarcely any physiological experiment," says Goltz, "which succeeds in so certain and regular a manner as this croaking experiment. . . . As I was delivering a discourse upon this subject before the meeting of the naturalists at Hannover, in the year 1865, I placed upon the table, for purposes of demonstration, several frogs operated upon several months previously, which I had brought with me from Königsberg. In the course of the session I asked Herr Von Wittich, who was present in the audience, how often each of the frogs, which were resting silently and still, should croak. The answer five times was given, and each of the frogs, upon being given five strokes, croaked exactly five times, to the evident gratification of the auditors, whereupon they all lapsed into silence."

The croaking of a brainless frog is a reflex set in operation by a particular localized external stimulus. In a normal specimen this reflex is subject to control from the higher nerve centers. It may be entirely checked by impulses down the spinal cord from the brain. The normal frog shows a spontaneity and freedom of action which is largely destroyed in individuals which have recently lost their cerebral hemispheres. The latter often croaks without any apparent exciting cause, while a brainless frog croaks only upon the application of an external stimulus to certain parts of the body.

The utility of the croaking reflex is not apparent. It has been suggested by Baglioni that, since in croaking air is pushed back and forth between the mouth and the lungs, the swelling thus produced enables the animal to push against anything that seizes it and make its escape, the sound being merely an incidental accompaniment of the process. Any one who picks up a frog in the hands may readily convince himself that the croaking movements are a means of enabling the creature to slip from his grasp. In fact, these movements often occur in the female without producing any sound whatever. It is a significant fact that the reflex is evoked by stimuli upon those parts which, as the body swells, press against whatever seizes the animal. It is not brought about by seizure of the head or hind legs; the swelling in such cases would be of no avail. The fact that the croaking reflex is brought about by gently stroking the side or back may indicate nothing but the extreme readiness with which the swelling reflex is initiated. When the animal is seized and there is a constant pressure stimulus, there is a repeated swelling of the body and accompanying croaks. If the animal is stroked once on the side, it croaks once and then stops because the stimulus is stopped.

The Clasping Reflex and the Recognition of Sex.—The tendency of the male frog to clasp the female is one of the strongest of its instincts, but it appears only for a short time, during the breeding period in the spring. At this time the male will clasp another male frog, one's fingers, or in fact almost any object that is placed between its fore legs, but objects other than females are after a time rejected, while the duration of ordinary copulation is commonly several days.

The clasping reflex may be evoked any time of the year by cutting through the medulla or, according to Busquet, by simply removing the cerebellum. Steinach found that the higher nerve centers exercise an inhibitory influence over the clasping reflex except during the breeding season when the internal secretion of the testes acts upon the higher centers so as to check their usual inhibitory function. Whether the seat of the normal inhibition is in the cerebellum or in the mid-brain, as held by Baglioni, or perhaps in more than one center, is not definitely established.

The clasping efforts of the male frog afford a typical illustration of instinctive action; nevertheless they occur in entire independence of the higher nerve centers. The Abbé Spallanzani showed that a male frog may have its head cut off during copulation without ceasing to cling tenaciously to the female. Goltz went still farther and cut off the head of a male, then cut the body through between the third and fourth vertebræ, and removed the viscera from the body cavity; the section of the frog that remained after these operations consisted of the first three vertebræ, the pectoral girdle, and the fore legs. Yet when the skin of the inner surfaces of the fore legs was rubbed with the fingers, this segment would show the same clasping efforts as a normal male frog. The clasping of the male frog is, therefore, a reflex action whose center lies in the brachial region of the spinal cord. If the skin on the inner surfaces of the fore legs and on the breast be removed, the clasping reflex is destroyed. It is probable, therefore, that the reflex is initiated through the stimulation of the sensory organs of these regions of the body.

Notwithstanding the almost mechanical character of this spinal reflex, the frog discriminates between two such similar objects as the males and females of its own species. When a number of frogs of both sexes are placed together during the breeding season, the males will be found to be clasping females instead of other males. The question naturally arises: How does the male frog distinguish the female from one of his own sex? That it is not, as in many animals, through the sense of smell, was shown by Goltz by cutting through the olfactory lobes of several male specimens; after this operation the mutilated males were placed among several females, and in a short time they were all in copulation with members of the other sex. Then several males which were blinded were placed among the females, with the same result as before. That it is not the sound produced by the female that reveals her sex, was shown by Goltz by placing several females, which had been rendered incapable of using their voice, among the males. These were as readily seized as normal females. After the destruction of both smell and sight, males were found to be still able to distinguish the females, although there was apparently a certain diminution of their ardor. The senses of sight, smell, and hearing are not, therefore, the exclusive or indispensable means of sex recognition, whatever be the part they play under normal conditions. Neither are the higher nerve centers necessary. Goltz cut through the skull of a male so as to cut off the cerebral hemispheres and eyes; the specimen almost immediately clasped a female that was presented to it, while a male that was offered was rejected.

The form of the body differs in the two sexes, especially when the female carries a large mass of eggs, but this alone does not enable the male to distinguish the female. Goltz found that if the bodies of males were filled with flesh and sewed up so as to resemble the form of the females, they would be clasped for a short time and then rejected. The bodies of freshly killed females, on the other hand, were held for a long time, the tension or cramp of the muscles increasing, the longer the bodies were held. Goltz has suggested that there is something that emanates from the body of the female that acts as a special excitant to the male, and some later observations support this view.

Banta, who has studied the mating behavior of the wood frog, finds that the males during the breeding season swim about actively in search of mates while the females are relatively less active. Males tend to seize almost any moving object that comes near. "Any individual which moves within a radius of several feet of another male is likely to be tested by him. The male thus approached sometimes swims away and sometimes actively resists but often pays no attention to the aggressor and the latter turns back, frequently without coming near enough to touch the male, and almost always the aggressor gives up the attack after the very beginning of an attempt to grasp the stranger with the fore-legs. . . . Seldom is an attempt made upon any but a moving individual. . . . Even a female may usually avoid pursuit as long as she remains quiet. On the other hand any small moving object at the surface of the water is most certain to be approached by an eager male. The writer twice observed the male approach a speckled tortoise when the latter thrust its head out of the water."

The different behavior of males to the two sexes of their species may be in part due to the peculiar reactions of the female, but, as Banta observed, "The readiness with which the attempt of a male to pair with another male is given up on near approach, the keenness of the male's pursuit after once approaching very near or touching a female, and the discrimination between a dead male and a dead female particularly in cases in which, to the human eye, the latter is indistinguishable in size, color and general features from a male, suggests that a chemical sense is involved in final sex-recognition though one experiment designed to test this hypothesis was unsuccessful."

Sex discrimination in frogs is not very precise. Males are sometimes held by other males for a long time, and copulation is not infrequently known to occur between the males of different species. Spallanzani records a male toad that was carrying around an individual of his own sex that had died some days previously and was in an advanced state of decay. Whether or not a male will clasp an object other than the female depends upon the length of time he has been separated from the sexual embrace. If a male is recently torn from a female, he is very sluggish, and will clasp the fingers or almost any object that is presented to him. If left for a time, he becomes more active and shows little tendency to clasp all sorts of objects. Male frogs which at first would be seized are now usually rejected, or held but for a short time; but if a female is presented, she is seized with eagerness.

Compensatory Motions.—If a frog is rotated on a circular disk with its head pointing away from the center, the head of the animal will turn opposite the direction of rotation. The turning of the head is often followed by locomotion in the same direction, so that the frog keeps circling around in one direction while the disk is rotating in another. If the frog is placed on a board, and tilted either up or down, the head is turned opposite the direction of motion. Combined movements of rotation and tilting are followed by corresponding combined movements of the head, the result being in all cases to keep the head as nearly as possible in its original position. Such movements are therefore called compensatory motions. They take place in response to very slight changes in the position of the body, and they occur with remarkable regularity, apparently independently of the animal's volition. They are performed after the destruction of all parts of the brain in front of the medulla, or even after the removal of the anterior part of the latter organ, provided the injury does not extend so far back as the trigeminus group of nerves. If the semicircular canals are destroyed or the auditory nerves cut, compensatory motions, according to Schrader, are no longer performed, but Steiner finds that compensatory motions of the head at least still take place.

The Functions of the Brain.—The brain is the great center of communication between the principal organs of sense and the rest of the body; through it are effected the numerous coördinations between a great variety of stimuli, sights, sounds, odors, etc., and the appropriate muscular actions which enable the animal to adjust itself to the environment. The number and nature of the connections established in the central nervous system determine to a large degree the character of the animal's instincts, and the possibilities and the limits of the development of its intelligence.

The brain of the frog is in one respect a favorable object for the study of function, inasmuch as large parts of it may be removed without causing the death of the animal. The shock effects following operations are much less in cold-blooded animals than in birds and mammals; the subjects recover more quickly, and will endure the removal of much larger portions of the brain. But even in the frog the after-effects of certain operations wear off very slowly. There is danger in removing parts of the brain, of attributing results to the loss of the part in question, which may be due to injuries produced by the operation. The behavior of the animal some months after being operated upon is often quite different from its behavior before complete recovery. For this reason different investigators of the functions of the frog's brain have arrived at contradictory results. It is only after waiting until the shock effects of the removal of a part of the brain have completely worn away, that we can arrive at a correct idea of the normal rôle of that part in the life of the animal.

