# Anatomy & Histology
# of the Channel Catfish

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# ANATOMY and HISTOLOGY

# OF

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# ACKNOWLEDGMENTS

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# CHAPTER ONE

# INTRODUCTION

The channel catfish, *Ictalurus punctatus* (Rafinesque), is an important commercial and sport species in the United States. It is also promising as an experimental animal because of its hardiness, adaptability to laboratory conditions, and availability.

Culture of channel catfish for commercial production and stocking for sport fishing has led to an interest in the diseases of this species. Bacteria, viruses, parasites, nutrition, and water quality can at times lead to serious mortality or reduced growth. In order to adequately study the diseases caused by these agents, the morphology of the undiseased fish should be known. The use of channel catfish for pharmacological or physiological experiments also requires a knowledge of their morphology.

The consideration of the morphology of one species or a group of closely related species is a promising way of presenting information on fish. The histology of trout has been described (Anderson and Mitchum, 1974) and additional publications dealing with single species or related species of fish seems desirable. Species which are important from an economic or research standpoint as well as those of comparative interest should be investigated.

Some of the organs of the channel catfish have been described previously by other authors. In order to validate the previous descriptions and obtain photographs for this study, sections of all organs were examined and described. Previous descriptions of channel catfish or related species were often useful in making these descriptions but discrepencies were occasionally found.

The genus *Ictalurus* (formerly *Ictalurus* and *Amiurus*) has received considerable attention from morphologists. Although taxonomically important differences exist between the species of this genus, most details of their anatomy and histology as described by previous authors are similar. The following descriptions probably apply generally to other *Ictalurus* spp. as well as *I. punctatus*.

The anatomy and histology of each anatomical system is described separately. Some systems include organs which are developmentally but not

functionally related. Many of the descriptions are superficial, but it is hoped that the illustrations and references cited will be useful in adding unstated details. The figure captions often contain information in addition to that in the text. Electron microscopy was used to supplement histological descriptions in a few cases.

Terminology is a problem in anatomical and histological descriptions. In most instances, the source or sources of the terminology used is given, and alternative terms are given in parentheses.

Both gross anatomy and microanatomy change as a catfish grows and ages, and the type of change and the rate of change varies depending on the organ considered. The most pronounced changes occur during growth of the juvenile. Early development of external features has been described by Mansueti and Hardy (1967), but after sexual maturity pronounced changes can occur such as the flattening and widening of the head of mature males. Unfortunately, the changes accompanying maturation have not been considered. In most cases, only the morphology of the adults or older juveniles has been described.

## Literature

Information concerning fish morphology is available in ichthyological texts and comparative anatomy texts but most of this information is very general and often does not apply to catfish. Comparative histology texts (Andrew, 1959; Patt and Patt, 1969) are useful sources of information concerning fish histology, and mammalian histology texts (Bloom and Fawcett, 1975) are useful for general histological information. The wide range of variation between fish species makes consideration of unrelated groups of fish difficult, although comparative fish histology is important.

Relevant literature is discussed in the sections in which it is applicable; however, one series of papers is particularly noteworthy. The Proceedings of the Canadian Institute for 1884 contained six papers dealing with the morphology of most systems of *"Amiurus catus"* (Macallum, 1884; McKenzie, 1884; McMurrich, 1884a and b; Wright, 1884a and b). The descriptions of the gross anat-

omy are accurate, although the terminology now in use is often different. The histological descriptions are sometimes inaccurate or misleading except for those of the nervous system. The species described in the above mentioned papers is probably *I. nebulosus* according to some authors (Shelden, 1937; Allis, 1908; Kindred, 1919), but accurate species identification is difficult to determine from the information presented.

## Materials and Methods

Specimens examined were obtained from ponds of the fisheries unit of the Auburn University Agricultural Experiment Station, from the Southeastern Fish Culture Laboratory, Marion, Ala., and from Lee County public lake, Lee Co., Ala. Additional specimens were examined from other sources, many being received for disease diagnosis at Auburn University by the Southeastern Cooperative Fish Disease Project.

Size of the specimens ranged from newly hatched fry to adults weighing 4 kg. Specimens smaller than 20 mm TL are not considered in most descriptions in this publication, but were useful in determining the development or overall organization of some systems.

Dissections were made of both fresh and formalin-preserved specimens for descriptions of gross anatomy. Serial sections of fingerlings were useful in determining positional relationships between organs. Frozen adult specimens were cut with a band saw into sections approximately 1 cm thick in transverse and sagittal planes. Figure 29 was drawn from sketches of these frozen sections

and from dissections of adult specimens.

Bouin's fixative, 10 percent buffered formalin, and Helly's fixative (Humason, 1967) were used for routine histological preparations. Most tissues were embedded in paraffin, but some tissues that were difficult to section were embedded in celloidin. Harris' hematoxylin and eosin (H & E) and Masson's trichrome stain (Masson's) were routinely used, but several other stains were used on selected tissues. The fixative and stain are indicated for each figure. Black and white photomicrographs were made with Panatomic-X film and most color photomicrographs were made with Ektachrome-X.

Tissues for electron microscopy were fixed in 3 percent glutaraldehyde in phosphate buffer followed by postfixation in 1 percent osmium tetroxide or were fixed directly in 1 percent osmium tetroxide in phosphate buffer. Fixation was at approximately 4°C. The tissue was embedded in an epoxy-araldite mixture (Mollenhauer, 1963) and sectioned with glass knives. Sections were double stained with uranyl acetate (Watson, 1958) followed by lead citrate (Reynolds, 1963). A Philips EM 300 electron microscope was used, and electron micrographs were made with glass projector slide high contrast plates.

Several methods were used only for a specific tissue or for only one system. Specialized techniques used include injection of blood vessels with latex, hematological techniques, dissection of muscles, and preparation of skeletal material. These techniques are discussed with the system in which they were used.

# CHAPTER TWO

# EXTERNAL ANATOMY

The channel catfish has a variable appearance depending on the age, sex, and geographical locality. This variability resulted in 20 different scientific names being applied to the channel catfish in the early and mid-1800's when much descriptive work of fishes was done (Jordan et al., 1930).

Color of the channel catfish is white to silvery on the undersides grading to a greyish slate-blue or steel-blue on the dorsum. Old specimens may be dark all over with the dorsal portion of the body being completely black. The small round to irregular dark spots on the body of young specimens usually are lost in large specimens.

Body shape is slender and elongate with the head slightly depressed. Head length is approximately one-fifth of total length (Fig. 1).

## Barbels

Eight barbels, four dorsal and four ventral, are located around a subterminal mouth. The maxillary barbels (Fig. 4), which are the largest, are located dorsolaterally to the mouth and are very dark in color. The nasal barbels are located dorsally at the anterior margins of the posterior nares. These barbels are lighter in color and about one-fifth as long as the maxillary barbels. Outer mandibulary barbels and mental barbels (Fig. 4) are located ventrally. The ventral barbels are light to almost white in color, and are intermediate in size between the two dorsal pairs with the mandibulary pair being longer.

## Fins

Immediately posterior to the head are the paired ventrolateral pectoral fins. Each of these fins has a hard ray (spine) made up of modified lepidotrichia, and nine soft rays. The posterior edge of the hard ray is serrated.

The dorsal fin originates on the dorsal midline about one-third of the body length from the anterior end. A serrated spine, composed of modified rays, and six soft rays make up the dorsal fin.

The paired pelvic fins, comprised of eight soft rays, are located ventrolaterally immediately anterior to the anus and urogenital openings, slightly anterior to body midlength.

The anal fin distal margin is rounded and has 24 to 30 rays. The anal fin size, shape, and ray count is one of the main distinguishing features of channel catfish and is used to separate it from closely related species.

The adipose fin is located on the dorsal midline posterior to the dorsal fin about two-thirds of the body length from the snout. The adipose fin does not have rays and is supported by fibrous connective tissue. It is described histologically in Chap. 7.
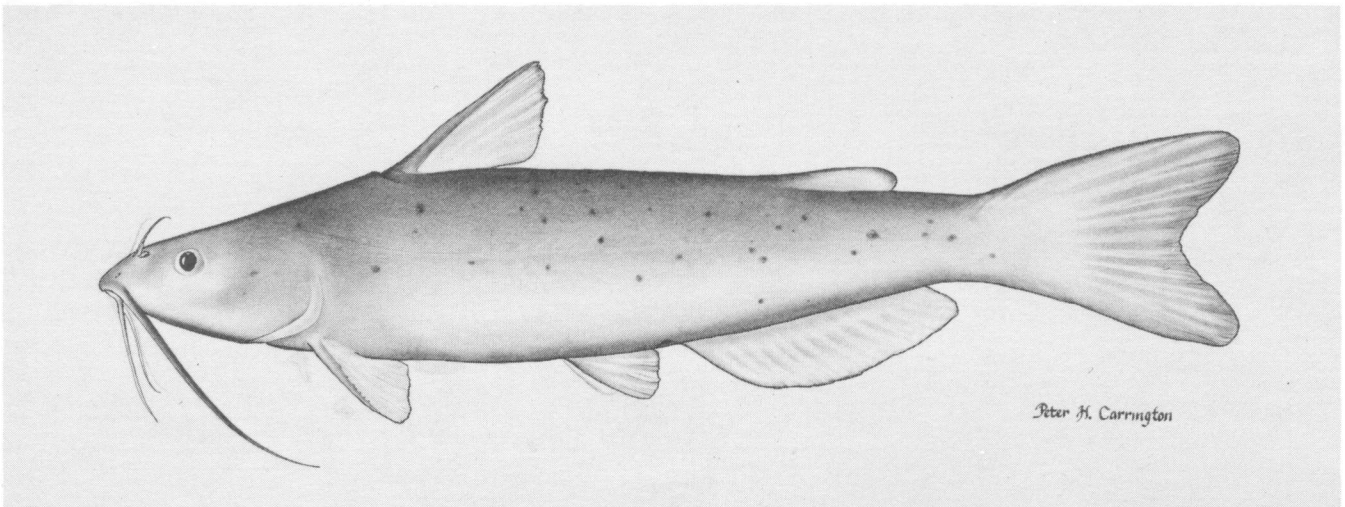


FIG. 1. Lateral view of adult channel catfish.

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The caudal fin is deeply forked in channel catfish and is another distinguishing feature of the species along with the anal fin.

## Lateral Line

The lateral line runs longitudinally from the caudal fin to the head with cephalic lateral-line canals (Chap. 9) extending onto the head. The lateral line on the trunk and tail is located at midbody except near the head where it arches dorsally. It is evident by a slightly lighter color and pores opening at intervals along the length of the line. The lateral line of some specimens has branches extending dorsally away from the main line. These branches can extend into the adipose fin.

## Sexual Differences

Sexual differentiation is possible on mature specimens using external features. The male has a distinct urogenital papilla (Fig. 2), a wide, flat head, and a darkly pigmented underbody and jaw. The female genital opening is separate from the urinary opening with small flaps covering the openings. Near spawning time the female genitalia become swollen and inflamed. The mature female has a more slender head, a fuller body,

and is much lighter colored than the male during the spawning period. Sexing of channel catfish with the use of a probe to determine if the genital and urinary ducts are separate (female) or united (male) has been suggested (Moen, 1959; Norton et al., 1976) but is usually not necessary.



FIG. 2. Ventral view of the urogenital area of adult channel catfish. The male (right) has a distinct urogenital papilla which is absent in the female (left). Courtesy of E. E. Prather, Auburn University.

# CHAPTER THREE

# CIRCULATORY SYSTEM

The circulatory system consists of arteries, veins, capillaries, heart, the lymphatic system, and fluids and blood cells they contain. The spleen, kidneys, and thymus are intimately associated with this system because of their involvement in the production or destruction of blood cells. A general schematic diagram of blood circulation is presented in Fig. 3.

## Anatomy of Arteries and Veins

The path of the major arteries and veins which carry blood from the heart to tissues and back to the heart can be determined most easily by injecting the vessels with latex. Uninjected specimens and serial sections of small specimens are useful in the study of vessels which are not easily injected. The branching of arteries and veins and their relationships to surrounding organs is highly variable between specimens. Only the most often encountered condition is described. The paths of the arteries and veins of the channel catfish are very similar to that described for *I. nebulosus* (McKenzie, 1884).

### METHODS FOR INJECTION OF BLOOD VESSELS WITH LATEX

Liquid latex (Carolina Biological Supply) was injected into arteries and veins of anesthetized fish (gills irrigated with 1 percent Quinaldine) for study of their gross relationships. A 20-guage needle and 10 ml syringe were used to inject the latex into the blood vessels. Injected fish were placed in 10 percent formalin with 2 percent acetic acid to harden the latex and preserve the specimen.

The caudal vein and artery were the usual sites for injection. In some specimens, these vessels were injected after removing the overlying muscles so that the hemal arches were exposed. The needle could then be accurately placed in the blood vessel. Injections were also accomplished by inserting the needle parallel to the pterygiophores of the anal fin and then probing for the blood vessel. With both methods, an incision was made in the ventral body wall so that the progress of the injection could be observed. Injection of latex

into other sites such as the heart or posterior cardinal vein were usually not successful.

Injection into the caudal artery results in filling all arteries except the afferent branchial arteries and ventral aorta between the heart and gills, therefore these arteries were examined without the aid of injection. Injection into the caudal vein resulted in filling branches of the caudal vein and the hepatic portal system which receives blood directly from the caudal vein. The remaining veins were usually not filled when the caudal vein was used because renal portal system capillaries lie between the caudal vein and the posterial cardinal veins which drain the trunk kidney. In a few specimens, latex flowed from the caudal vein into the posterior cardinal vein filling all veins except the hepatic vein. This may have resulted from rupture of venules or capillaries because of excessive pressure, or natural connections may exist in some specimens.

### ARTERIAL CIRCULATION

The arterial system consists of arteries and arterioles which carry blood from the bulbus arteriosus of the heart to the capillaries of the various tissues. The blood flows from the heart to the gill lamellae where it is oxygenated before being distributed to the body. Blood pressure is reduced in the gills so that postbranchial arteries have low blood pressure compared to arteries of higher vertebrates.