Cerebral Hemispheres.—It is frequently stated that a frog which has lost its cerebral hemispheres loses nearly all its spontaneity; that it remains sitting in one position for an indefinite time, if not disturbed; and that it takes no food unless it is forced into its mouth. While it is still able to hop and swim, avoid obstacles placed in its path, and perform many other movements in an apparently normal manner, it is said to lose the power of originating actions independently of outer stimuli. The experiments of Schrader showed the incorrectness of these commonly accepted conclusions. The symptoms so frequently ascribed to loss of the cerebral hemispheres are those which follow when a part of the thalamencephalon is also removed or subjected to severe injury. Schrader found that if the cerebral hemispheres were carefully removed without injuring the thalami, and the animal kept some months after the operation, spontaneity of action is by no means lost; the animals move about from land to water, bury themselves in the mud on the approach of winter, and snap at flies which move within their reach. Their conduct, in fact, resembles very closely that of normal frogs; and in just what respect it differs Schrader does not make clear. After loss of the cerebral hemispheres all fear, according to Kato, disappears, and the frog no longer croaks spontaneously, but how long after the operation these results were observed is not stated.

In higher animals the cerebral hemispheres are the seat of intelligence and voluntary control. Dr. T. C. Burnett removed the cerebral hemispheres from several frogs and endeavored to ascertain if the animals could learn the simple things which ordinary frogs are able to learn. He found that the decerebrate frogs were unable to learn a very simple path to water, nor would they avoid a path in which they repeatedly received a strong electric shock. Removal of the cerebral hemispheres seems, therefore, to affect the frog much as it does a bird or a mammal in destroying the power of associative memory.

Removal of one cerebral hemisphere is not followed by so severe shock effects as the removal of the entire cerebrum. The frog thus operated upon is, according to Kato, more active, it springs more readily, and manifests fear upon seeing the approach of large objects. It tends at first to avoid obstacles placed in its path by turning away from the operated side, but in four days after the operation its behavior, according to Loeser, becomes entirely normal.

If the parietal region of the cerebral hemisphere is stimulated by a very weak current of electricity, movements of the limbs are brought about on the opposite side of the body, and usually also, although to a less extent, on the same side, whereas stimulation of other parts of the cerebral hemispheres produces no such effect (Krawzoff, Kato). No definite localization of motor functions such as has been established in the brains of the higher mammals has yet been worked out.

Thalamencephalon.—Removal of the thalamencephalon along with the cerebral hemispheres results, as before remarked, in an almost complete loss of spontaneous movements. The animal rests quietly, and seldom makes a move unless in response to some external stimulus, and shows a general insensibility to touch (Loeser). Since the optic nerves enter the thalamencephalon, removal of this part causes complete blindness; the frog no longer avoids obstacles placed in its path, or shows any reaction involving the power of vision. When placed on a piece of wood that is slowly tilted upward it will not climb to the upper side and balance there, like a frog that has lost its cerebral hemispheres, but it responds only by movements of the head, lowering that part when the anterior part of the body is raised and raising it when the reverse movement is performed (Steiner, Schrader). If the animal is rotated on a horizontal disk it responds by turning; soon after the operation it shows no compensatory motions; later, it responds by turning the head opposite to the direction of rotation, and, after complete recovery, performs circus movements of the body in the same direction as those of the head. The same movements are also performed after loss of the optic lobes. The loss of the power to balance the body on the edge of a tilted board is apparently permanent.

The Optic Lobes.—According to Steiner the center for coördinated motion is in the optic lobes. Frogs from which this part of the brain was removed were found by Steiner to swim with alternate movements of the legs instead of combined strokes. Schrader showed, however, that this was the result of shock effects, and that frogs carefully operated upon and given time to recover, performed coördinated jumping and swimming movements remarkably well. The center for locomotion cannot, therefore, be located in the optic lobes. Removal of the optic lobes was found by Loeser to produce forced movements, an abnormal retention of urine, and a slight loss of sight, but later these symptoms gradually disappear. Frogs with the brain removed as far back as the medulla locomote normally, perform the croaking reflex, breathe regularly, and show the usual compensatory motions.

The optic lobes exercise an inhibiting influence on the reflex activity of the spinal cord. Removal of the optic lobes results in an increased irritability of the cord, while stimulation of the optic lobes may greatly check spinal reflexes. If one optic lobe is stimulated, the spinal reflexes on the opposite side of the body are inhibited, while those on the same sides are not noticeably affected (Langendorff).

The Cerebellum.—The cerebellum of the frog is so small compared with that of most other vertebrates, that it would not be expected to have an important function. Steiner found that frogs from which the cerebellum had been removed were apparently unaffected by the operation, and other investigators have confirmed this conclusion. Goltz, however, found that coördinated locomotion was disturbed after extirpation of the cerebellum, but, as was admitted later, somewhat more than the cerebellum alone was removed. Recently, however, Loeser has arrived at results similar to those of Goltz. After removal of the cerebellum, according to Loeser, "the jumps became very unsteady and were weakened in force, but not much reduced in rate. Most of the time the frog lay stretched in contact with the floor of the vessel and covered with moss. The unsteady and weakened condition of the limbs persisted in a marked degree two and a half months after the operation (especially when the frog was greatly excited)." It seems not improbable that the discrepant results of the different investigators of this subject may be mainly due to differences in the amount of nervous material removed by the operation.

The conclusion of Goltz that the optic lobes and the cerebellum contain the centers for locomotion cannot be sustained, since Schrader and others have shown that coordinated locomotion is still possible after the cerebellum and all parts of the brain lying in front of it are destroyed. According to Steiner, if the cerebral hemispheres are removed along with the cerebellum, the frog shows certain symptoms that do not appear after loss of the cerebral hemispheres alone. Frogs deprived of both these parts of the brain were found, when attempting to jump from one object to another, either to fall short of the goal, or to jump too far, whereas animals from which the cerebral hemispheres alone were removed were able to adjust more accurately the length of their spring.

The Medulla.—A frog with the brain removed as far back as the medulla is still capable of performing regular leaps and swimming movements of the hind limbs. When thrown on its back it rights itself, and it still performs compensatory motions when tilted or rotated. Breathing is normal, and the animal swallows pieces of food that are placed in its mouth.

If the anterior portion (*pars commissuralis*) of the medulla is removed, the frog becomes possessed of an uncontrollable tendency to move about, whereas if the medulla is intact, the movements of the animal are sluggish. It creeps about restlessly, coming to rest only when it has arrived in some protected nook or corner. Locomotion is effected mainly by creeping, but the frog is nevertheless capable of springing in the ordinary manner. In the water it swims by alternate movements of the limbs. The resting position assumed is not quite normal, the body is more flattened than usual, and the hind limbs are not drawn up to the sides. The breathing and swallowing reflexes are still normal, but the croaking reflex is no longer performed. The reflex of snapping at food is not destroyed, although in the absence of connection with the eyes it is not performed in response to visual stimuli. If a piece of meat is rubbed against the frog's nose, the animal snaps at it and uses the fore legs to stuff it into the mouth. The same reaction may be brought about by using the finger, but after the finger is seized and it is found that the object is too large to be stuffed into the mouth, the frog begins to reject the morsel, and uses the fore legs to push it away. Truly a remarkable combination of reflexes!

The snapping reflex is also brought about by contact with the fore legs, or even other parts of the body. If several frogs, whose brains are cut through just behind the cerebellum, be placed together in a box, they frequently snap at each other when they accidentally come into contact, as if they were defending themselves against attack. Flies creeping over the nose are usually not snapped at, but the stimulus produces another reflex, the fore leg being brought forward to brush the insect away.

The snapping reflex is prevented if the facial nerve is cut, or if the region of the medulla from which the fifth and seventh nerves originate is destroyed. These nerves form the afferent and efferent channls respectively of the nervous impulses involved in the snapping reflex. The extrusion of the tongue, which goes along with this process, is dependent upon the hypoglossus nerve, which has its origin further back in the medulla. Destruction of the root of this nerve prevents the extrusion of the tongue, but the snapping of the jaws may still occur. The two parts of the reflex of seizing food may therefore take place independently, although they are normally almost always associated.

The swallowing reflexes persist after destruction of the center for snapping. They are dependent upon the vagus group of nerves, and disappear only when the region of the medulla is injured from which the roots of the vagus group arise. Normal breathing movements still occur when the medulla is cut across just behind the cerebellum and the parts in front of the cut entirely removed. They are not destroyed if the medulla is also cut across at the tip of the calamus scriptorius, but if the region between these two cuts is removed, respiratory movements entirely cease. This region includes, therefore, the centers for the movements of respiration.

The posterior region of the medulla contains those parts of the brain most essential for the maintenance of life. So long as this region remains, the animal may live for a long time. Removal of the medulla farther back than the pars commissuralis results in making locomotion more difficult, although it is still possible when the brain is cut in two as far back as the tip of the calamus scriptorius. The restlessness of the animal disappears and the body tends to assume an abnormal attitude.

There is no center for coördinated locomotion in the medulla. Disturbances of locomotion begin with the fore limbs. If the medulla is cut across at the tip of the calamus scriptorius, the animal sinks on its breast, and the fore limbs are for a considerable time helpless, although the hind limbs are capable of performing vigorous coördinated movements. The reason for this is that the injury lies so near the region from which the nerves of the fore limbs arise that the movements of these members are very naturally affected.

The Segmental Character of the Functions of the Nervous System.—The functions of the central nervous system of the frog bear out the segmental theory of the action of the higher nerve centers which was first suggested by Schrader and more fully elaborated by Loeb. The nervous system of such forms as worms, crustaceans, and insects consists of a series of pairs of ganglia connected by a double nerve cord, there being typically one pair to each segment of the body; and as a rule each pair of ganglia forms the center of the movements of the parts of the segment in which it lies. Schrader at the close of his paper on the functions of the brain of the frog gives expression to the segmental theory as follows: "The series of experiments we have given teaches us that the central nervous system of the frog can be divided into a series of sections, each of which is capable of performing an independent function. It brings the central nervous system of the frog into closer relation with the central nervous system of the lower forms, which consists of a series of distinct ganglia that are connected by commissures. It speaks against the absolute monarchy of a single central apparatus and against the existence of different kinds of centers, and invites us to seek for the centralization in the many-sided coupling of relatively independent stations."

Loeb has attempted to show that "the more complicated instincts are for the most part nothing but a series of segmental reflexes." "I am inclined," he says, "to recommend using the word chain-reflexes whereby the performance of one reflex acts at the same time as the stimulus for setting free a second reflex. The taking of food may serve as an illustration of such a chain-reflex. The optic reflex of the moving fly produced the snapping reflex; the contact of the mouth epithelium with the fly produces the swallowing reflex. Each of these reflexes is purely segmental. By taking into account the act of transmission, complicated acts can thus be resolved into a few segmental reflexes."

The action of the lower nerve centers is much influenced by the inhibitory action of the parts lying in front of them. That a frog with the optic thalamus or optic lobes removed loses much of its spontaneity is due not to the fact that these parts contain the centers for locomotion, but to the inhibiting influence of these organs on the lower nervous centers. This is shown by the fact that if the brain is removed still farther back so as to include the anterior part of the medulla, spontaneous movements will again make their appearance. One of the most important functions of the higher nerve centers is that of checking the movements of the lower centers that would otherwise occur. In this way the frog's actions are subject to a control which makes them more adequately subservient to the needs of the animal. Locomotion may be effected by the nerve centers of the spinal cord, but when locomotion is set up, and when stopped, and how it is directed are determined by impulses from the higher nerve centers in response to sights, sounds, etc., from the organs of special sense. The higher centers of the brain are comparable to the captain of a steamer who issues orders to the man running the engine when to start and when to stop, and who has his hand on the wheel so as to guide the course of the vessel. The machinery of locomotion works away by itself, but it works blindly. The captain sees and avoids the obstacles in the way and determines the direction and the limits of the journey. In a similar manner the reflex machinery of the lower nerve centers of the frog is guided by those parts whose organs of sense put them into more intimate connection with the outer world.

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CHAPTER XVII

THE SENSE ORGANS

The sense organs are the means through which stimuli are received from the outer world. They are always connected with the central nervous system by nerve fibers which carry the impulses derived from the various objects in the environment which act upon the organism. The sense organs in general are specialized so that they are exceedingly sensitive to certain forms of stimulation, and but very slightly so to others. The eye is affected ordinarily only by light, the auditory organ only by sound, the olfactory organ only by contact with certain substances. The specific functions of the sense organs are determined by their structure, each being specialized in relation to some particular source of stimulation from the outside world.

Sense Organs of the Skin.—The skin is richly supplied with sensory nerve endings both in the epidermis and in the corium. The epidermis is supplied by fine fibers which repeatedly branch and form a sort of network between the cells. The free ends of the ultimate branches are often enlarged into a disk (Retzius). The corium contains special end organs, the so-called *touch corpuscles*, which lie under small papillæ of the epidermis. Each touch corpuscle is composed of a small heap of flattened cells between which are found the terminal branches of the nerve with which each organ is supplied. The temporary papillæ of the female of *Rana fusca*, according to Huber, possess a structure in some respects resembling that of the touch bodies.

The skin of the frog is an organ of unusual sensibility. It is sensitive not only to touch and chemical stimuli, but it is affected in no small degree by light. A. H. Morgan has shown that the frog's foot reacts differently to warm and to cold water, and that the reactions are destroyed by removing the skin of the foot. Not improbably it has different sense organs for heat and cold. The skin is also readily influenced by changes in the moisture of the air, as is indicated by the behavior of the animal under different conditions of the atmosphere.

Fig. 104.—Touch corpuscle of the frog with its supplying nerve. The branches of the nerve may be seen ramifying between the flattened cells of the sense organ. (From Gaupp, after Merkel.)

Sense Organs of the Mouth.—In the mouth there are in addition to the nerve endings in the general epithelium numerous sense organs which have been supposed to be concerned with the sense of taste. They occur on the flattened surfaces of the fungiform papillæ of the tongue and also on the floor and roof of the mouth, where they assume a more rounded form although possessing essentially the same structure in both regions (Bethe). The surface of these organs is covered by cylindrical epithelial cells between which are scattered various forms of elongated cells which are connected usually by means of branching processes, with the ramifications of the supplying nerve.

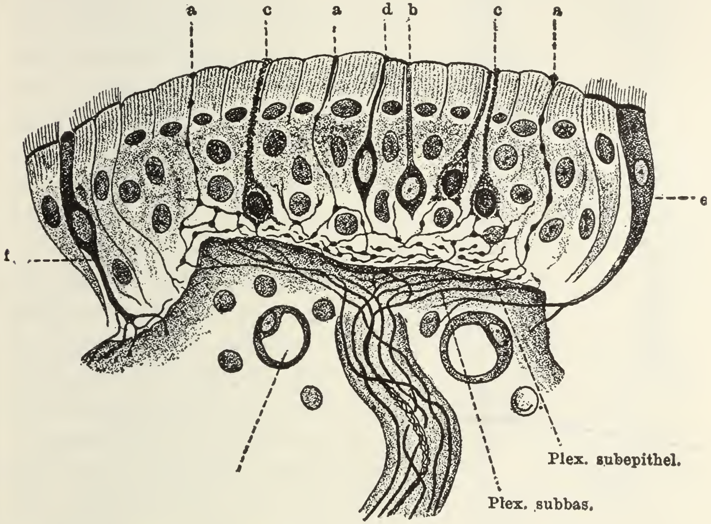

Fig. 105.—Section through a fungiform papilla. A bundle of nerve fibers enters the papilla from below, breaking up into first the subbasal plexus, and second the subepithelial plexus around the bases of the cells of columnar epithelium. The latter plexus forms connections with the branches of the sensory cells. *a*, free nerve endings; *b*, *c*, *d*, nerve cells; *e*, *f*, cells connected with the subepithelial plexus. (From Gaupp, after Niemack.)

The Olfactory Organs.—The seat of smell is in the nasal cavity, the walls of which are supplied with the olfactory nerves. The nasal cavity is lined by a mucous membrane which is composed of a connective tissue substratum and an outer layer of olfactory epithelium. In the regions to which the olfactory nerves are distributed the epithelium consists of three kinds of cells: (1) *interstitial cells,* which are very much elongated and cylindrical in form; (2) *basal cells* (Krause), which are of stellate form and lie next to the connective tissue; and (3) the *olfactory cells.* The latter, which represent the true sensory cells, are very variable in form. They are usually very long and narrow, much swollen out where the nucleus occurs, and furnished at the outer free end with a tuft of fine cilia. At their inner ends they are drawn out into a fine process which is connected with the olfactory nerve.

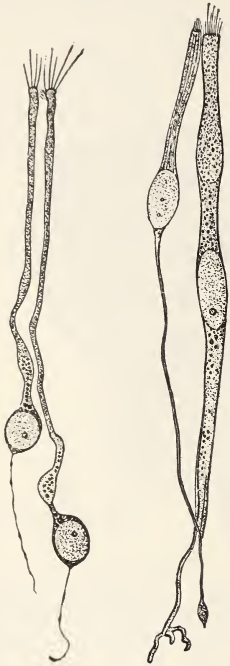
FIG. 106.—Cells of the olfactory epithelium. On the left two sensory cells with ciliated outer ends, enlarged nuclei, and fine basal fibers. On the right two interstitial cells. (After Dogiel.)

Knauer found that ill-smelling substances held near the nostrils caused the frog to turn away the head, but whether the olfactory sense plays an important rôle in the life of the animal is not known.

The Eyes.—The eyes of the frog are nearly spherical in form, and they are lodged in large cavities in the sides of the head called the orbits, within which they are freely movable. The outer or exposed portion of the eye is covered by a transparent membrane known as the *cornea;* the remaining portion, which constitutes about two thirds of the surface, is formed by the *sclerotic coat.* This is an opaque, white covering mainly inclosed within the orbit; it is composed of an outer fibrous membrane, and an inner layer of hyaline cartilage; on the side next to the cranium it is perforated by an aperture; the *optic foramen,* through which the optic nerve enters the eye.