*Branchial arteries.* Blood flows from the heart to the gills through the ventral aorta. Afferent branchial arteries branch from the ventral aorta, enter each of the eight gill arches, and send a branch to each gill filament (Chap. 11) where the blood enters the gill lamellae. Blood leaves the filaments, enters the efferent branchial arteries, and flows to the dorsal side of the pharynx where the efferent branchials form the carotids and dorsal aorta (Fig. 4).

The first and second efferent branchial arteries also have branches ventral to the pharynx. A small branch from the first efferent artery goes anteriorly to the ventral hyoid region. The first and second efferent arteries contribute to the median hypo-
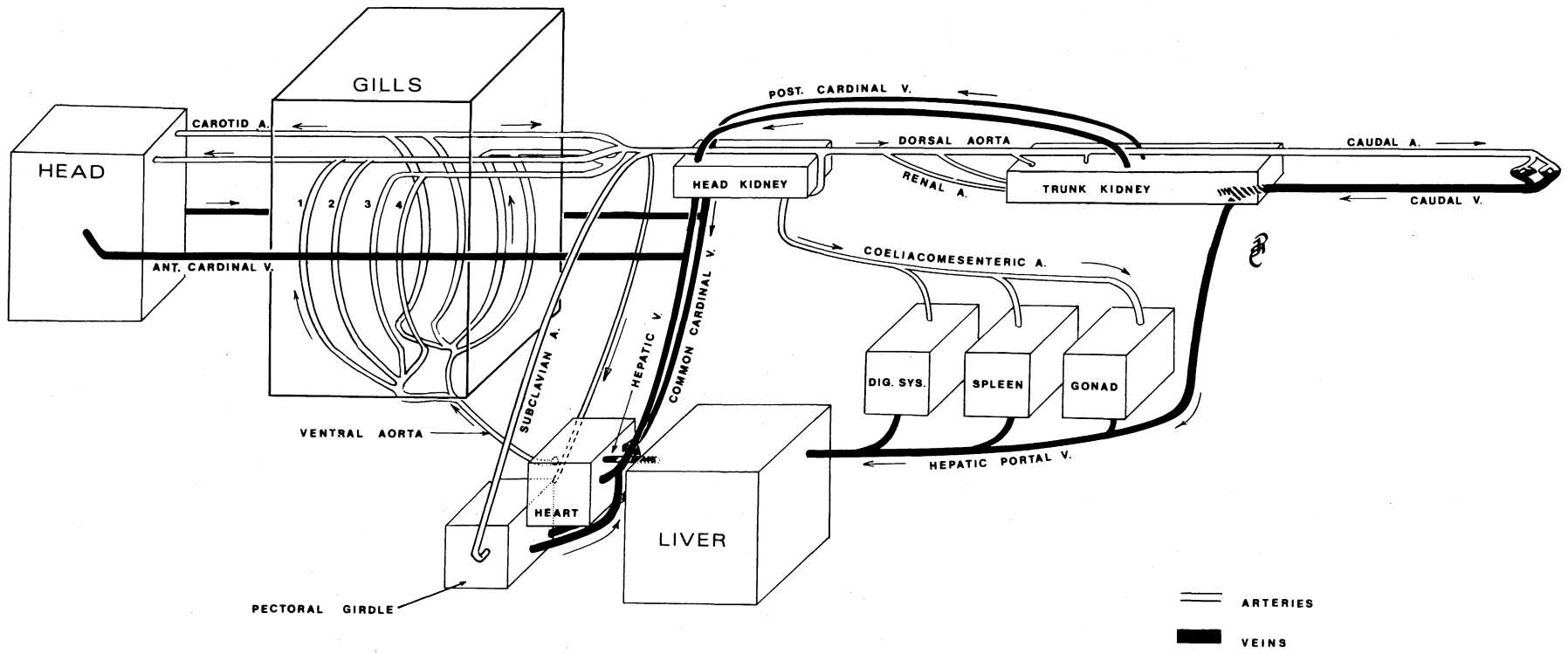
FIG. 3. A diagram of the major arteries and veins.
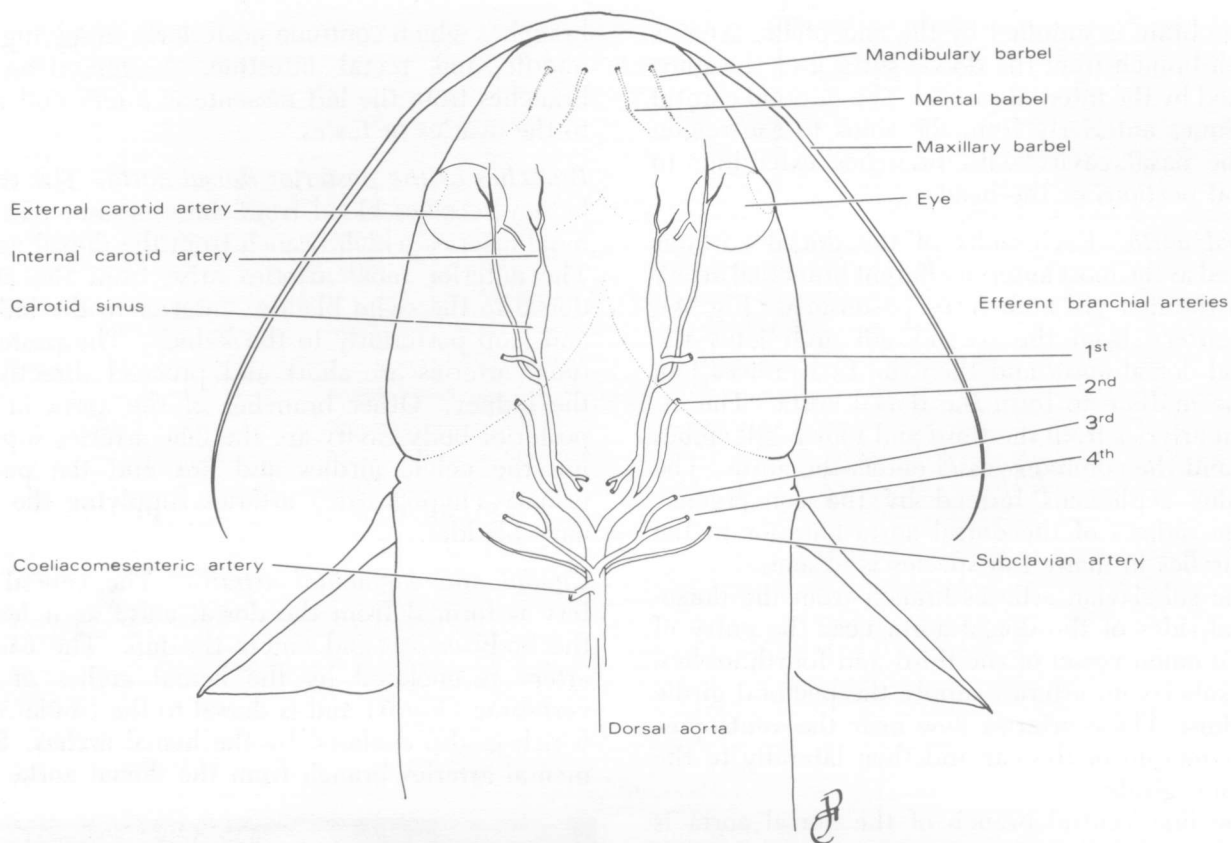
FIG. 4. Ventral view of the efferent branchial arteries, carotid arteries, and anterior dorsal aorta. The internal and external carotid arteries branch from the first efferent branchial artery which continues posteriorly to form the radix of the dorsal aorta. These vessels lie on the ventral surface of the neurocranium and vertebrae.

branchial artery which passes posteriorly along the ventral aorta to the heart. The median hypobranchial sends branches to the ventral aorta, thyroid, and pericardial sac before becoming the coronary artery as it branches over the surface of the heart.

*Carotid arteries.* Most of the head is supplied with blood by the carotid arteries which branch from the first efferent branchial arteries dorsal to the pharynx (Fig 4). The first efferent artery goes toward the midline from the gill and then turns to run posteriorly. At this turn, the external carotid arises from the dorsal surface and the internal carotid passes directly anteriad. The external carotids supply the lateral portions of the head including the regions of the eye, nasal capsule, roof of the mouth, and maxillary barbel.

The internal carotids thicken into an irregularly divided, oblong sinus (Fig. 5) immediately anterior to its origin from the first efferent branchial artery. This sinus was thought to be a degenerate pseudobranch by McKenzie (1884), although the development of this structure was not determined. The primary evidence supporting this opinion is the large artery supplying the eye which arises

from the sinus. This is similar to the condition in some other teleosts in which the ophthalmic artery arises from the pseudobranch (Goodrich, 1930). More recent studies (Allis 1908) have refuted the presence of pseudobranchia in *Ictalurus*.



FIG. 5. The internal carotid forms an irregularly divided sinus just anterior to its origin from the first efferent branchial artery. This sinus is ventral to the brain, near the optic nerve (O). Several arteries (A) branch from this sinus. Transverse section; Bouin's; H & E; × 60.

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The brain is supplied by the encephalic arteries which branch from the dorsal surface of the sinus formed by the internal carotid. The internal carotid continues anteriorly from the sinus to the region of the nasal cavity with branches extending to lateral portions of the head.
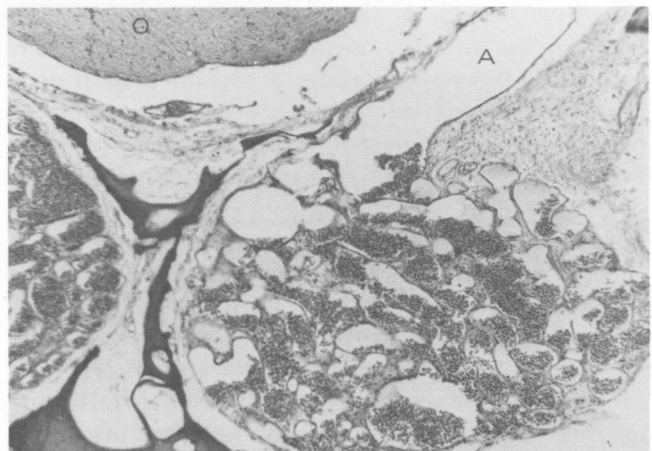
*Dorsal aorta.* Each radix of the dorsal aorta is formed as the most anterior efferent branchial artery from the first gill arch turns posteriorly (Fig. 4). The artery from the second gill arch joins the lateral dorsal aorta and then the two radices join at the midline to form the dorsal aorta. The efferent arteries from the third and fourth gill arches join and the common vessel enters the aorta. The circulus cephalicus formed by the convergence of the radices of the dorsal aorta anterior to the gill arches in many fish species is absent.

The subclavian arteries branch from the dorsolateral sides of the dorsal aorta near the entry of the common vessel of the third and fourth arches. The subclavian arteries supply the pectoral girdle and fins. These arteries flow near the ventroposterior margin of the ear and then laterally to the pectoral girdle.

The first ventral branch of the dorsal aorta is usually too small to locate except in serial sections and goes to the head kidney. The coeliacomesenteric artery originates immediately posterior to the origin of the head kidney artery. Both of these arteries arise near the entry of the combined third and fourth efferent branchial artery. The coeliacomesenteric artery supplies most of the organs of the visceral cavity.

*Coeliacomesenteric artery.* This artery passes between the head kidney and swim bladder after branching from the ventral side of the dorsal aorta. The first branch is the pneumatic artery which supplies the anterior portion of the swim bladder. Ventral to the swim bladder, a second branch goes to the esophagus, and then the coeliacomesenteric divides into the gastric artery and mesenteric (coeliac) artery. The gastric artery supplies most of the stomach and the mesenteric artery supplies the remaining visceral organs.

The first branch of the mesenteric artery divides into the cystic artery to the gall bladder and the hepatic artery going to the liver. Several anterior intestinal arteries branch from the mesenteric and supply the different regions of the pyloric intestine. The usual number of anterior intestinal arteries is four. Posterior to the anterior intestinal arteries, a small splenic artery branches from the mesenteric.

The mesenteric artery divides into right and left branches which continue posteriorly supplying the middle and rectal intestine. A genital artery branches from the left mesenteric artery and goes to the ovaries or testes.

*Branches of the posterior dorsal aorta.* The trunk kidney receives blood from three or four pairs of renal arteries which branch from the dorsal aorta. The anterior renal arteries arise from the aorta dorsal to the swim bladder anterior to the kidney and loop posteriorly to the kidney. The posterior renal arteries are short and proceed directly to the kidney. Other branches of the aorta in the posterior body cavity are the iliac arteries supplying the pelvic girdles and fins and the paired urinary (hypogastric) arteries supplying the urinary bladder.

*Caudal and segmental arteries.* The caudal artery is formed from the dorsal aorta as it leaves the body cavity and enters the tail. The caudal artery is enclosed by the hemal arches of the vertebrae (Fig 6) and is dorsal to the caudal vein which is also enclosed by the hemal arches. Segmental arteries branch from the dorsal aorta and



FIG. 6. The caudal artery (A) and caudal vien (V) are protected by the hemal arches (H) of the vertebrae. Transverse section; Bouin's; H & E; × 175.

caudal artery at regular intervals to supply the muscle and skin of the body and tail. These segmental arteries are somewhat reduced in number compared to the number of vertebrae or myomeres with one segmental artery occasionally supplying several myomeres.

## VENOUS CIRCULATION

Blood returns to the heart from capillaries through venules and veins. Two portal systems are present in which blood returning to the heart passes through an additional capillary network before reaching the heart.

*Renal portal system.* The caudal vein is located in the hemal arches of the caudal vertebrae and enters the trunk kidney immediately upon reaching the body cavity. The caudal vein collects blood from segmental veins of the tail. Renal portal veins branch from the caudal vein while in the kidney and then the caudal vein proceeds anteriorly from the ventral surface of the trunk kidney to form the hepatic portal vein.

Blood from the renal portal veins and from intercostal veins which enter the trunk kidney from the body wall adjacent to the kidney flow through renal portal capillaries of the kidney. The blood from these capillaries is collected by the paired posterior cardinal veins. The right posterior cardinal is much larger than the left and both receive segmental veins from somatic muscles before entering the common cardinal veins. The most anterior intercostal veins enter the head kidney and form capillaries which then enter the posterior cardinal veins.

*Hepatic portal system.* The caudal vein branches as it passes through the trunk kidney. Some of these branches are renal portal veins but most anastomose near the ventral surface of the kidney. The paired iliac veins from the pelvic girdle and fins join these anastomosing veins as they emerge from the kidney. The large vein formed on the ventral surface of the kidney is the hepatic portal vein which continues anteriorly to the liver. Blood from the gonads, spleen, swim bladder, and alimentary tract enters the hepatic portal vein.

After emerging from the kidney, the hepatic portal vein passes between the gonads and receives blood from numerous genital veins. A small pneumatic vein enters the hepatic portal vein just posterior to the spleen. The spleen is closely attached to the hepatic portal vein by extremely short splenic veins. Several intestinal veins enter the hepatic portal vein just anterior to the spleen. The gastric vein from the stomach enters near the anterior end of the hepatic portal vein. The hepatic portal vein branches before entering the liver with the branches extending to different regions of the liver.

Within the liver, the branches of the hepatic portal vein are surrounded by pancreas (See Chap. 4) and supply blood to the hepatic sinusoids. Blood drains from the sinusoids into central veins and then into the hepatic vein which pierces the transverse septum and enters the sinus venosus.

*Cephalic veins.* Most blood from the head enters the anterior cardinal veins. Branches enter this vein from the upper and lower jaw, operculum, pharynx, dorsolateral head, cranium, and dorsal fin. The anterior cardinal and posterior cardinal veins join to form the common cardinal vein (duct of Cuvier).

The inferior jugular vein receives blood from the ventral portions of the head and then enters the common cardinal vein near the sinus venosus. The common cardinals are located in the transverse septum and enter the sinus venosus laterally.

## Histology of Blood Vessels

### ARTERIES

The structure of channel catfish arteries varies, depending on the location of the artery. A tunica intima, tunica media, and tunica adventitia are generally present but are often not distinct. The tunica intima lines the vessel and consists of a layer of simple squamous epithelium (endothelium) and sometimes a thin layer of fibrous connective tissue. The tunica media varies greatly but generally consists of elastic connective tissue and smooth muscle. The tunica adventitia is the outermost layer and is composed of fibrous connective tissue which merges with surrounding tissue.

The ventral aorta and afferent branchial arteries (Fig. 7) are elastic arteries with a tunica media composed primarily of elastic fibers which absorb some of the pressure shock resulting from ventricular systole. Smooth muscle fibers are also present in the tunica media. The tunica intima is composed of prominent endothelial cells and a very thin connective tissue layer. The tunica adventitia is composed of loose connective tissue which merges with adjacent tissues including unencapsulated thyroid follicles.

The dorsal aorta, especially in the area dorsal to the swim bladder (Fig. 8), is slightly modified. Most of the wall is composed of collagen fibers, and a dorsomedial projection protrudes into the vessel. The tunica intima and tunica adventitia are thin compared to the tunica media.
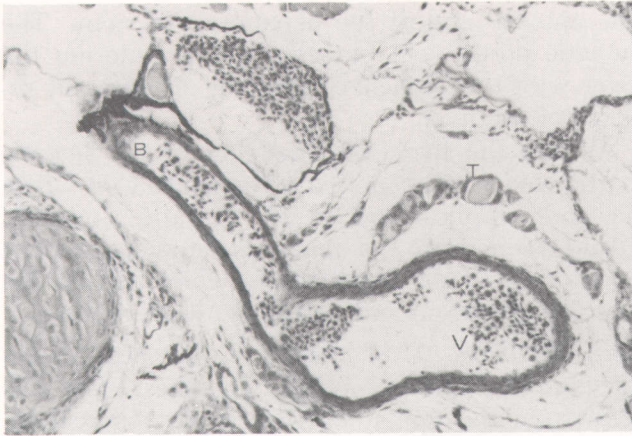
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FIG. 7. The afferent branchial arteries (B) branch from the ven'ral aorta (V) just anterior to the heart. These vessels are elastic arteries and are surrounded by thyroid follicles (T). Transverse section of 30 mm TL juvenile; Bouin's; H & E; × 160.



FIG. 8. The dorsal aorta, dorsal to the swim bladder, has very thin tunica intima and tunica adventitia and a thick tunica media (M) composed entirely of collagen fibers. The aorta is located in a groove in the vertebrae so that bone (B) partially surrounds it. A projection of the dorsal wall (P) into the lumen is characteristic of the dorsal aorta and in some regions this projection almost completely divides the lumen. Bouin's; H & E; × 120.

The remaining large arteries are muscular arteries (Fig. 9) with a tunica media composed largely of smooth muscle. The tunica intima usually has an internal elastic membrane in addition to the endothelium. The tunica adventitia is thicker than in other types of arteries, and consists of connective tissue and scattered longitudinally oriented muscle fibers.

Arterioles are the smallest arteries and have relatively simple structure. All three layers are thin and not easily distinguished by light microscopy but are clearly seen in electron micrographs (Krementz and Chapman, 1975). The endothelial cells are often prominent with the nuclei protruding into the lumen.

## CAPILLARIES AND RELATED STRUCTURES

Capillaries are tube-shaped with the wall one cell thick. Most tissues receive their blood supply from capillaries. Some organs such as the liver and spleen do not have distinct capillaries with definite boundaries; instead, they have sinusoids which vary in shape and sometimes have no endothelial cells separating the sinusoidal space from the surrounding tissue.

The terminal blood vessels of the gill lamellae are also not typical capillaries because of their shape and the nature of the cells lining them. These vessels are described in Chapter 11.

Some teleosts have retia mirabilia consisting of capillary beds with blood flow of adjacent vessels being antiparallel. These structures are usually associated with the gas gland of the swim bladder, choroid of the eye, or certain muscles (Lagler et al., 1962). Structures of this type have not been described in channel catfish.

### VEINS

Veins have thinner walls and larger diameters than the corresponding arteries (Fig. 10). The layers of the wall are not distinct. The endothelium of the tunica intima is present and the remainder of the wall is composed of fibrous connective tissue. Valves are not present in any of the veins.

### Heart

The heart consists of four chambers; sinus venosus, atrium, ventricle, and bulbus arteriosus (Fig. 11 and 12). The heart is located ventral to the pharynx and just anterior to the liver. It is protected ventrally by the heavy pectoral girdle. The
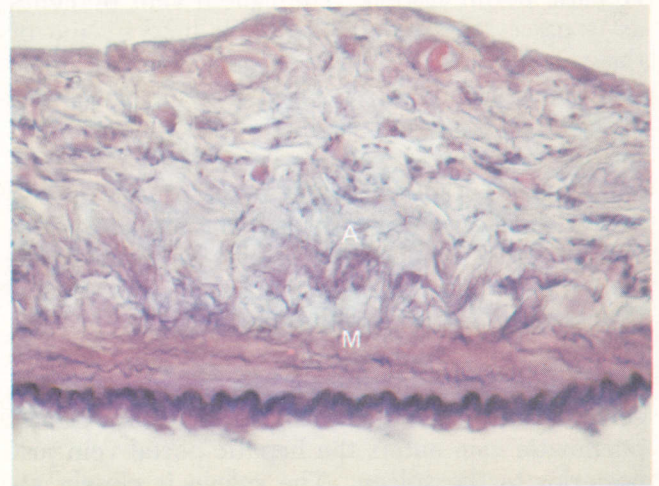


FIG. 9. Muscular arteries have an elastic membrane which stains darkly in the tunica intima, a tunica media (M) composed primarily of smooth muscle, and a relatively thick tunica adventitia (A) composed primarily of light staining connective tissue which has longitudinally oriented smooth muscle. Helly's; aldehyde fuchsin trichrome (Epple, 1967); × 600.
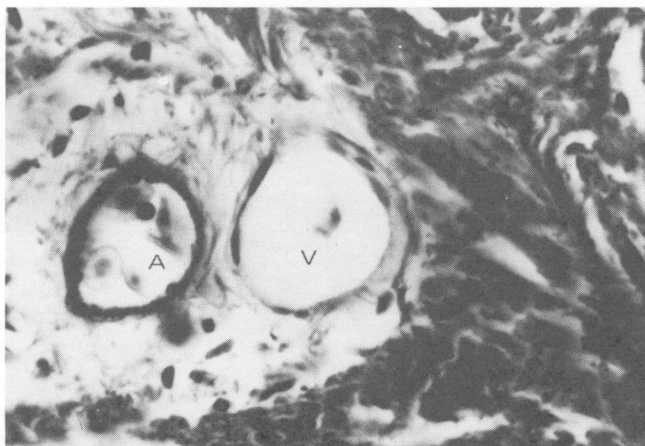
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FIG. 10. An artery (A) has a thicker wall and smaller lumen than a vein (V) serving the same tissue. These vessels are in the dorsal wall of the swim bladder. Bouin's; H & E; × 650.
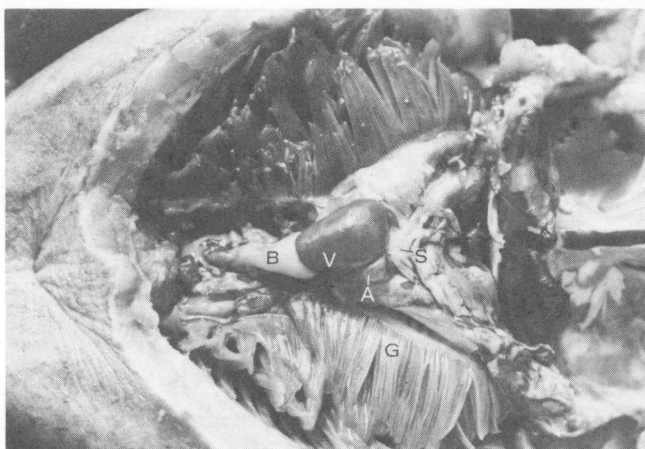


FIG. 11. This ventral view of the heart illustrates the relationship between the heart and gills (G). S, sinus venosus; A, atrium; V, ventricle; B, bulbus arteriosus.

chambers are separated by paired semi-lunar valves.

The heart is located in the pericardial sac which is lined by a serous membrane. The surface of the heart is covered by the epicardium consisting of pericardial mesothelium and sparse connective tissue. Blood vessels are located between the epicardium and the underlying cardiac muscle, especially in the ventricle.

Cardiac muscle (Fig. 13) of channel catfish is like that of other vertebrates. Striations, branching of muscle fibers, and nuclei located in the center of fibers distinguish cardiac muscle from smooth or skeletal muscle. Many fibers of cardiac muscle are separated from adjacent muscle fibers and are covered by the endothelium which lines the heart. Nuclei of the endothelial cells are often seen on the outer edges of fibers giving an appearance of peripherally located nuclei. However, the endothelial nuclei can be distinguished by their flattened profile.

## SINUS VENOSUS

The sinus venosus is extremely thin walled and almost devoid of cardiac muscle (Fig. 14). Most of the wall is composed of the epicardium and an inner layer of endothelium, the endocardium. Isolated fibers of cardiac muscle and melanin are located between the epicardium and endocardium.

The sinus venosus is closely associated with the transverse septum which separates the pericardial cavity from the visceral cavity. The hepatic and common cardinal veins pass through the transverse septum before entering the posterior and lateral portions of the sinus venosus. The sinus venosus is sometimes difficult to distinguish in dissections of small fish.

## ATRIUM

The atrium lies anterior to the sinus venosus and dorsal to the ventricle. The wall of this chamber (Fig. 15) is thin but has much more cardiac
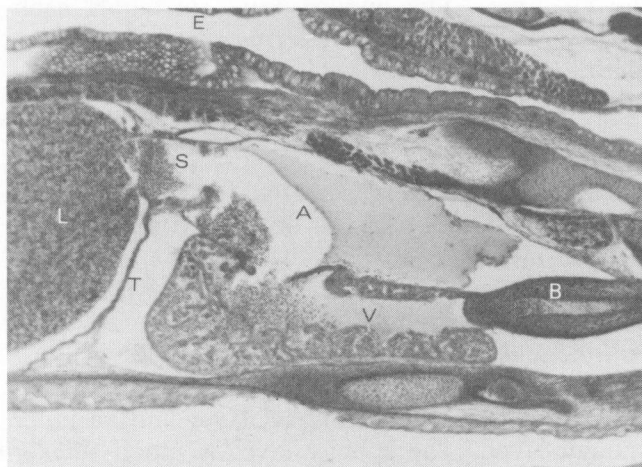


FIG. 12. The four chambers of the heart and its location are seen in this sagittal section of a 7-day old fry. S, sinus venosus; A, atrium; V, ventricle; B, bulbus arteriosus; T, tranverse septum; L, liver; E, esophagus. Bouin's; H & E; × 60.
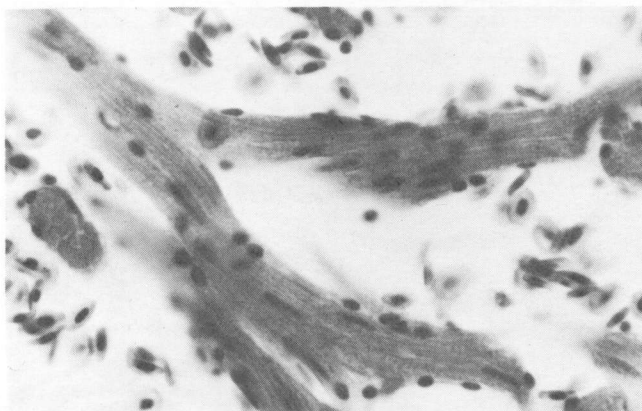


FIG. 13. Cardiac muscle fibers are found isolated in the spongy layer of the ventricle. These fibers have weak striations, branch, and have centrally located nuclei. Blood cells are scattered around the muscle fibers. Bouin's; H & E; × 600.
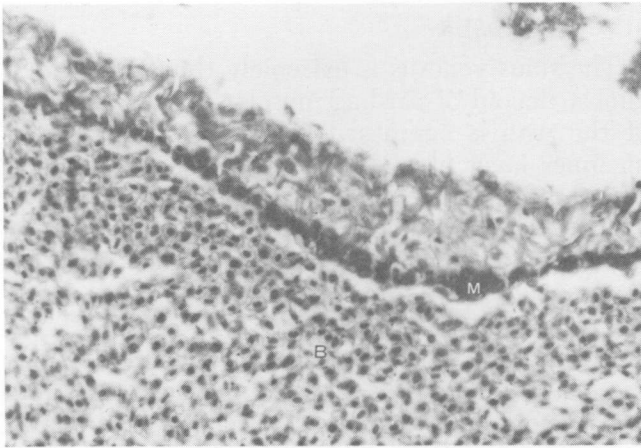
FIG. 14. The sinus venosus has a very thin wall composed primarily of connective tissue. Melanin (M) and cardiac muscle are scattered. Blood cells (B) fill the lumen in this specimen. Bouin's; H & E; × 320.