At its outer margin the cornea is continuous with a membrane, the *conjunctiva,* which passes backward a short distance (about 2 mm.) over the sclerotic, and is then reflected over the inner surface of the upper and lower eyelids. The *upper eyelid* is a narrow, thick fold extending from the upper edge of the orbit. It has no power of independent motion, but may be raised or lowered by the movements of the eyeball. What appears as the *lower lid* is really made up of two elements, the lower lid proper, and the *nictitating membrane.* In most animals these folds are quite distinct, but in the frog the nictitating membrane is continuous with the upper portion of what corresponds to the true lower eyelid of other forms. The lower lid consists of a lower thick portion and an upper thinner part, which is folded in behind the former when the eye is uncovered. The nictitating membrane is a thin semilunar fold somewhat more transparent than the upper portion of the lower eyelid, from which it is separated by a slight furrow. At the anterior and posterior ends of its slightly thickened upper margin it is attached to the two ends of a tendon which passes behind the eyeball, thus encircling the greater part of the eye. The closing of the eye of the frog does not occur through the independent movements of the eyelids as it does in ourselves, but is a consequence of the retraction of the eye within the orbit. If one watches the closing of the eye of the frog, it will be seen that every time the lids are drawn together the eye sinks into the head. The withdrawal of the eye by producing a tension on the tendon of the nictitating membrane causes the latter to be pulled up, although one might easily gain the impression that the eye is pressed into the head by the closure of the lids. The opening of the eye, on the other hand, while generally accompanied by the protrusion of the eyeball through the contraction of the *levator bulbi* muscle, is partly effected by means of an independent muscle, the *depressor membranæ nictitantis.* In the closure of the eye the lower lid and nictitating membrane are pulled over all but a small part of the exposed surface.

Through the transparent cornea may be seen the colored *iris,* in the center of which is an oval aperture, the *pupil.* Just behind the pupil lies the transparent *crystalline lens,* which, unlike the lens of higher animals, is of a nearly spherical form, although somewhat more flattened on the anterior face. It is made up of concentric layers like the coats of an onion. On its outer surface is a single layer of epithelial cells, the remaining portion consisting of transparent fibers whose general direction is parallel with the optical axis of the eye. The whole lens is surrounded by a very delicate transparent capsule which is attached along the outer margin to the ciliary body by means of radiating fibers.

The cavity of the eye is divided by the lens and its supporting fibers into an outer chamber which contains a transparent watery fluid, the *aqueous humor,* and a larger inner chamber filled by a more solid transparent substance known as the *vitreous humor.* The vitreous humor is permeated by numerous fibers which form a sort of supporting network which contains free cellular elements and numerous blood vessels. The circulation in the latter as seen by the ophthalmoscope has been described by several observers and with especial fullness by Hirschberg and Schleich.

The wall of the posterior chamber of the eye is formed of three tunics, the *sclerotic coat,* which has been described above, the *choroid,* and the *retina.* The *choroid* is a vascular, pigmented layer lying next to the sclerotic. Next within the choroid lies the *retina* which is continued anteriorly over the posterior surface of the iris as far as the pupil. It is composed of two principal layers, an outer thin layer of pigmented cells, and an inner much thicker layer which forms the sensitive portion of the retina. Over the ciliary body and posterior side of the iris the retina is much thinner than it is elsewhere and does not contain nervous tissue. The optical portion of the retina which lines the whole posterior region of the eye and extends as far forward as the ciliary body, is a complex structure formed mainly of nervous elements. It is the part of the eye which is especially sensitive to light and upon which images of external objects are thrown. In addition to the outer pig-

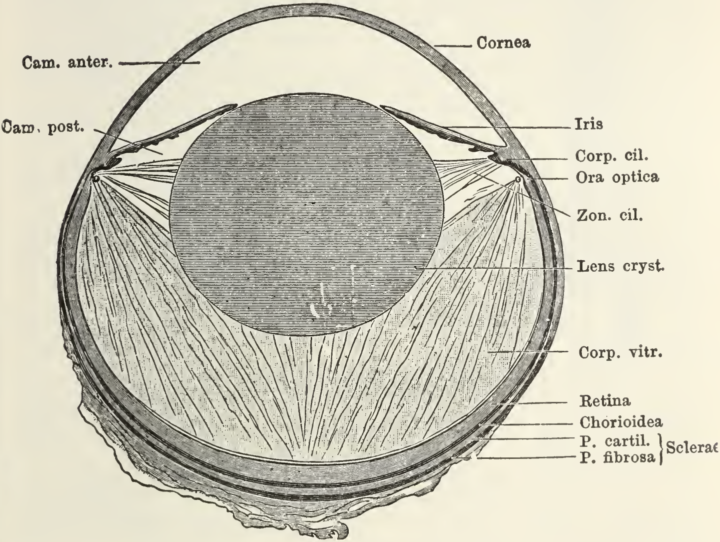

Fig. 107.—Section through the optical axis of the eye of the frog. *Cam.anter*, outer chamber containing the aqueous humor; *Cam. post*, inner chamber containing the vitreous body; *Corp.cil*, ciliary body; *Corp.vitr*, vitreous body; *P.cartil*, and *P.fibrosa Scleræ*, cartilaginous and fibrous layers of the sclerotic coat; *Zon.cil*, zonula ciliaris. (From Gaupp, after G. Retzius.)

mented epithelium it is composed, as in the higher vertebrates, of nine layers, the latter forming the inner or thicker stratum of this structure. These layers taken in order from within outward are as follows:—

1. The *inner limiting membrane,* a thin supporting membrane lying next to the vitreous humor. It is connected with elongated cells (Müller's fibers) which extend to the outer limiting membrane and give off branches which form a sort of supporting network for the nervous elements of the retina.
2. A layer of *nerve fibers,* formed by the ramifications of the optic nerve.
3. The *inner ganglionic layer,* formed by comparatively large ganglion cells whose processes extend into the preceding and following layers.
4. The *inner reticular layer,* formed by a network of nerve fibers.
5. *The inner nuclear layer,* composed of several layers of ganglion cells whose processes extend into both of the adjacent layers.
6. The *outer reticular layer,* a narrow layer formed by a network of nerve fibers derived from the inner nuclear layer and the layer of rods and cones.
7. The *outer nuclear layer* contains the nucleated portions of the cells forming the rods and cones and a few isolated ganglia.
8. The *outer limiting membrane,* a very thin supporting membrane, perforated in numerous places by the cells of the outer layer.
9. The layer of *rods* and *cones.*

The latter layer lies next to the pigmented epithelium of the retina, and processes from the pigmented cells extend between the rods and cones. It forms the receptive surface of the retina, although the light must pass through all of the other layers before reaching it. The rods, which are larger and more numerous than the cones, are very much elongated cells; their outer ends are cylindrical and show a cross striation which marks their division into transverse disks, into which they may be separated by treatment with certain reagents. Behind the cylindrical portion comes a lens-shaped, refractive body with a flat inner and a very convex outer surface. The nucleus lies in the part of the cell on the inner side of the outer limiting membrane. The inner end of the cell tapers into a fiber which extends into the outer reticular layer. The rods are of two kinds, the red and the green. The former are more abundant and have a much longer cylindrical segment, which is permeated by a peculiar reddish purple pigment which is known as *visual purple.* The green rods have a short, cylindrical segment which is followed by an elongated narrow neck; the cylindrical portion contains a green substance (*visual green*).

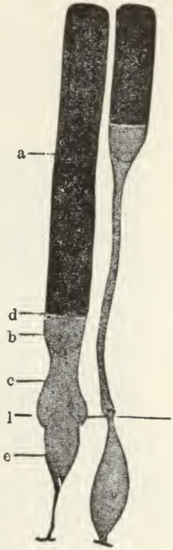

FIG. 108.—Rods from the retina of the frog: a green rod on the right, a red one on the left. *a*, outer segment; *b*, refractive body; *c*, inner segment; *d*, intermediate disk; *e*, inner enlargement containing the nucleus; *l*, external limiting membrane. (From Gaupp, after Greeff.)

The cones have a conical outer segment which shows a cross striation like the corresponding portion of the rods. This is followed by a refractive lens-shaped body, beyond which the cone becomes constricted. The nucleus lies in an enlargement on the inner side of the outer limiting membrane. The inner end of the cone, like that of the rods, runs out into a fiber which enters the outer reticular layer. The cones vary in size and form, as many as three varieties being distinguished (M. Schultze, van Genderen Stort). Some of these are movable, expanding in the dark until they may reach the periphery, and contracting under the influence of light. Ordinarily most of the cones do not reach the outer surface of the retina.

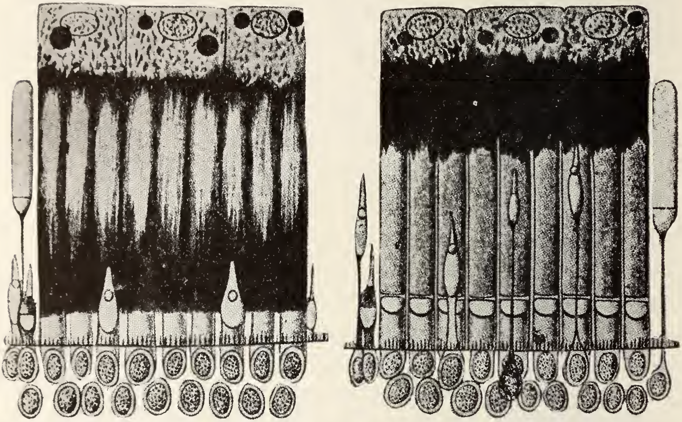

FIG. 109.—Sections through the outer part of the frog's retina with its pigmented epithelium. The figure on the left is taken from a frog which had been exposed to daylight for five hours. The processes of the three outer pigment cells extend inward to the external limiting membrane, and the pigment they contain has streamed inward, surrounding the rods and cones nearly to their base. The cones are strongly retracted, so that their outer segments lie near the limiting membrane. The figure on the right is taken from a frog that had been kept for forty-eight hours in darkness. The pigment in the processes of the pigment cells is drawn back toward the center of the cells, and the cones are extended outward between the rods. The nuclei of the rod and cone cells are shown below the limiting membrane. (From Gaupp, after Van Genderen Stort.)