FIG. 16. The wall of the ventricle has compact (C) and spongy (S) layers. Both are composed of cardiac muscle, but the muscle fibers of the spongy layer are widely spaced with blood flowing between fibers. Bouin's; H & E; × 240.

muscle than the sinus venosus. Much of the muscle forms a network of widely spaced muscle fibers that are bathed by the blood contained within the chamber. The endocardium surrounds each of these fibers as well as covering the inner surface of the wall. The thin wall of the atrium is composed of cardiac muscle covered by epicardium.

## VENTRICLE

The ventricle is responsible for almost all of the pumping action of the heart, and most of the cardiac muscle is in this chamber. It is located ventral to the antrium, and the bulbus arteriosus continues anteriorly from it. This is the most conspicuous chamber upon gross dissections.

The thick wall (Fig. 16) has two layers of cardiac muscle, an outer compact layer and an inner spongy layer. The spongy layer is much thicker than the compact layer and is composed of widely spaced muscle fibers which are bathed by the

blood in the lumen. The fibers of the spongy layer anastomose resulting in a loose arrangement of the cardiac muscle. The compact cortical layer is composed of tightly packed muscle fibers and is supplied with blood from the coronary artery.

The endocardial endothelium surrounds each muscle fiber of the spongy layer and covers the inner surface of the compact layer as it does in the atrium. The epicardium covers the outer surface.

## BULBUS ARTERIOSUS

This chamber has a thick wall composed of fibrous connective tissue and smooth muscle (Fig. 17). Cardiac muscle is totally absent from the bulbus arteriosus and elastic fibers are abundant. The endothelium has rounded nuclei protruding into the lumen, and epicardium covers the outer surface. The bulbus arteriosus becomes the ventral aorta as it leaves the pericardial cavity.
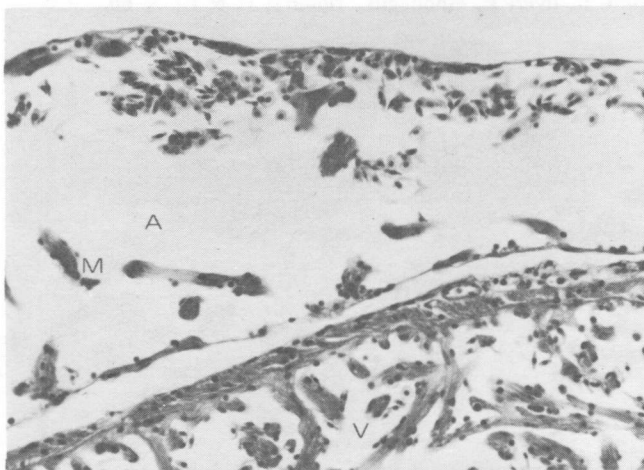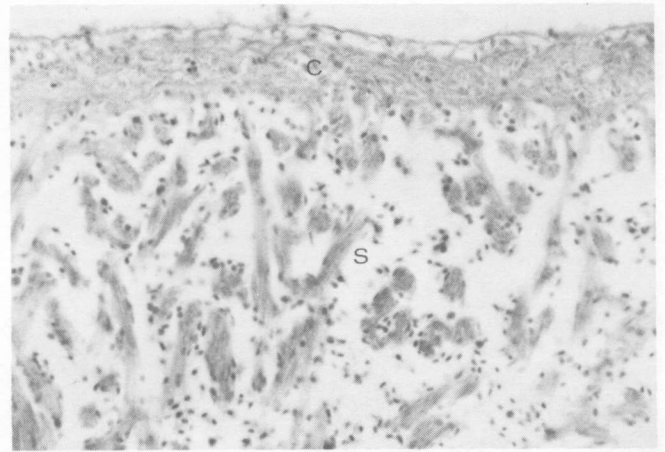


FIG. 15. The atrium (A) has a very thin wall composed primarily of cardiac muscle. Isolated muscle fibers (M) are found in the lumen. V, ventricle. Bouin's; H & E; × 240.



FIG. 17. The bulbus arteriosus (B) is separated from the ventricle (V) by semilunar valves (S). The wall of the bulbus arteriosus is composed of connective tissue fibers and smooth muscle. Longitudinal section; formalin; H & E; × 33.

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The bulbus arteriosus is very important in regulating the pressure of the blood leaving the heart (Licht and Harris, 1973). The elastic fibers allow this chamber to expand during the high pressure of ventricular systole protecting the delicate vessels of the gill lamellae from excessive distention. During diastole the elastic fibers shorten so that the bulbus contracts and forces blood into the ventral aorta resulting in more even pressure.

## Lymphatic System

Teleosts have lymph vessels which originate as blind capillaries in tissues, anastomose freely forming larger vessels, and eventually empty into the venous system (Bertin, 1958a). Krementz and Chapman (1975) found that the serosa of the channel catfish intestine contained numerous small and large lymph vessels. From electron micrographs they determined that the highly convoluted vessels had thin, flat endothelium without fenestrations or pericytes. These vessels are similar to those of other vertebrates.

Some Osteichthyes including the European catfish (*Silurus*) have chambered lymph hearts located in the caudal region which pump lymph into veins (Patt and Patt, 1969). These structures were not found in channel catfish.

## Hemopoietic Tissues

Blood formation occurs in the head kidney (Chap. 5; Fig. 54), trunk kidney (Chap. 6; Fig. 69), spleen, and perhaps the thymus. Tissue imprints of the kidneys (Fig. 18) were made using the techniques of Ashley and Smith (1963). These imprints contain numerous hemoblasts and other immature blood cells indicating the importance of these organs in hemopoiesis. Macrophages which have engulfed erythrocytes are also present, so some blood cell destruction also occurs in these organs. Tissue imprints of the spleen indicate that it is more important in blood cell destruction and less important in hemopoiesis than the kidneys.

## Spleen

The spleen is a dark red disk-shaped organ located between the fundic stomach and the swim bladder (Fig. 29) and is attached to the hepatic portal vein. The edges are smooth, but peripheral blood sinuses are sometimes visible grossly as protruding red spots.

The surface is covered by simple squamous epithelium (mesothelium) overlying a capsule of dense fibrous connective tissues (Fig. 20). A
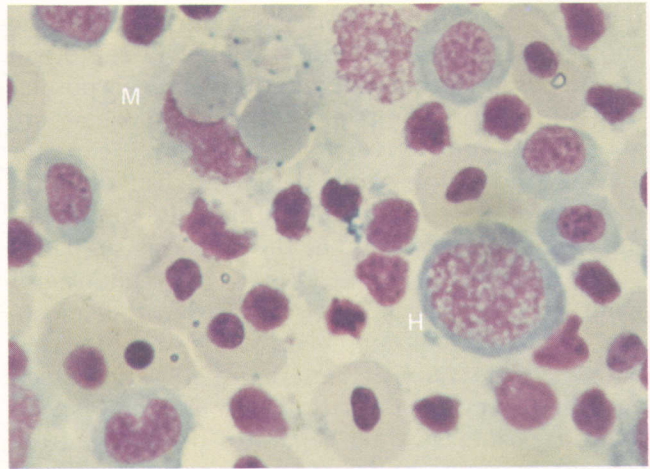


FIG. 18. Hemoblasts (H) are abundant in tissue imprints of the head and trunk kidneys indicating their importance in hemopoiesis. Other immature blood cells as well as mature blood cells are also present. Macrophages (M) which have engulfed erythrocytes are present but much less abundant than in the spleen. Head kidney tissue imprint; air dried; Wright-Giemsa; × 1200.
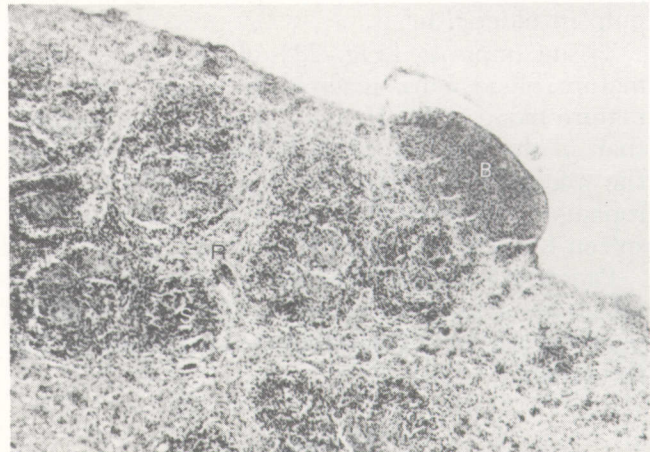


FIG. 19. The spleen consists of splenic corpuscles (S) surrounded by red pulp (R). Large blood sinuses are located immediately beneath the outer capsule and are sometimes swollen with blood (B). Bouin's; H & E; × 90.
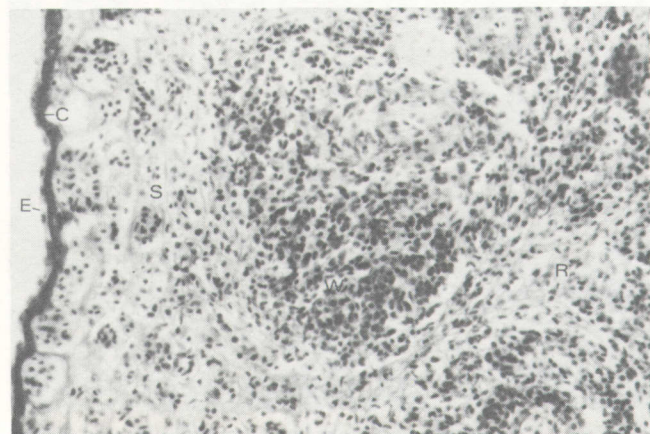


FIG. 20. Simple squamous epithelium (E) and a connective tissue capsule (C) cover the spleen. A zone of blood sinuses (S) separates the capsule from the underlying red (R) and white (W) pulp. Bouin's; H & E; × 240.

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region of large blood sinuses is found beneath the connective tissue, and the remainder of the organ is composed of red pulp and splenic corpuscles containing white pulp (Fig. 19). Trabeculae are absent and connective tissue is scarce except for arteries and veins. Young and old fish differ in the discreteness of the red and white pulp, but the general organization of the spleen is similar.

The splenic corpuscles (Fig. 21) are nodules of white pulp surrounding arteries within the spleen. The white pulp is more basophilic than the red pulp because its cells are more closely spaced and there are fewer erythrocytes. In some specimens a germinal center separates the artery from the white pulp, and hemosiderin is sometimes present in the splenic corpuscle.

Red pulp is composed of sinusoids filled with blood. Reticular fibers form the walls of the sinusoids which tend to be arranged circularly around the splenic corpuscles. The red pulp is more organized and more sharply separated from white pulp in older fish.

Tissue imprints (Fig. 22) of the spleen have mature blood cells, macrophages, and some immature blood cells. Hemoblasts are less abundant than in the head or trunk kidney indicating that the spleen is less important in hemopoiesis. Macrophages often contain erythrocytes indicating the spleen is a site of blood cell destruction.

Pancreas is attached to the hepatic portal vein which lies against the spleen, and acini of exocrine pancreas are frequently found along veins within the spleen.

### Thymus

The thymus is located in the posterior portion



FIG. 22. Macrophages, often containing portions of erythrocytes, are very abundant in tissue imprints of the spleen. Blast cells are also present but not abundant. Most cells in spleen tissue imprints are mature blood cells. Air dried; Wright-Giemsa; × 1200.

of the dorsal wall of the pharynx (Fig. 23) and is usually not grossly visible. It is composed of closely spaced lymphocytes termed thymocytes because of their location (Fig. 24). Reticular cells support the lymphocytes which may vary in density in various regions resembling cortical and medullary zones of the mammalian thymus. Lobes are not formed, and the organ is located between the dermis and the epithelium of the opercular cavity.

The thymus is sometimes considered an endocrine organ (Lagler et al., 1962) but its most important function is its role in immunogenesis (Patt and Patt, 1969). It is probably most important in small fish because the thymus of the adult is very small, about the same size as in fingerlings.
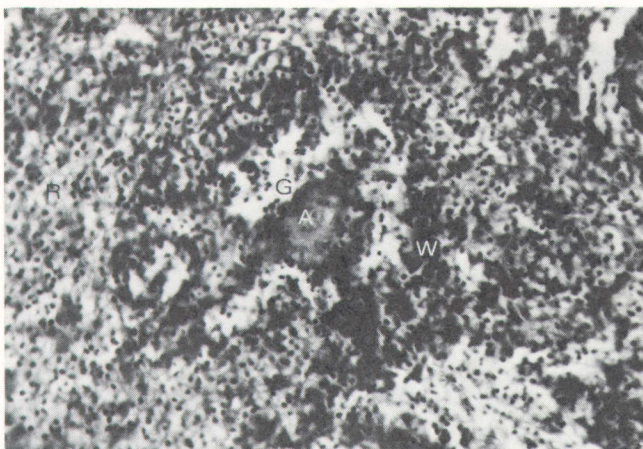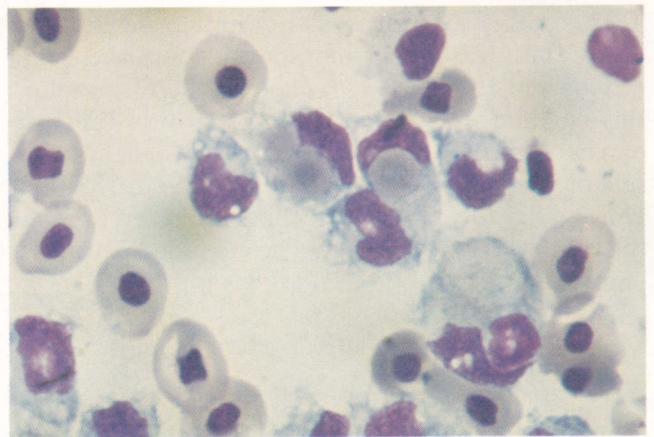


FIG. 21. This splenic corpuscle has a centrally located artery (A) surrounded by a germinal center (G) and an outer zone of white pulp (W). Red pulp (R) surrounds the corpuscle. The location of the artery and development of the germinal center is variable. Bouin's; H & E; × 240.



FIG. 23. The thymus (T) is a prominent structure in this parasagittal section of a 7-day old larva. It is located in the dorsoposterior portion of the gill chamber. Bouin's; H & E; × 65.

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## Blood Cells

Mature erythrocytes (red blood cells), mature leukocytes (white blood cells), and immature blood cells are found in the peripheral circulation where some hemopoiesis occurs. The amount of hemopoiesis occurring in circulation compared to that of hemopoietic tissue is not known, but the presence of immature cells complicates the identification of mature blood cells. The formation of blood cells of teleosts is not clearly understood but may involve a common stem cell or hemoblast from which all types of blood cells are formed (Catton, 1951; Watson et al., 1963). Hemoblasts have been referred to as large lymphocytes (Jordan and Speidel, 1924), and the distinction between these cells is not clear.

The terminology of fish blood cells is not uniform and is complicated by the differences between species. Most of our terminology is based on the generalized descriptions of teleost blood cells by Jakowska (1956). Blood cells of the brown bullhead (Weinberg et al., 1972) and goldfish (Watson et al., 1963; Weinreb, 1963) are similar to those of channel catfish. Williams and Warner (1976) described the blood cells of channel catfish, and their descriptions are similar to those of the present study except they report the presence of basophils and use the term monocyte in place of macrophage.

The number of various blood cells per mm³ from channel catfish in this study, in Haws and Goodnight (1962), and in Dodgen and Sullivan (1969) are compared in Table 1 (Page 18).

A variety of sizes of channel catfish juveniles and adults were used in the blood studies. Blood was collected from fingerlings by excising the tail, and with a syringe from the caudal vein of adults. Blood was collected without anticoagulants when possible or in heparinized capillary tubes. Blood smears were air-dried and stained with Wright's, Jenner-Giemsa, or Wright-Giemsa (Humason, 1967). Some smears were fixed with absolute methanol before staining. Wright-Giemsa give best results and most descriptions in this chapter are based on Wright-Giemsa stained smears. Hematocrits values were obtained by centrifuging for 15 minutes in heparinized microhematocrit tubes. Blood cell counts were made from 1:100 dilutions of heparinized blood in a hemocytometer. The diluting fluid was that used by Yokoyama (1960) and was satisfactory, although thrombocytes could not be reliably distinguished from other leukocytes. Differential counts of the various types of leukocytes were
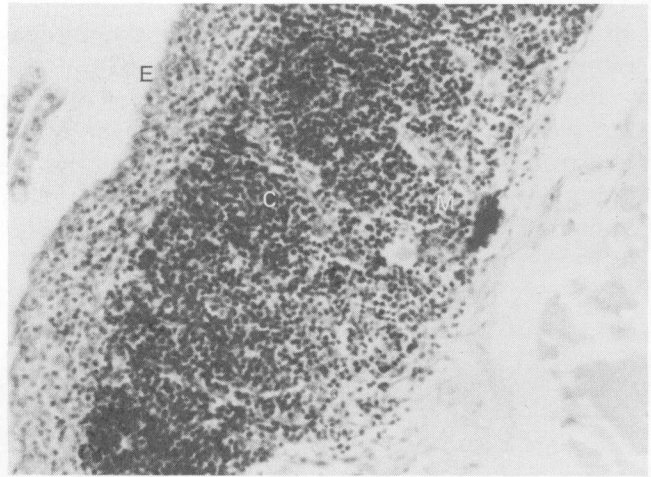


FIG. 24. The thymus of fingerlings has poorly delineated cortical (C) and medullary (M) zones and is located between the dermis and epithelium (E). The epithelium covering the thymus and lining most of the gill chamber has no alarm substance cells. Bouin's; H & E; × 240.

made from the stained smears, and the number of each type of leukocyte was calculated from these counts. Blood cell measurements were made with an ocular micrometer.

### ERYTHROCYTES

Erythrocytes are the most abundant cells in the blood (Table 1). Mature erythrocytes are elliptical in shape with a centrally located oval nucleus and pink cytoplasm (Fig. 25, 26, 27, and 28). Cell size is relatively constant, usually between $7 \times 10$ $\mu$ to $9 \times 12 \mu$. The nucleus is usually about $3 \times 5 \mu$ and stains a uniform dark violet.

Erythroblasts (Fig. 26) and reticulocytes (forms of immature erythrocytes), including some cells very early in the erythropoietic series, are present in the blood. Reticulocytes are distinguished by the presence of a reticular network after staining with brilliant cresyl blue. The percentage of reticulocytes present in two control groups of brown bullheads was 13.0 percent and 8.79 percent of the erythroid cells (Weinberg et al., 1972). Erythroblasts have basophilic cytoplasm and a nucleus larger than that of a mature erythrocyte.

Nuclear shadows are frequently seen in smears and are probably the disintegrated nuclei of erythrocytes (Yuki, 1960). These nuclear shadows stain pale pink and have an irregular outline. Nuclear shadows are an artifact resulting from smear preparation but may be indicative of the number of old or fragile erythrocytes (Yuki, 1960).

### LEUKOCYTES

Identification of leukocytes is sometimes difficult because of intermediate stages of immature cells. Thrombocytes are included with the discussion of leukocytes and in leukocyte counts,

although some authors have treated them separately (Romer, 1955; Watson et al., 1963).

Basophils are found in many species of teleosts but were not found in the channel catfish. Some neutrophils of channel catfish have basophilic granules, but these granules are smaller and less numerous than in basophils of species such as goldfish (Weinreb, 1963).

Monocytes were not found in channel catfish. Every leukocyte could be identified as a hemoblast,

channel catfish but do not describe them.

*Hemoblasts (Fig. 26).* These are found in smears but are much more abundant in hemopoietic tissues (Fig. 18). The shape of these cells varies but is often round. Cytoplasm is medium to dark blue and the large nucleus (6 to 11 $\mu$) has fine chromatin filaments and a pale background. Separation of these cells from lymphocytes is difficult. Weinberg et al. (1972) differentiate between these cells by cytoplasm color, an arbitrary difference
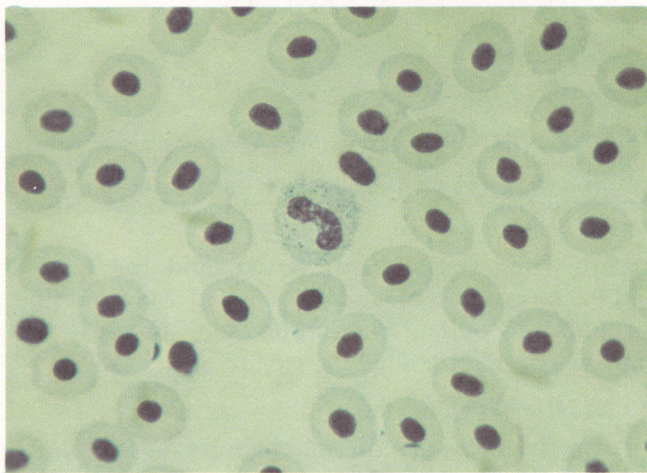


FIG. 25. Blood smear with several erythrocytes. The large round cell in the center is a neutrophil. A round thrombocyte (lower left) and an elongate thrombocyte (above neutrophil) are present. Methanol; Wright-Giemsa; × 800.



FIG. 27. This blood smear has a clump of round thrombocytes. A neutrophil is left of the clumped thrombocytes. Methanol; Wright-Giemsa; × 1600.
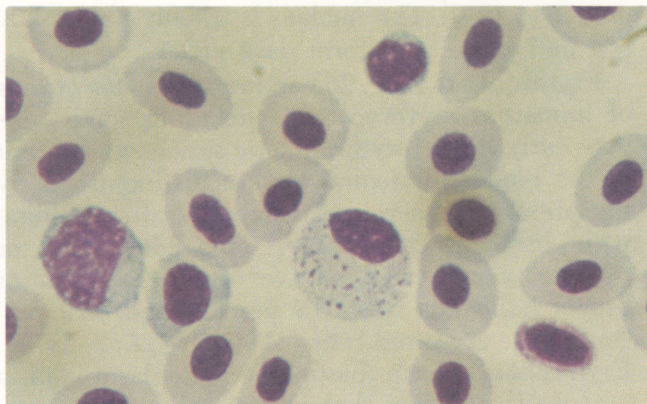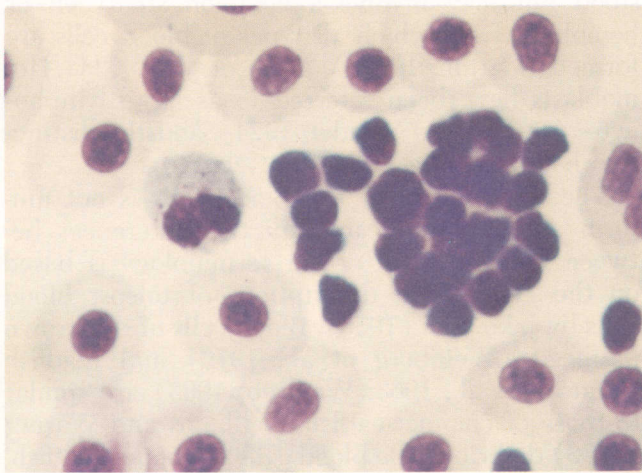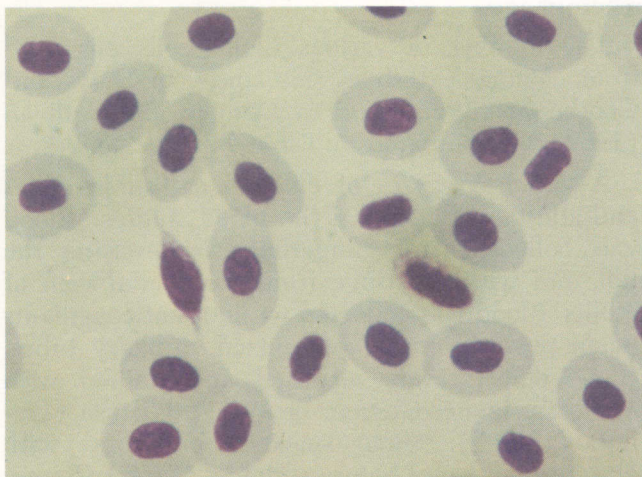


FIG. 26. The large leukocytes present in this blood smear are a hemoblast (left) and a neutrophil (center) which has large granules. An elongate thrombocyte (lower right) and a lymphocyte (top) are also seen. An erythroblast is just right of the hemoblast and has a larger nucleus than the adjacent erythrocytes. Methanol; Wright-Giemsa; × 1200.



FIG. 28. Blood smear with an elongate thrombocyte (right) and a fusiform thrombocyte (left). Methanol; Wright-Giemsa; × 1200.

lymphocyte, granulocyte, or an intermediate stage. Jakowska (1956) did not find monocytes as a distinct cell type in teleost blood and notes that the circulating hemoblasts sometimes resemble human monocytes. Watson et al. (1963) suggests that the monocytes of some authors are either neutrophils, hemoblasts, or large lymphocytes. Dodgen and Sullivan (1969) report monocytes in

in size (lymphocytes, 5 to 7 $\mu$; hemoblasts, 8 to 12 $\mu$), and nuclear staining. These criteria were applied in differential counts except that cells larger than 8 $\mu$ which had the other characteristics of lymphocytes were classified as lymphocytes.

*Lymphocytes (Fig. 26).* Most lymphocytes are smaller and have lighter blue cytoplasm than hem-

oblasts. Size of lymphocytes varies from 5 to 11 $\mu$ with the nucleus occupying most of the cell. The nucleus is usually idented and very basophilic with chromatin filaments barely distinguishable. Pseudopodia and irregular cell outline are characteristic of lymphocytes although many are round. Small vacuoles and red granules are sometimes present in the cytoplasm. Lymphocytes are frequently found migrating in epithelial tissue, although the significance of this is unknown. The fine structure of lymphocytes which have migrated into epithelium is highly modified (Andrew, 1965).

*Thrombocytes.* These cells are found in three distinct shapes; round (Fig. 25, 27), elongate (Fig. 25, 26, 28), and fusiform (Fig. 28). The relationship of these cell types is not clear but Weinberg et al. (1972) suggests that the elongate thrombocytes are immature thrombocytes. Thrombocytes are thought to be involved in blood clotting (Srivastava, 1969; Watson et al., 1963) and the clumping of thrombocytes (Fig. 27) seen in this study supports this hypothesis.

Round thrombocytes are often found clumped in smears but are also found separated. These cells are somewhat round but are often slightly irregular in shape especially when clumped. Cells range from 3 to 6 $\mu$ but are usually about 4 $\mu$. The nucleus occupies most of the cells and cytoplasm is very sparse or not visible. The cytoplasm stains pink or pale blue and the nucleus stains very dark and is sometimes indented.

Elongate thrombocytes vary from 3 × 7 $\mu$ to 4.5 × 11 $\mu$ and have elongate nuclei, 2 × 6 $\mu$ to 4.5 × 10 $\mu$. Mottled pink cytoplasm is usually visible surrounding the dark nucleus. The nucleus of elongate thrombocytes stains lighter than those of other types of thrombocytes and is often indented on one or both sides.