The retina is marked by a thickening or papilla where the optic nerve enters. Above this papilla there extends in an antero-posterior direction a thickened portion of the retina known as the *area centralis,* which probably marks the region of most acute vision, like the yellow spot in the eye of man. The cones are relatively more numerous in this region than in other parts (1 c. : 2.4 r. instead of 1 c. : 3 or 4 r., as elsewhere), and the rods are of relatively small size.

The action of light upon the retina results in the production of several visible changes. In addition to the contraction of the cones which has been mentioned above, there is a bleaching of the pigment in the outer ends of the rods; this takes place more rapidly in the visual purple than in the green pigment. After a short exposure in the dark both pigments are restored, even in the extirpated eye. It is probable that the chemical changes produced in the retinal pigments through the influence of light, play some part in the stimulation of the sensitive cells. Light also affects the cells of the outer pigmented layer of the retina, causing the

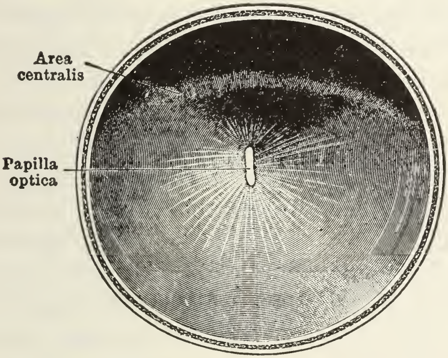

Fig. 110.—Inner surface of the inner half of the eye of *Rana esculenta,* showing the area centralis as a light-colored band above the papilla optica where the optic nerve enters. (After Gaupp.)

pigment to stream out into the processes which extend between the rods and cones. With intense illumination the pigment may spread as far as the inner limiting membrane, in from ten to fifteen minutes, which is about the time which it takes the visual purple to disappear under the same conditions (Boll, Angellucci).

The amount of light falling upon the retina is regulated by the iris which acts as a sort of screen or curtain, admitting the rays only through its central aperture, the pupil. The iris lies directly in front of the lens. Its outer margin is joined to the ciliary body behind and the juncture of the sclerotic and cornea in front. It contains numerous black pigment cells and several golden ones which give it its bright yellow spots. Near the margin of the pupil there is a ring of smooth muscle cells forming a *sphincter pupillæ* which causes the pupil to contract. Strong light causes a contraction of the pupil and consequently a diminution of the amount of light that falls on the retina, thus checking the excessive stimulation of the sensitive part of the eye. This effect is produced, at least in part, through the direct action of the light upon the muscle cells of the iris, since it occurs in eyes that have been removed from the body (Steinach, Guth).

The optical arrangements of the eye of the frog are such as to throw images of objects upon the retina. The sensitive surface of this layer is thereby stimulated and impulses carried through the optic nerve to the brain, there giving rise to sensations of sight. The eye of the frog has no power of accommodation for viewing both near and distant objects such as our own eyes have. The lens cannot either be changed in form or brought nearer to or farther from the retina, so that only objects are in focus which are at a particular distance from the eye. Images of objects at other distances are not clearly outlined, and there consequently results imperfect vision. In the air the frog is myopic, or near-sighted (Plateau, Hirschberg, Beer); *i.e.* it can see clearly only objects which are near at hand. In the water, on the contrary, it is hypermetropic, or far-sighted. The myopia of the frog is evidently an advantage to the animal in securing food, as it is important to see clearly objects which are sufficiently near to be snapped at. It is evident that the frog responds to the perception of movement much more than of form, and for that purpose images which are somewhat indefinite and blurred will suffice. Large moving objects mean enemies, and consequently the necessity of getting out of the way, even if there be no clear perception of the outline or the distance of the portentous creature that is coming.

NB

The frog can be said to possess the power of binocular vision only in a very small degree, since, owing to the fact that the eyes are so laterally situated, their fields of vision overlap anteriorly only to a very slight extent.

The eyes may be moved in various directions by means of special muscles. Four of these are the straight or *recti* muscles,—a *superior,* an *inferior,* an *anterior* or *median,* and a *posterior* or *lateral rectus* muscle, which roll the eyeball upward, downward, forward, and backward respectively. There are two *oblique* muscles, the *superior oblique,* which rotates the eye around its optic axis so that its upper margin turns forward, and an *inferior oblique,* which produces the reverse movement. The eye is pulled into the orbit by means of the strong *retractor bulbi* muscle, which arises from the angle between the lateral and median portions of the parasphenoid bone and is broadly inserted upon the posterior and median sides of the eyeball. The eye are pushed outward by the contraction of the *levator bulb* a broad sheet of muscle running obliquely across the ventr side of the orbit.

The Ear.—In the ear of the frog there are two sets of organs which are fundamentally different in origin and in function. The one constitutes the *inner ear* which forms the sensory apparatus; the other, the *middle ear,* being composed of accessory structures for the transmission of sound waves to the sensitive part of the organs.

The inner ear is composed of the membranous *labyrinth,* which lies within the auditory capsule, which is formed by the proötic and exoccipital bones of the skull. The labyrinth is a complicated sac formed originally by invagination of the ectoderm of the surface of the body from which it is subsequently constricted off. It is divisible into an upper portion, the *utriculus,* and a lower, smaller part, the *sacculus.* The former is an oblong sac lying nearly horizontal. It gives rise to the three *semicircular canals,* which lie in planes approximately at right angles to each other. These canals are membranous tubes embedded within the cartilage of the auditory capsule and communicating with the utriculus at each end. There is an anterior canal which lies in a vertical plane, a lateral canal which lies in a nearly horizontal plane on the outer side of the utriculus, and a posterior canal which extends transversely nearly at right angles to the two others. At one end each of the canals is furnished with an enlargement, or *ampulla,* which contains an important sensory apparatus.

The *sacculus,* or lower division of the labyrinth, is an irregular oval sac which projects downward and forward from the utriculus, with which its interior is connected through an aperture. There are four small outpocketings from the base of the sacculus, and from the median side there is given off a narrow tube, the *ductus endolymphaticus,* which extends dorsally where it penetrates the cranial cavity and ends in a large sac, the *saccus endolymphaticus.*

which is filled with a milky white fluid containing numerous white crystals of carbonate of lime. The utriculus, the sacculus, and the larger outpocketings of the latter contain masses of similar crystals which are commonly called the *otoliths.*

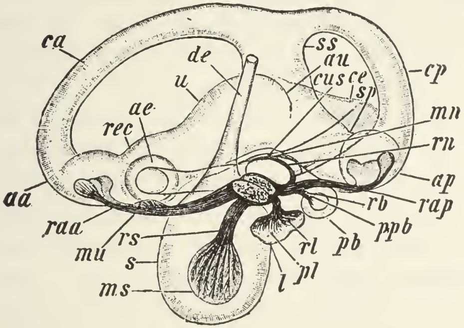

FIG. 111.—Right membranous labyrinth of the frog from the inner side. *aa, ae, ap,* anterior, external, and posterior ampulla; *au,* aperture of utriculus; *ca, ce, cp,* anterior, external, and posterior semicircular canals; *cus,* utriculo-saccular canal; *de,* ductus endolymphaticus; *l,* lagena; *mu, ms, mn,* macula acustica of the recessus utriculi, sacculus, and pars neglecta respectively; *pb,* pars basilaris; *pl, ppb,* papilla acustica lagenæ and basilaris; *raa, rap, rs, rn, rl, rb,* branches of auditory nerve to anterior ampulla, posterior ampulla, sacculus, macula neglecta, lagena, and pars basilaris respectively; *s,* sacculus; *ss, sp,* sinus utriculi superior and posterior; *u,* utriculus. (After G. Retzius.)

The different parts of the ear are all supplied by the branches of the auditory nerve. In the regions of the nerve endings the epithelium contains sensory cells with hairlike processes at their outer ends. These are especially abundant and well developed in the walls of the ampullæ. The whole labyrinth is filled with a fluid called the *endolymph,* and it is surrounded by another fluid, the *perilymph,* which fills the space between the labyrinth and the wall of the auditory capsule. On the outer side the wall of the auditory capsule is perforated by an aperture, the *fenestra ovalis,* which is closed with a small plug of cartilage.