Fusiform thrombocytes have projections of pink or very pale blue cytoplasm from one or both ends. Little or no cytoplasm is visible on the sides of the nucleus. Cells range from 2.5 × 7 $\mu$ to 3.5 × 12 $\mu$ and the dark oval nuclei from 2 × 5 $\mu$ to 3 × 7 $\mu$. The nuclei of some cells are indented.

The relative abundance of the various shapes of thrombocytes varies but the round and elongate forms predominate. Many thrombocytes are found that are intermediate in shape suggesting that their shape may change due to maturation or other factors. It was also noticed that thrombocytes in clumps were usually round, even in smears containing large numbers of elongated thrombocytes. Collection of blood in heparinized tubes before making blood smears decreased the per-centage of round thrombocytes and increased the percentage of elongate thrombocytes. These two observations suggest that a transformation from the elongate form to the round form is involved in the clotting process.

Round thrombocytes and small lymphocytes can be confused while making differential counts (Watson et al., 1963), but these cells can be distinguished by the smaller size, denser nucleus, and scarcity of cytoplasm of the thrombocyte. The cytoplasm of the round thrombocytes is often not visible. If visible in Wright-Giemsa stained smears it is usually clear or light pink while a lymphocyte's cytoplasm is blue. Cells with characteristics intermediate between lymphocytes and thrombocytes are occasionally found, supporting the hypothesis of Jordan and Speidel (1924) that thrombocytes develop from small lymphocytes.

*Neutrophils (Fig. 25, 26, 27)* These are the only common granulocyte since eosinophils are rare and basophils are absent. These cells range from 8 to 13 $\mu$ and contain very fine to coarse granules in the mostly clear cytoplasm. The eccentrically located nucleus may be round, oblong or bilobed. The nucleus is usually much smaller than the cell and contains dark staining coarse chromatin filaments on a lighter background. The difference in granule size (Haider, 1968) and nucleus shape (Sanders, 1967) may be related to cell age with older cells having larger granules and more nuclear lobes.

*Eosinophils.* These cells are rare and were not found during differential counts so that the number of eosinophils is zero in Table 1. Most eosinophils seen in smears were round, 7 to 10 $\mu$ in diameter with round or band shaped nucleus. Large eosinophilic granules fill the cytoplasm.

*Macrophages.* These are abundant in the spleen (Fig. 22) and kidneys (Fig. 18) but were rarely found in the peripheral circulation. They are probably formed directly from hemoblasts (Jakowska, 1956) from which they are distinguished by the presence of large, debris filled vacuoles. Large lymphocytes and hemoblasts were frequently found with small clear vacuoles but were not considered macrophages. Cells which were clearly macrophages were not seen while differential counts were being made, so the number per mm$^3$ is zero in Table 1.

## HEMATOCRITS

Hematocrits for channel catfish varied greatly (Table 2), and nutritional factors and age affect the variation. Well nourished fingerlings had

TABLE 1. BLOOD CELL COUNTS OF CHANNEL CATFISH[1] COMPARED WITH DODGEN AND SULLIVAN (1969)[2] AND HAWS AND GOODNIGHT (1962)[3]

| Blood cells | Average cells/mm³ |
|---|---|
| Erythrocytes: | |
| This study | $2.44 \times 10^6$ |
| Dodgen and Sullivan | $2.23 \times 10^6$ |
| Haws and Goodnight | $2.16 \times 10^6$ |
| Total Leukocytes: | |
| This study | $164.0 \times 10^3$ |
| Dodgen and Sullivan | $146.3 \times 10^3$ |
| Lymphocytes: | |
| This study | $89.9 \times 10^3$ |
| Dodgen and Sullivan | $105.7 \times 10^3$ |
| Thrombocytes: | |
| This study | $68.4 \times 10^3$ |
| Dodgen and Sullivan | $34.2 \times 10^3$ |
| Neutrophils: | |
| This study | $5.2 \times 10^3$ |
| Dodgen and Sullivan | $3.7 \times 10^3$ |
| Hemoblasts: | |
| This study | $0.5 \times 10^3$ |
| Dodgen and Sullivan | $1.6 \times 10^3$ |
| Eosinophils: | |
| This study | 0 |
| Dodgen and Sullivan | $0.3 \times 10^3$ |
| Macrophages: | |
| This study | 0 |
| Dodgen and Sullivan | $0.4 \times 10^3$ |
| Monocytes: | |
| This study | Not used as cell type |
| Dodgen and Sullivan | $0.4 \times 10^3$ |

[1] Based on 35 fish.
[2] Based on 90 fish.
[3] Based on 31 fish.

higher hematocrits than adults or poorly fed fingerlings. The general health of the fish may be involved because feeding a complete diet for 28 days to fingerlings in poor condition did not sig-

TABLE 2. HEMATOCRITS OF CHANNEL CATFISH

| Description of sample | Average Hematocrit and Range |
|---|---|
| 142 adults from Auburn University ponds during all seasons of the year[1] | 40 (30-50) |
| 35 fingerlings (50 to 85 mm TL) in poor condition, held in indoor 500 l trough and fed nutritionally complete feed for various lengths of time (0-28 days)[2] | 31 (22-39) |
| 50 fingerlings (10 to 15 cm TL) kept in indoor aquaria at 28°C and fed nutritionally complete feed | 46 (39-53) |
| 20 fingerlings (50 to 75 mm TL) fed insufficient thiamine for 120 days in indoor flowing water trough at 28° C (Camacho, 1974) | 30 (24-35) |
| 40 fingerlings fed sufficient thiamine for controls in above experiment (Camacho, 1974) | 47 (32-55) |
| 32 specimens from Wabash River near Lafayette, Indiana (Haws and Goodnight, 1962) | 29.4) (17.0-41.5) |

[1] No significant difference was found in samples taken in different months between males and females although sexually mature fish were not sampled during the spawning season. Data collected by Dr. John Gaines.
[2] No significant difference was found between fish sampled at different times.

nificantly increase the hematocrit. No significant difference was found in hematocrits at different times of the year or in males and females; however, sexually mature fish were not sampled during late spring or early summer so a difference may occur during spawning.

# CHAPTER FOUR

# DIGESTIVE SYSTEM

The digestive system includes the alimentary tract consisting of the oral cavity, pharynx, esophagus, stomach, and intestine; and accessory digestive organs including the pancreas, liver, and gall bladder. The swim bladder will also be discussed in this chapter since it is derived from the foregut.

The digestive tract and pancreas of the channel catfish were described by Gammon (1970), and the digestive system and swim bladder of *Ictalurus nebulosus* were described by Macallum (1884). The description by Macallum, particularly concerning the pancreas and liver, is inadequate. The esophagus of *I. nebulosus* was described by Reifel and Travill (1977). The liver (Kendall and Hawkins, 1975; Hinton and Pool, 1976), swim bladder (Al-Rawi, 1967), stomach (Wargo, 1978), and posterior intestine (Krementz and Chapman, 1975) of channel catfish have also been described.

The channel catfish is omnivorous (Jearld, 1970; Cross, 1967) and the digestive system reflects this adaptation. The length of the alimentary canal from mouth to anus divided by the fish's total length varied from 0.99 to 3.17 in 15 specimens examined by Gammon (1970). The stomach is highly expandable and can accommodate large food items. Changes in the relative position of the digestive organs occur when they are full.

## Alimentary Canal

### ORAL CAVITY AND PHARYNX

The oral cavity and pharynx are grossly distinct because the pharynx is bounded laterally by gill slits (Fig. 29). The oral cavity and pharynx (Fig. 30) are histologically similar with an epithelium similar to that covering the external surface of the body (Chap. 7). There is a decrease in the number of alarm substance cells (see Chap. 7) and an increase in goblet cells posteriorly, and taste buds are abundant in all areas. A dense lamina propria and a submucosa of areolar connective tissue underlie the mucosal epithelium. The lining of the posterior pharynx forms longitudinal folds which are often flattened. The opercular cavity surrounding the gills has a thick epithelium with very few goblet or alarm substance cells (Fig 24). Teeth are present on the premaxilla and dentary bones of the mouth. Pharyngeal teeth are found
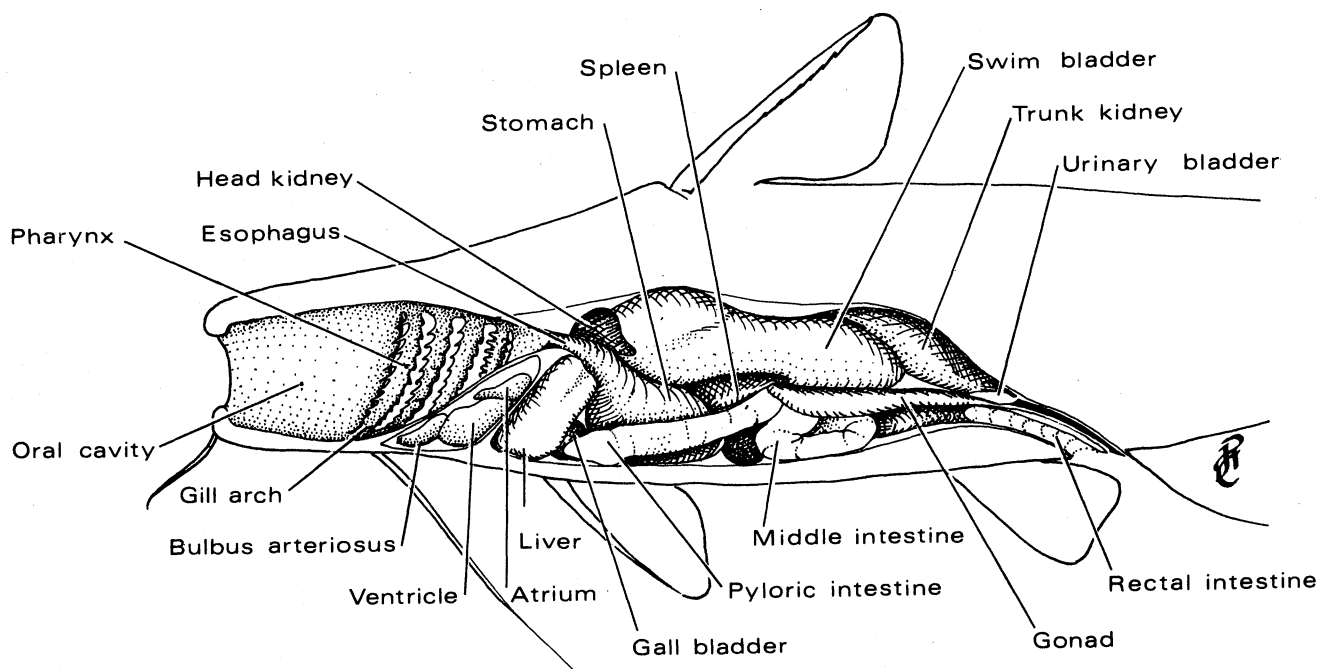


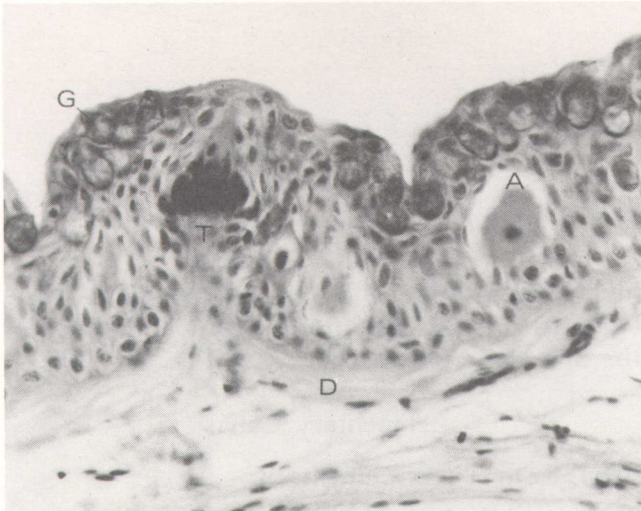FIG. 29. Lateral view of the internal anatomy of the channel catfish.

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FIG. 30. The pharynx is lined with epithelium which has goblet cells (G) and alarm substance cells (A). A lamina propria (D) and submucosa lie beneath the epithelium. Taste buds (T) are numerous in the pharynx. Bouin's; H & E; × 320.

on the lower and upper pharyngeal bones.

Teeth of the jaws and pharynx are small and numerous. Because they are of similar size, closely spaced, and form pads, they can be classified as cardiform. The teeth (Fig. 31) are formed of a dentine-like material surrounding a pulp cavity containing nerves, blood vessels, and fibrous connective tissue. Each tooth is covered with a very thin layer of enamel-like material. They are ankylosed to the underlying bone and are surrounded by modified epithelial cells.

## ESOPHAGUS

The esophagus (Fig. 29) extends from the pharynx to the stomach. Longitudinal folds permit expansion of the esophagus during swallowing. Gammon (1970) refers to primary, secondary, and tertiary folds of the esophagus, but only primary folds are present in small juveniles (Fig. 32).

The esophagus, stomach, and intestine have four basic layers which vary in composition between and within each of these organs (Table 3). The innermost layer is the mucosa (tunica mucosa) composed of epithelium, a lamina propria of fibrous connective tissue, and sometimes a muscularis mucosae. The submucosa (tela submucosa), composed of fibrous connective tissue, lies between the mucosa and the muscularis (tunica muscularis externa) which is formed from muscle. The outer layer is the serosa (tunica serosa) composed of fibrous connective tissue and simple squamous epithelium. This epithelium, which is the visceral peritoneum, is often termed a mesothelium because of its location.

The esophagus has several distinctive histologi-

cal features (Fig. 32 and 33) including a mucosa composed primarily of goblet cells, taste buds located on the ends of longitudinal folds, longitudinal bundles of striated muscle in the submucosa, a muscularis composed of circular striated muscle, and absence of a serosa in the anterior region. The mucosa and submucosa are not sharply separated since the lamina propria of the mucosa composed of connective tissue is difficult to differentiate from the submucosa.

The striated muscles of the esophagus are arranged in two layers. An outer circular layer composes the muscularis, and the submucosal muscle is composed of longitudinal bundles which continue anteriorly with some fibers inserting on the upper and lower pharyngeal bones. The submucosal muscle diminishes posteriorly and is absent in the posterior portion of the esophagus.

In previous descriptions of the digestive system, the submucosal muscle has been described as the muscularis mucosae (Gammon, 1970) although
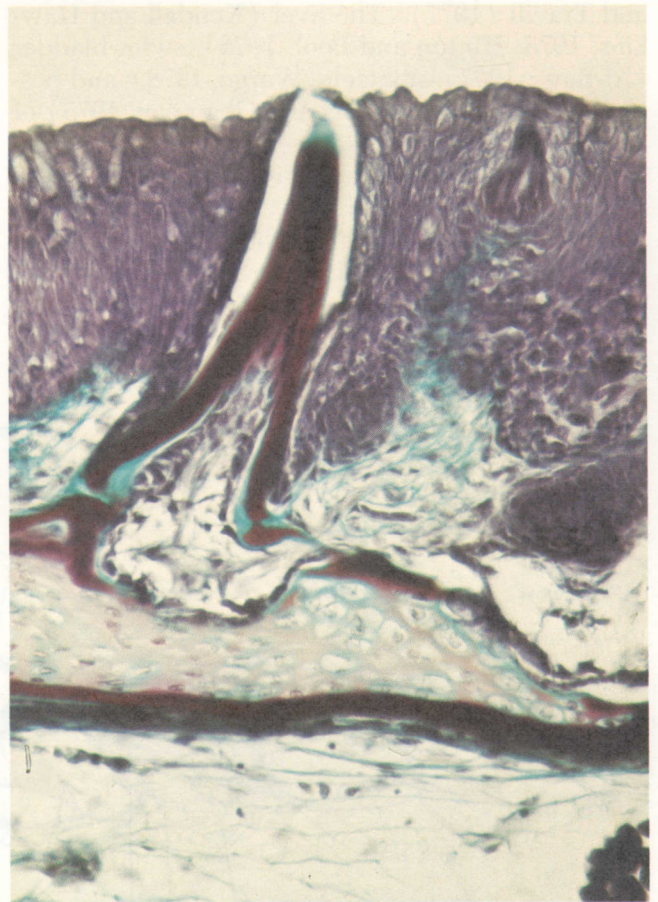


FIG. 31. This pharyngeal tooth of a fingerling is ankylosed to the underlying bone which has a cartilaginous core. The central pulp cavity and the dentine-like material of the tooth are seen in this photograph. The epithelium is thick and has goblet cells and a taste bud. The part of the tooth which protrudes through the epithelium was missed in this section. Bouin's; Masson's; × 350.

| Organ | Mucosal epithelium | Goblet cells | Gastric glands | Muscularis mucosae | Submucosal muscle | Layers of muscularis | Type of muscle |
|---|---|---|---|---|---|---|---|
| Esophagus | stratified squamous | extremely abundant | absent | absent | present | one | striated |
| Fundic stomach | simple columnar | absent | present | present | absent | usually two | smooth |
| Pyloric stomach | simple columnar | very rare | absent | present | absent | two | smooth |
| Intestine | simple columnar | moderate number | absent | absent | absent | two | smooth |

Al-Rawi (1967) states that the muscularis mucosae is absent from the channel catfish esophagus. This discrepancy is undoubtedly due to a confusion in terminology. Mehrotra and Khanna (1969), Al-Hussaini (1947), and Liem (1967) described



FIG. 33. The mucosa of the esophagus is stratified squamous epithelium, but the large goblet cells (G) are more prominent than the non-glandular epithelial cells. A lamina propria (P) lies beneath the epithelium but can not be distinctly separated from the submucosa. T, tangential section of taste bud. Bouin's; H & E; × 240.



FIG. 32. The esophagus has a mucosa composed of a thin lamina propria and an epithelium with numerous goblet cells surrounding the lumen. The submucosa (stained green) is composed of fibrous connective tissue and forms longitudinal folds. The submucosal muscle (S) is formed of striated muscle oriented longitudinally in the submucosa and becomes less abundant near the stomach. The muscularis (M) is composed of a circular layer of striated muscle. The outer layer in this section is the adventitia (A) composed of loose fibrous connective tissue which binds the esophagus to adjacent organs, but more posterior portions have serosa as an outer layer which is composed of fibrous connective tissue covered by mesothelium. Bouin's; Masson's; × 90.

similar longitudinal muscle bundles inside of the circular layer of the muscularis of other fish species as an inner layer of the muscularis.

Confusion in terminology of the submucosal muscles of the esophagus has resulted because the distinctiveness of these muscles has not been realized. The muscularis is composed of inner circular and outer longitudinal layers in most vertebrates (Patt and Patt, 1969) and a muscularis mucosae is part of the mucosa. The submucosal muscle is located within the submucosa and is not a part of the muscularis or mucosa. Their function is probably related to the coordination of the contractions of the esophagus with movements of the pharyngeal teeth.

## STOMACH

The junction of the esophagus and stomach occurs just posterior to the connection of the pneumatic duct to the esophagus. The stomach is J-shaped with the ascending limb ending at the pyloric sphincter. The stomach has two distinct regions, fundic and pyloric, which can usually be distinguished grossly by the larger folds of the
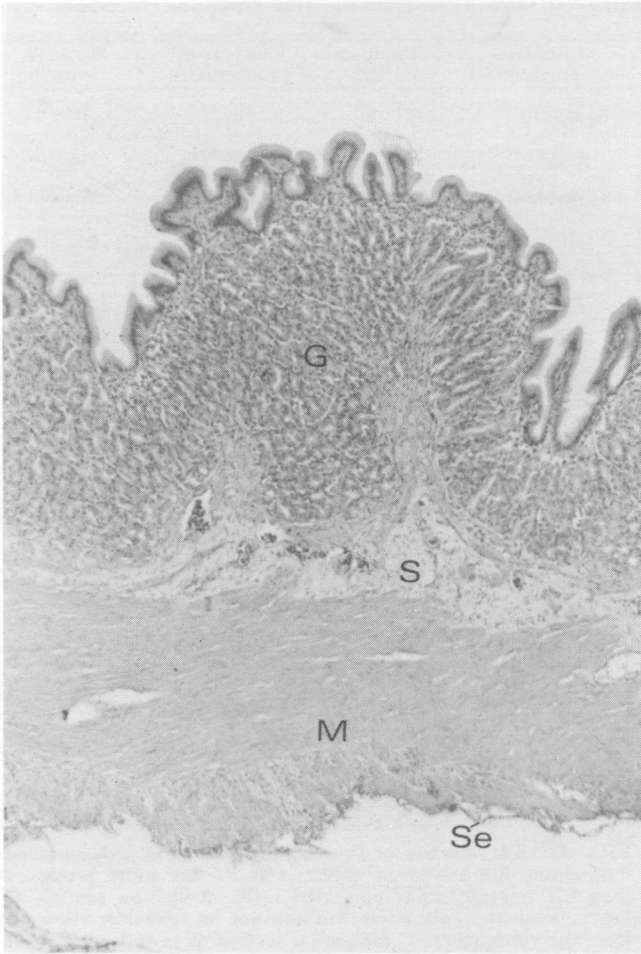
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FIG. 34. The fundic portion of the stomach has a thick mucosa due to the presence of gastric glands (G). The submucosa (S) has numerous blood vessels and supports the large folds characteristic of the fundic stomach. The muscularis (M) has two or three layers of smooth muscle. The serosa (Se) is composed of fibrous connective tissue and mesothelium. Bouin's; H & E; × 90.

fundic region. The stomach of teleosts is sometimes divided into three regions (Weinreb and Bilstad, 1955; Gammon, 1970), but this does not seem justified in the channel catfish because of lack of histological differentiation.

*Fundic region.* The mucosa is much thicker in the fundic region of the stomach (Fig. 34 and 35) than in other regions of the alimentary canal. The mucosa is composed of simple columnar epithelium without goblet cells, gastric glands supported by the lamina propria, and the muscularis mucosae. The gastric glands are simple tubular and composed of uniform secretory cells. The submucosa, multilayered muscularis, and serosa are also present. All muscle in the stomach is smooth muscle.

*Pyloric region.* The absence of gastric glands in the pyloric region (Fig. 36) is the most significant difference between it and the fundic area of the

stomach. Other tissues are basically similar in both areas. Goblet cells were found in the mucosa of some specimens but were rare. The pyloric region usually begins as the stomach curves anteriorly toward the pyloric sphincter with the muscularis increasing in thickness near the sphincter. The pyloric sphincter is similar to other areas of the fundic region except that the circular layer of the muscularis is much thicker.

### INTESTINE

The intestine begins at the pyloric sphincter and is not clearly differentiated into regions, and no pyloric ceca are present. Gammon (1970) designated the anterior portion from the pyloric sphincter to the first loop posterior to the stomach as the pyloric intestine (Fig. 37 and 38), the coiled portion as the middle intestine, and the portion posterior to the last loop as the rectal intestine
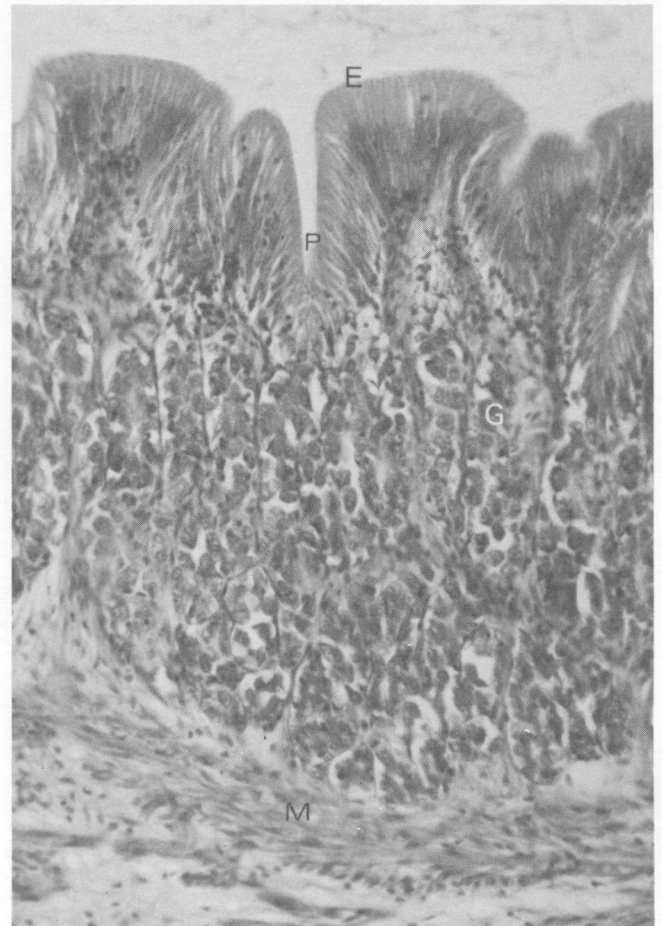


FIG. 35. The mucosa of the fundic stomach has simple columnar epithelium (E) with basally located nuclei and light staining apical portion. Several cells which appear to be lymphocytes are present in the epithelium and immediately below it. Tubular gastric glands (G) are supported by the lamina propria and empty into gastric pits (P). The muscularis mucosae (M) separates the lamina propria from the submucosa. Bouin's; H & E; × 235.
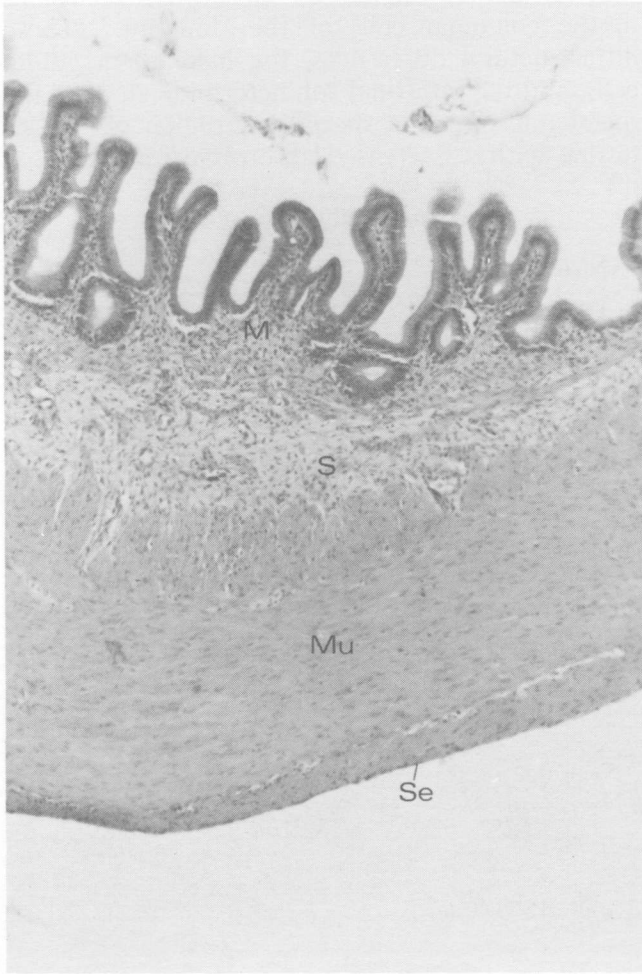
FIG. 36. The pyloric region of the stomach is easily distinguished from the fundic region by the absence of gastric glands. The mucosa (M) has simple columnar epithelium, a lamina propria, and a muscularis mucosae. Folds of the mucosa are supported by the lamina propria and are similar to the gastric pits of the fundic stomach. Submucosal folds are sometimes present in the pyloric stomach as in the fundic stomach. The remainder of the wall is similar to that of the fundic stomach except near the pylorus where the thickness of the muscularis increases. S, submucosa; Mu, muscularis; Se, serosa. Bouin's; H & E; × 90.