The accessory auditory apparatus consists of the structures which in higher forms constitute the middle ear, there being nothing in the frog which corresponds to the external ear of mammals. The cavity of the middle ear communicates through the Eustachian tube with the mouth cavity near the angle of the jaw. It is closed externally by the *tympanic membrane,* which is readily seen at the side of the head behind the eye. This membrane is nearly circular in form and is attached by its outer margin to a ring of cartilage, the *annulus tympanicus.* Near its middle it gives attachment to the outer head of a rod, the *columella,* which extends across the cavity of the middle ear, and joins the small cartilage lying over the fenestra ovalis. It is through this rod that the vibrations which are produced by the sound waves impinging upon the tympanic membrane are carried to the inner ear. Here they set the contents of the labyrinth into vibration and thus stimulate the sensory end organs of the auditory nerve. The nervous impulses set up in this way are conveyed to the brain, where they give rise to the sensation of sound.

The ear is not only concerned in the perception of sound, but it has a very important function in the relation to the maintenance of equilibrium. Removal of the labyrinth on both sides of the body is followed by loss of ability to maintain an upright position. Frogs upon which this operation is performed no longer balance themselves on a tilted board so readily as a normal frog will, and when thrown upon the back, they lie there for a long time, and finally right themselves, if at all, only with the greatest difficulty (Goltz). They are able to swim through the water in a tolerably straight course, but very frequently with the ventral side up, which a normal frog does not do (Breuer).

When stimulated, they jump about irregularly and move the fore and hind legs in a disconnected and uncoördinated manner (Girard, Ewald). According to Girard and Schrader there is a complete loss of compensatory motions, but this is disputed by Steiner. If the labyrinth is destroyed only on one side, the frog takes an asymmetrical attitude. If the operation is performed on the left side, the head is slightly inclined to the left, the right fore limb is held straighter than the left (Girard), the body is bent toward the operated side, and the right hind foot is more extended than the left and seldom drawn up to the body (Ewald). The same attitudes are assumed, according to Ewald, for a year after the operation.

After injury to one of the horizontal canals, the frog tends to move in a circle; injury to the vertical canals causes abnormal movements in a vertical direction (Hensen).

If the otoliths are removed from both of the auditory organs, the behavior of the frog, according to Ach, differs from that of a normal individual in several particulars. If the brow of the injured animal is rubbed with the finger, the creature will close its eyes, bow down its head, elevate its back, and remain in this attitude, with its muscles in a state of tonic contraction often for half an hour. A normal frog of the species experimented with (*R. esculenta*) does not show this response except in a slight degree, and then only after it has become fatigued. Frogs devoid of otoliths were found to utter the so-called "pain cry" upon slight provocation, whereas this response is rarely elicited from normal specimens. Locomotion may take place in a normal manner, but the muscular tonus seems to be low, and the animal quickly becomes fatigued. The compensatory motions are unaffected.

Frogs have a well-developed sense of hearing, although they do not usually manifest it by any clearly evident sign.

In croaking, one frog frequently responds to the croak of another individual, so that one often hears a pair answering each other by regularly alternating notes. If, after a concert of frogs has been silenced by some one who intrudes too near their haunts, one individual ventures to resume its croaking, it is speedily followed by one after another of its comrades. Landois tells of a tree frog which he kept in captivity which would give an answering cry every time that he would imitate its note. Yerkes observed that when he caused a frog to croak by rubbing its sides, the other frogs under observation occasionally gave signs of attention by straightening up and raising the head as if listening. The same observer noticed, when carrying on experiments with frogs in a labyrinth, that the animals often gave signs of hearing the sound made when other individuals jumped into the water. They would "straighten up and hold the listening or attentive attitude for some seconds. As the animals could not see one another, there is good evidence of their ability to hear the splash made by a frog when it strikes the water." This, according to Yerkes, explains the fact that "it is never possible to get near to any frogs in the same region after one has jumped in." The splash sound is significant to them and puts them on their guard.

On the other hand, many other sounds, varying greatly in loudness and pitch, do not elicit any marked response. "One may approach to within a few feet of a green frog or a bullfrog and make all sorts of noises without causing it to give any signs of uneasiness. Just as soon, however, as a quick movement is made by the observer, the animal jumps. . . . Sounds like the splash of a plunging frog, or the croak or pain scream of another member of the same species, serve as warnings, but the animals do not jump into the water until they see some sign of an unusual or dangerous object."

It must not be inferred that frogs do not hear a great variety of sounds simply because they give manifest signs of attending to only a few sounds in which they have some particular interest. Yerkes found that frogs which give no other signs of perceiving sound, show a difference between the rates of their respiratory movements before and after the sound is made. The sound of a tuning fork, falling water, a shrill whistle, the ringing of a bell, and other noises were employed. Some of these produced little or no effect. The shrill whistle and the ringing of a bell caused a decrease in the rate of respiration, owing perhaps to fear, while the sound of falling water caused the rate of respiratory movements slightly to increase. The green frog (*Rana clamitans*) was found to respond to sounds varying in pitch between fifty and ten thousand vibrations per second.

The reaction time of frogs to visual stimuli is also influenced by sound. Yerkes found that frogs which were placed in a glass aquarium so surrounded that the movements of the observer could not be detected, would jump vigorously at a small red card which was moved near them. If a tuning fork was sounded just before the card was presented, it "became evident that the sound put the frog on the alert, and, when the object came into view, it jumped at it more quickly and a greater number of times than when the visual stimulus was given without the auditory. . . . When the red card was shown, it was often several seconds before the frog would notice it and attempt to get it, but when the sound also was given, the animal usually noticed and jumped toward the moving card almost immediately." It is probable that this habit of getting into readiness for a spring upon hearing a sound near by is of value to the frog, since insects and other creatures that serve as food often manifest their presence by some sort of noise before they come into the frog's field of vision. If the frog prepares himself he is more apt to seize his prey when it appears.

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CHAPTER XVIII

INSTINCTS AND TROPISMS AS RELATED TO REFLEX ACTION

We have already treated of some of the reflex actions of the frog and have shown that they exhibit a purposive character, often in a very striking degree. They are far from being mere random responses to stimuli, notwithstanding the fact that they may take place independently of intelligent control. It is generally recognized that there is a close connection between reflex actions and instincts, it being, in fact, very difficult to draw the line between them. The behavior of an animal is usually called instinctive when it takes place without previous instruction and with no consciousness of the end to which it is directed. A digger wasp, for instance, makes a nest of a particular type in the ground, catches only certain species of insects, which it stings in the ventral ganglia, so as to produce paralysis without causing death, and, after depositing an egg upon its prey, buries it in the nest as provision for its future offspring. The wasp is utterly unaware of the significance of its complex behavior; of the wriggling grub which it has labored so industriously to provision it knows nothing and cares less; it is impelled by blind impulses to a particular line of activity, which, although of no service to the individual wasp, is essential to the continuance of the race. It is guided neither by previous experience nor by imitation, and has no basis for drawing any conclusion regarding the utility of its conduct, even were it capable of so doing.

Such behavior affords a typical illustration of instinct; and throughout the animal kingdom it is instinct which is the dominant element in conduct.

The behavior of the frog is almost entirely made up of instinctive actions. Nature has equipped this animal with the means of getting through the world without relying, to any great extent, upon the lessons of experience. The frog has intelligence of a rudimentary sort, to be sure, but it plays a very subordinate rôle in directing the creature's activities. It is truly a marvelous thing that an animal should be endowed with the power of successfully adapting its conduct to a complex environment without any perception of the consequences of its actions. How can the existence of such a power be explained, or brought into relation with our knowledge of the other features of the animal's life?

It was formerly customary to regard instinct as a property *sui generis,* something having no necessary affiliation with the other functions of the organisms, a sort of power with which animals are mysteriously endowed for their guidance. It is but another illustration of the effect of increasing knowledge in bringing different fields of biological inquiry into closer and more organic connection that the instinctive behavior of animals is now shown to be intimately connected with their structure and physiological activities. Instinct is but a phase of the general life process, exhibiting the same purposiveness that is shown in the activities of the heart or alimentary canal. All parts of the body are continually responding to stimuli in ways that are beneficial to the organism. When the stomach pours out its secretion and begins its peristaltic movements upon the receipt of food and allows the material when digested to escape through the pylorus, it is performing actions which we do not commonly call instinctive, but which are as well adapted to the end achieved as the diving of a frog upon the approach of an enemy, or its burrowing into the mud in cold weather. All of these actions are adaptive responses to stimuli. Those of the stomach we call reflex acts, while the diving and burrowing into the mud are usually called instincts. The chief distinction between the two is that the one involves the action merely of a part, while in the other there is a response by the organism as a whole. There are so many intermediate types of reaction, however, that it is no easy matter to decide how some of them should be classed. If a frog withdraws its foot when its toe is stimulated, we call the act reflex, but how shall we designate the act of bringing the foot forward to wipe away a drop of acid from the side of the body? As we have seen, the latter act may be performed by a frog whose spinal cord is cut across near the brain; if, therefore, we call the action reflex, what shall we say of the struggles of a frog when, after being picked up in the fingers, it uses both hind legs to push against the hand, and at the same time inflates the lungs with air, causing the body to swell? These struggles to escape will take place in a frog which has lost the greater part of its brain, but nevertheless, they would, I think, generally be regarded as instinctive actions. The use of the hind limbs and the swelling of the body may be regarded as two complex reflexes excited by the same cause. The frog is so organized as to respond to seizure by two methods which coöperate to effect its escape, both of which are reflexly brought into play.

Many of the more complex instincts of the frog may be resolved into a series of reflex acts. We have seen that the tendency of the male frog to clasp the female during the breeding season depends upon the reflex irritability of the brachial region of the spinal cord. It is a tendency independent of the higher nervous centers, and it is brought about by certain changes that take place in the organism during the spring, probably as an indirect result of the ripening of the sexual products.

Most of the things that the frog does fall into a comparatively few categories. Its actions do not show an indefinite diversity like those of an ape or a human being. It uses its hind limbs, for instance, in leaping and swimming, and occasionally for pushing against some object or removing an irritating substance from the skin. The two former movements are much alike and the two latter both consist in bringing the legs forward to the point of stimulation. The legs of a frog are not moved about in a great variety of ways for different purposes like the arms of a man. They have a few simple tricks which they are admirably adapted to perform, but beyond these the range of their powers is very limited. The same is true of the fore legs, the head, and the body as a whole. Movements of the fore and hind limbs may be combined in various ways, as in leaping, diving, crawling, burrowing, righting movements, but the number of combined actions employed is much less than in higher forms. The frog is a sort of mechanism beautifully adapted to the performance of a number of actions, but its repertoire is not at all extensive, and it has little power of improvising new rôles. Its modes of response are dependent upon the way it is organized, for as a machine is constructed so will it work. A frog is as incapable of leading a life like that of a cat as a machine made for grinding corn is incapable of weaving cloth or printing books. Its kind of life is laid out for it by the forces that have shaped its bodily structure.

Reactions to Light.—In addition to responding to various objects of sight, frogs react to light in a very peculiar manner by placing their bodies so that they face the region of strongest illumination; frequently also they move toward it. Animals which orient themselves to light in this manner are said to be *phototactic* or *heliotropic*. Those which move toward the light are called positive; those which move away from it negative. This orientation is generally regarded as brought about in a reflex manner through the unequal stimulation of the two sides of the body, either through the eyes or other parts of the organism. When the body is oblique to the rays, it receives more stimulus from the light on one side than the other, and if the light has any directive effect upon the animal's movements, it will naturally cause the body to turn until equally illuminated on the two sides; then, as both sides receive the same amount of stimulation, the animal tends to go either toward or away from the light in a straight line.

Graber, who experimented with *Rana esculenta,* came to the conclusion that this species is negatively phototactic. The specimens were placed in a box in which were two compartments, one of which was darkened while the other was exposed to diffuse daylight. The animals showed a tendency to collect in the darker of the two compartments. If the frogs were given a choice between red and blue, they collected under the red light.

The responses of *Rana pipiens* and *R. clamitans* to light have been studied by Miss Torelle, who arrived at results quite different from those of Graber. Frogs placed in a box one half of which was exposed to diffuse light, while the other half was shaded, moved into the light end of the box and oriented the body so as to face the incoming rays. When one half of the box was exposed to direct sunlight, the frogs first moved into the illuminated area, and then, after a short time, retreated into the shade, where they sat with their heads pointing toward the light. The same result occurred when the heat rays were eliminated by passing the light through a vessel of water before it entered the box, showing that it was not the heat alone that caused the frogs to retreat into the shade. If light be admitted from below, which may be done by making the floor of the box of glass, the frogs leap into the lighted area as before. If the whole lower side of the box be exposed, the animal takes a normal resting position, but if a half or two thirds of it be covered, the frog moves toward the light and the body assumes a greater angle to the horizontal, the angle increasing, the smaller the area through which the light enters. When light is thrown upon the frog from above, the anterior part of the body becomes raised. Miss Torelle found that when a frog was placed in a tall glass cylinder the bottom and sides of which were covered with black cloth, "the body was raised so that the fore legs were as nearly as possible at right angles to the horizontal bottom of the jar. This made the inclination of the body 60° or over. Frequently the frog assumed an almost erect position, by means of placing the fore feet against the side of the jar."

As these and other experiments show, the frog has a strong tendency to place its body so as to face the light; yet notwithstanding its marked orienting response, it manifests a strong proclivity to seek the shade. Frogs placed out of doors, near the shadows of trees or buildings, soon hop into the shade and remain there even if they have to travel at right angles to the rays of light. Miss Torelle tried the experiment of placing dark objects in the vicinity of the frog to find if the animal showed any tendency to approach them. "The side of a large wooden box was covered with black cloth, and the frog placed near the black perpendicular surface. It hopped close to this, remained a couple of minutes, then moved close to the wall of the gray-colored building, where it remained at rest in the angle formed by the wall and the ground. When placed near the uncovered box (pine) on the side in full sunlight, there was no movement toward it. When the box was raised on one edge and propped, so that the other edge was about four inches from the ground, the frog moved toward the shadow thus formed, crept well under the box, placed its body between the floor and the ground, where it remained with its head directed outward. A black cloth was fastened close to the ground in the center of a sun-illuminated area, and a frog placed near it moved on to it, crept along the edge as if seeking cover, then hopped off. A second frog also hopped on to the cloth, but almost immediately moved off. Apparently a dark surface, brightly illuminated, does not produce the effect of a shadow or of diffuse light." It may be, however, that frogs are attracted to such surfaces just as they are to shadows, but finding different conditions of stimulation when they get there they do not remain.

It is clear that the frog manifests two quite different responses in its behavior toward light. The orienting response, in which the animal puts itself in line with the direction of the rays, affords a good illustration of phototaxis. The proclivity to seek and rest in the shade is more nearly akin to what is commonly called *photopathy.* Under ordinary conditions the frog may be considered as positively phototactic, but negatively photopathic. Many animals collect in the shade, not because they are negatively phototactic, but because when they happen to reach the shade in the course of their moving about, they come to rest there. The collection of frogs in shady spots may be partly explained in this way, but there appears to be also a perception of shaded regions at a distance and a tendency to make for them, which is not merely a matter of photopathy as that term is usually employed. It is possible that the latter peculiarity is not a primary instinctive response, but a habit acquired by experience. It is known that the frog is capable of forming simple associations, and it may learn in the course of its experiences with light and shade to connect moving toward the latter with a sense of comfort or respite from the disagreeable effects of strong light.

The reactions of the frog to light are influenced by temperature to a marked degree. At 25° C. the positive response becomes considerably accelerated, the frog moving more quickly and more directly toward the light end of the box. Above 30° C. the movements become irregular, owing to the predominant effect of heat. When the temperature is lowered, the positive reaction becomes less decided, and according to Miss Torelle, when a temperature of 8° C. is reached, the animal becomes negatively phototactic both in air and in water. The evidence cited in favor of this conclusion is, however, not convincing, inasmuch as other reactions, such as the tendency to dive downward and to crawl under objects, are evoked when the temperature is lowered to this point. These relations were brought about both when light came in from above the aquarium, and when the top and the upper two thirds of the aquarium were covered by an opaque cloth.

As in most animals thus far investigated, it is the blue and violet rays that are the most influential in evoking the phototactic response; the effectiveness of the other colors of the spectrum diminishes in order from blue to red. Miss Torelle found that if frogs are placed in a box illuminated through one end with blue light and through the other with red, they soon gather at the blue end. If they have the choice between yellow and green, they go toward the green; in general it may be said that where they are able to go toward one of two colors of equal intensity they move to the color lying nearest the violet end of the spectrum. The same conclusions were drawn by Pearse who experimented upon *Rana palustris* and Bufo.

The eyes would naturally be regarded as the organs through which the phototactic response is effected, and in fact they play an important part in the process, but, as has been shown by Parker and by Pearse, orientation may be brought about merely by the photic stimulation of the skin. In order to determine the rôle played by the eyes in phototaxis Dr. Parker covered a frog with the skin of a somewhat larger individual leaving only the eyes, feet, and snout exposed. Four specimens thus covered were tested, and it was found that they "turned toward the light and jumped toward it much as normal frogs do." When a normal frog was introduced for comparison, it was found that in most instances it "responded more quickly than the covered one, but the difference was not so great that it might not have been due to the purely mechanical interference of the covering skin." When the eyes of the frog were covered as well as the skin, there was no longer any response to light, thus showing that it was not the light, which may have penetrated the covering of dead skin, that effected the orientation.

That phototaxis may be produced through the skin alone as well as through the eyes alone was shown by Parker in the following experiment. Eleven frogs were taken, and "by a single vertical, transverse cut just behind the eyes, these organs and the cerebral hemispheres were removed with the snout of the animal. It is well known that frogs in this condition may with a little care be kept alive for many weeks, and that the chief difference between these and normal frogs is the great reduction in spontaneous movements shown by the former." Of these frogs nine showed an unmistakable phototactic response, turning by the shortest course to face the light, where they remained "for a considerable period, usually terminated by a jump toward the light." This reaction occurs when the exposed portions of the brain are covered by an opaque object or a shadow cast over the head. The skin, therefore, is in all probability the organ which is sensitive to stimulation by light. Pearse found that eyeless toads would also orient toward light, but they showed no discrimination between lights of different colors. A sensitivity to light is shown by the blinded urodeles Triton, Triturus and Cryptobranchus, as well as by the naturally blind Proteus.

Thigmotaxis.—Many animals tend to remain in situations which afford contact stimuli over a considerable surface of the body. Such forms are called positively thigmotactic; those which avoid contact are called negatively thigmotactic. The tendency so common among insects and worms to crawl under stones and lie within crevices, is to a great extent the manifestation of a thigmotactic response, although, in some cases, it may be due in part to a negative phototaxis or photopathy.

Frogs often show a propensity to crawl under stones or to get between objects, where they remain quiet. The same tendency seems to be somewhat more marked in toads. It is apparently stronger when the temperature is lowered. Miss Torelle in experimenting with frogs placed in a jar of cold water found that "when a rock was lowered into the jar in such a way that a small space was formed between it and the wall of the jar, the frog crawled into this space and remained there. When a space was formed between the bottom of the jar and the rock, it crawled into that. This was tested several times, and was also observed when the temperature of the water in the aquarium in which the frogs were kept was lowered to 10° C. and below. When this was done, all the frogs responded, either by flattening their bodies against the stone floor, or by creeping under the rocks usually kept there. It therefore seems that the frog is stereotropic [thigmotactic] in temperatures between 10° C. and 4° C."

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CHAPTER XIX

THE INTELLIGENCE OF THE FROG

THE frog is admirably endowed by nature with a number of instincts which enable it to cope successfully with most of the situations that present themselves in the ordinary course of its life. Its behavior is, to a great extent, stereotyped, the result of specific adaptive responses which are dependent upon its inherited organization. Nevertheless it shows at least the beginnings of intelligence. It is capable of learning simple things and of guiding its conduct by the light of its previous experience. By thus increasing the range and delicacy of its responses it is able to perfect its adjustment to its conditions of existence.

Intelligence at its first appearance is very closely associated with instinct and rises out of the latter by almost insensible gradations. A step of fundamental importance in its development is taken in the acquisition of the power of forming associations between different experiences. These associations may be at first of a very simple nature and formed only after much repetition, but they mark the important transition from instinctive to intelligent behavior.

Abbott, who has devoted some attention to the intelligence of batrachians, concludes that frogs are exceedingly stupid. "Hoping," he says, "to find that in the pursuit of prey, which is principally insects, frogs would display some intelligence, I tried several experiments to test their ingenuity, but it was of no avail. Unless the food could be easily reached by making the exertion of a single leap, the frogs would go hungry. Subsequently I placed a large fly upon a piece of thin mica, and surrounded it with a circle of fine needles, piercing the plate. The fly thus protected could only be seized by the frog suffering a severe pricking of the jaws. This I found a frog would suffer indefinitely in its attempts to secure the fly. In one instance the frog, which had been fasting for seventy-two hours, continued to snap at the needle-protected fly until it had entirely skinned its upper jaw. I concluded from this that the wits of a frog were too limited to be demonstrated."

Knauer finds that frogs persist for a long time in snapping at worms from which they are separated by a glass partition without becoming aware of the futility of their efforts. They will keep up their endeavors at intervals all day; how much more time would be required to convince them that their efforts are vain is uncertain.

Wood frogs, according to Abbott, exhibit much more ingenuity in the pursuit of prey than the ordinary aquatic species. "I have frequently noticed," says Abbott, "when I placed flies in the case, that the wood frog singled out one and approached it in a very stealthy manner, squatting closely to the moss, hiding behind ferns and dragging itself along, until it had reached a position suitable for making a successful leap. If the fly moved, the frog would alter its position accordingly, and follow up the chase with great patience and unquestionable skill. At times it would happen that some one of the smaller batrachians kept in the case snapped at the coveted prize, when the disgust of the wood frog would be plainly shown by its manner, but such an occurrence never led to a quarrel."

Yerkes has studied the power of forming associations in frogs, and has come to the conclusion that their learning is slow, but that habits once formed are hard to change. The frogs experimented with were placed in a labyrinth (Fig.

112) formed by a box 72 cm. long, 28 cm. wide, and 28 cm. deep. The frog enters the box through a small opening at one end *A*. At the other end of the box an opening at one side leads to a tank of water, into which the frog is naturally desirous of getting. Near *A* the box is divided so that a choice of two paths is given. If the frog passes to the right, its course is blocked off by the partition *P*. Near the other end of the box two alternatives are also presented, in that the frog can go either to the left, where its course is cut off by the glass plate *G*, or to the right path, which leads to the water. The sides of the box were fitted so that colored cardboard could be placed in the positions marked *W* and *R*, and the color of the sides of the labyrinth could thus be varied at will. The partition *P* was also movable and could be shifted to the other side of the box so as to reverse the closed and free passages. A frog entering the box at *A* usually does not go at first by the most direct route to the water, but after several trials it comes to avoid the closed passages and travels to the water by the shortest route. The frog learns this path very slowly, as it was found to take from fifty to one hundred trials before it would take the direct route without being liable to make a mistake. Associations once formed, however, were found to persist for over a month. If, after the frog had learned to go to the water by the

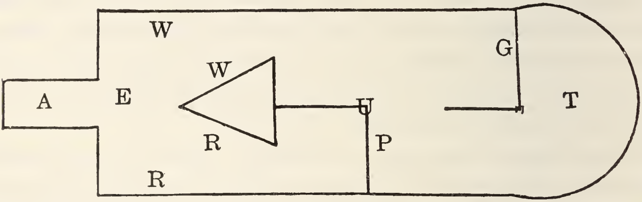

FIG. 112.—Labyrinth used in studying the formation of habits by the frog. From *A* the frog enters at *E*. *G*, glass plate; *P*, partition; *R*, red surface; *W*, white surface; *T*, tank. (After Yerkes.)

nearest path, the colored cardboards lining the sides of the box were exchanged, so that the side that was red before was made white, the animal would become confused and frequently take the wrong route. Yerkes comes to the conclusion that the frog is guided by color vision as well as by "complex sensations of turning."

Fear exercises a strong inhibiting effect on the formation of associations. The frogs experimented with by Yerkes, although they "gave little evidence of fear by movements, after being kept in the laboratory for a few weeks, they were really very timid, and the presence of any strange object influenced all their reactions. Quiescence, it is to be remembered, is as frequently a sign of fear as movement, and one is never safe in saying that the frog is not disturbed just because it does not jump. The influence of the experimenter's presence in the room with the frogs which were being tried in the labyrinth became apparent when the animals were tried in a room by themselves. They escaped much more quickly when alone." If after the frogs had learned to escape by the nearest route from the labyrinth into the water they were frightened by being poked about with a stick, their movements became confused, and they would as frequently as not take the wrong path.

The experiments of Schaeffer on the feeding reactions of frogs showed that learning is not necessarily slow. Frogs were given hairy caterpillars which were seized but quickly rejected. In some cases even two trials were sufficient to prevent the frog from snapping at hairy caterpillars although they would continue to seize other kinds of prey. The frogs also learned, after a very few trials, to avoid seizing earthworms which had been treated with a disagreeable chemical. The habit of avoiding irritating caterpillars was found to persist for ten days.

It is not surprising that frogs learn to discriminate between different kinds of food more readily than they learn to take the right path to water. They are continually making trials of various moving objects and they have probably become endowed with an aptitude for associating such objects with avoiding reactions. An irritating stimulus produced by a disagreeable caterpillar is apt to make more of an impression than a simple error in the choice of a path. Under natural conditions the frog has little experience in learning routes, but it cannot fail to acquire considerable experience in the proper choice of food.

Toads are generally credited with greater intelligence than frogs. Their space perceptions are quite well developed, since they find their way back to their regular habitations after making journeys of considerable distance. They may be readily tamed so that they come toward one and eat out of the hand, and allow themselves to be stroked without showing the usual instinctive reaction of bowing down the head and swelling the body. According to Knauer, they are endowed with no small amount of curiosity. After this observer had placed a glass cage of snakes near a similar cage containing a number of toads it was found that each group of animals was apparently contemplating the other with much interest. The toads were all gathered on the side of the cage nearest the snakes, engaged in what seemed to be a close inspection of their neighbors. Whether the toads' actions were manifestations of curiosity may be questioned, but they probably indicate at least a certain power of attention.

The emotional endowment of frogs and toads is meager. Aside from their sexual impulses, they show little emotional susceptibility beyond that of fear. It is doubtful if they ever show anger, which is one of the most primitive of all emotional feelings. While there is often rivalry among them for the possession of food, their struggles are peaceable and betray no ill temper. The "angry and envious glances" with which, according to Knauer, toads regard one of their number which is fortunate enough to seize a worm for which they are all struggling, are more matters of subjective interpretation on the part of the observer than any real emotional expression on the part of the animals. How the countenance of the toad is modified to express an angry glance we are not informed. L. E. Adams[1] comments on the "pugnacious propensities" of a frog which snapped repeatedly at the tip of an umbrella moved near its head. It seems more probable that this somewhat unusual behavior was a manifestation of the food taking response instead of the fighting instinct.

Of sympathy or affection for its kind the frog or the toad shows no trace. Care for offspring is almost of necessity absent owing to the methods employed in reproduction, since the young shift for themselves in entire independence of their parents. The formation of groups in hibernation is doubtless brought about either by the animals happening to get into the same nooks, or through the tendency to seek the slight degree of warmth afforded by each other's bodies. The frog and the toad are pure egoists. Their only acts which have any reference to other members of their species are those prompted by the blind impulses to reproduction which nature has implanted in these animals in the interests of their posterity.

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