FIG. 37. The pyloric intestine has simple columnar epithelium (E) with scattered goblet cells. A thin lamina propria is part of the mucosa but is not clearly separated from the submucosa (S). Tall, longitudinal folds which often branch, project into the lumen. The muscularis (M) has inner circular and outer longitudinal layers of smooth muscle. The serosa is composed of a very thin layer of connective tissue covered by mesothelium. Formalin; H & E; × 120.
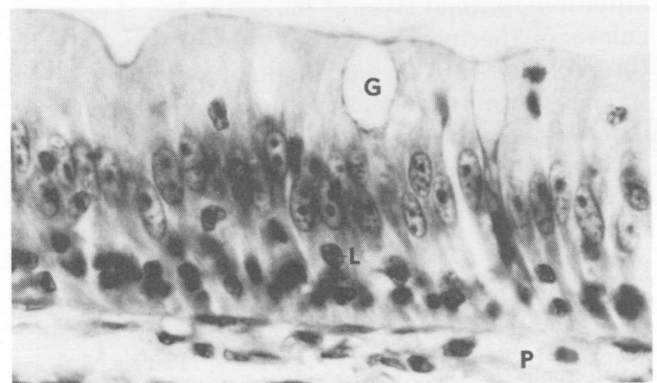


FIG. 38. The mucosa of the intestine has tall columnar epithelium with a striated border and nuclei near the center of the cell. Goblet cells (G) and lymphocytes (L) are found among the epithelial cells. The lamina propria (P) is composed of fibrous connective tissue and also has lymphocytes. Bouin's; H & E; × 800.

(Fig. 39). Digestive enzymes and bile enter the pyloric intestine through the common bile duct and pancreatic ducts. An intestinal sphincter (Fig. 40) (Lane, 1973) is located between the middle and rectal intestines. The only glands present in the intestine are goblet cells. Multicellular glands were mentioned by Gammon, but they are probably not glands since the cells are not specialized for secretion.

The pyloric and middle intestines are very similar, although the lumen of the pyloric intestine is usually larger. The rectal intestine has an increase in the number of goblet cells with the amount of increase being much greater in some specimens. The longitudinal folds of the rectal intestine are also different since they are some-

times stretched out in completely extended intestines (Fig. 39). The columnar cells of the mucosa of the posterior middle intestine and rectal
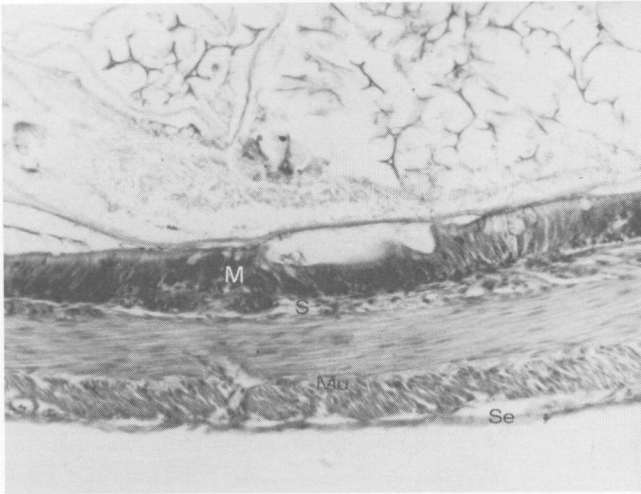
FIG. 39. The rectal intestine, which is posterior to the intestinal sphincter, has thick folds which flatten when the wall is extended. The mucosa (M), submucosa (S), muscularis (Mu), and serosa (Se) are similar to those of other regions of the intestine. More goblet cells are present in this portion of the intestine than in other regions. Bouin's; H & E; × 160.

intestine have clear staining apical portions in some specimens.

The most modified portion of the intestine is in the region of the intestinal sphincter (Fig. 40) which was apparently overlooked by Gammon (1970) and Krementz and Chapman (1975). A similar structure is present in *I. nebulosus* (Macallum, 1884). The muscularis is thickened at the sphincter, and most specimens have a circular fold supported by circular smooth muscle forming a valve. The fold would increase the effectiveness of this structure in preventing the passage of food. Both layers of the muscularis are thickened anteriorly and posteriorly from the sphincter, but the circular layer becomes much thicker than the outer longitudinal layer at the sphincter. The muscularis of the intestine is not thickened except in the proximity of the intestinal sphincter.

The fibrous connective tissue between the mucosal epithelium and the muscularis can be divided into submucosa and lamina propria, although a distinct separation is usually not present since a muscularis mucosae is absent. The lamina propria, lying immediately beneath the epithelium, is usually more compact than the submucosa and has been termed stratum compactum of the submucosa by some authors (Curry, 1939; McVay and Kaan, 1940; Weinreb and Bilstad, 1955; Krementz and Chapman, 1975). Gammon (1970) used the term lamina propria in reference to this layer in the channel catfish.

The ultrastructure of the posterior intestine of the channel catfish has been described by Krementz and Chapman (1975). Ultrastructural differences between the "midgut" and "hindgut" were

shorter microvilli and fewer absorptive inclusions in the columnar cells of the "hindgut." These ultrastructural differences, the increase in goblet cells, and the intestinal sphincter indicate that the rectal intestine is a specialized region of the intestine with a decreased absorptive function.

### Accessory Digestive Organs

PANCREAS

The pancreas (Fig. 41 and 42) consists of scattered white nodules (Brockman bodies) in mesenteries in the vicinity of the bile duct, along the
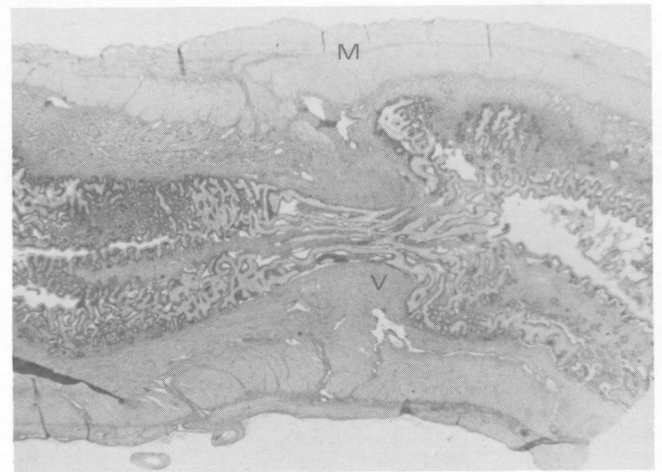


FIG. 40. The intestinal sphincter has an increase in thickness of the muscularis (M) and a fold of the wall forming a valve (V). Longitudinal section; Bouin's; H & E; × 11.



FIG. 41. This nodule of pancreas from mesentery near the spleen has acini of exocrine tissue (E) and a pancreatic islet (P). The acini of exocrine pancreas are formed of cells with basophilic cytoplasm containing eosinophilic zymogen granules. A capsule surrounds the islet, but exocrine pancreas is often found within the capsule. The cells of the islet appear as cords separated by capillaries. The various cell types of the islet are not differentiated by hematoxylin and eosin. V, vein; N, nerve. Bouin's; H & E; × 120.

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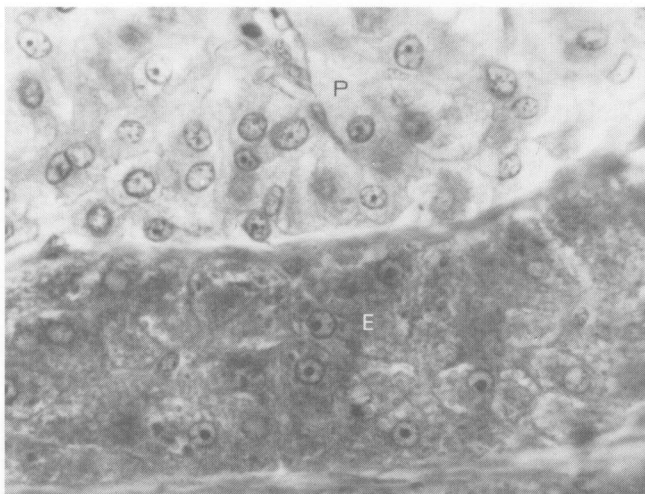FIG. 42. The two types of tissue of the pancreas are exocrine tissue (E) and pancreatic islets (P). Bouin's; H & E; × 600.



FIG. 43. Branches of the hepatic portal vein in the liver are surrounded by acini of exocrine pancreas (E). The vacuolated appearance of the hepatocytes is a result of the high glycogen content (compare to Fig. 44 from a starved specimen). Bouin's; H & E; × 240.

hepatic portal vein between the spleen and liver, in tissue surrounding branches of the hepatic portal vein within the liver (Fig. 43) and occasionally within the spleen. Pancreas includes exocrine tissue which produces digestive enzymes and endocrine tissue concentrated in pancreatic islets (Chap. 5). The larger nodules of pancreas in the mesenteries have pancreatic islets surrounded by acini of exocrine pancreas.

Several ducts connect the scattered exocrine pancreas to the pyloric intestine. Near the intestine, the pancreatic ducts closely parallel the common bile duct. Each of the pancreatic ducts enters the intestine separately and do not enter the common bile duct as reported by Gammon (1970), although they are tightly connected to its external surface. The ducts have the same basic layers found in the alimentary canal but are distinctive by having no folds in the mucosa.

Goblet cells are absent from the mucosa of columnar epithelium, and the serosa surrounding adjacent ducts is often continuous.

## LIVER

The liver (Fig. 29) is large and varies from yellowish brown to dark red in color. The parenchyma (Fig. 43) is not divided into distinct lobules and is composed of branching, two-cell thick laminae of hepatocytes separated by sinusoids. The appearance of the hepatocytes varies between specimens. The principle difference is the degree of vacuolation in routine preparations which results from the removal of glycogen and fat during slide preparation. Well fed specimens (Fig. 43) have greater vacuolation than starved specimens (Fig. 44). The gross variation in the color of the fresh liver may also be related to difference in glycogen and fat content.

The hepatic portal vein branches before enter-



FIG. 44. The liver is composed of laminae of hepatocytes which are two cells in thickness. The laminae are arranged around central veins (V) into which blood flows from the sinusoids which separate the laminae. Bouin's; H & E; × 240.

ing the posterior side of the liver, and the hepatic vein leaves the anterior side and passes through the transverse septum to the heart (Fig. 3). Blood flows from branches of the hepatic portal vein and hepatic artery through the sinusoids to central veins which empty into the hepatic vein. Hepatic arteries are small and contribute little of the blood going to the liver. Pancreatic tissue surrounds branches of the hepatic portal vein within the liver.

Bile canaliculi (Fig. 45) within the laminae of hepatocytes drain bile from hepatocytes to bile ducts which carry it to the gall bladder. Bile canaliculi are usually not visible with the light microscope. Electron microscopy has shown that they do not have their own wall but are expan-
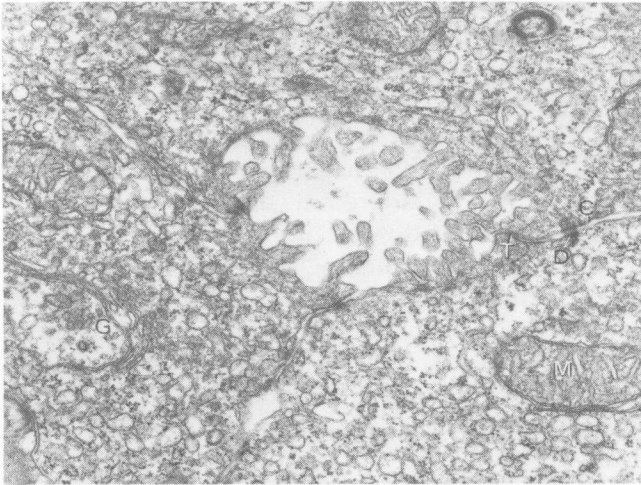
FIG. 45. Electron micrograph of the liver. The bile canaliculi of the liver are formed by the expansion of the intercellular space between hepatocytes. Microvilli project from the hepatocytes into the bile canaliculus. M, mitochondria; C, cell membrane; T, tight junction; D, desmosome; G, golgi complex. Osmium tetroxide; uranyl acetate and lead citrate; × 18,000.

sions of intercellular spaces between hepatocytes.

Kendall and Hawkins (1975) used a staining technique of Williams (1960) to demonstrate that argyrophilic reticular fibers form a meshwork supporting the hepatocytes. These fibers were also in the walls of blood vessels and around the acini of exocrine pancreas surrounding the branches of the hepatic portal vein.

## GALL BLADDER AND BILE DUCTS

The gall bladder, used to store the green bile, is located on the right, posterior side of the liver. The common bile duct connects the gall bladder to the pyloric intestine (Fig. 46) as the intestine passes ventral to the esophagus and just posterior to the liver. Several short, small hepatic ducts
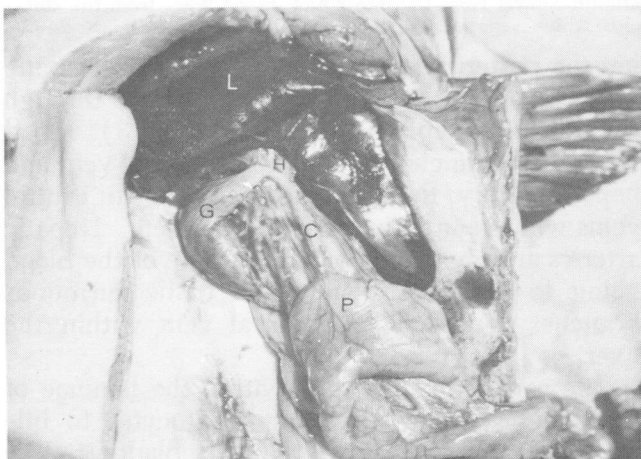


FIG. 46. The common bile duct (C) connects the gall bladder (G) to the pyloric intestine (P). Hepatic ducts connect the liver (L) to the common bile duct in this area (H). Ventral view of 4 kg channel catfish.

connect the liver to the upper portion of the common bile duct. A distinct cystic duct is not present because the hepatic ducts enter the common bile duct at several points beginning at the neck of the
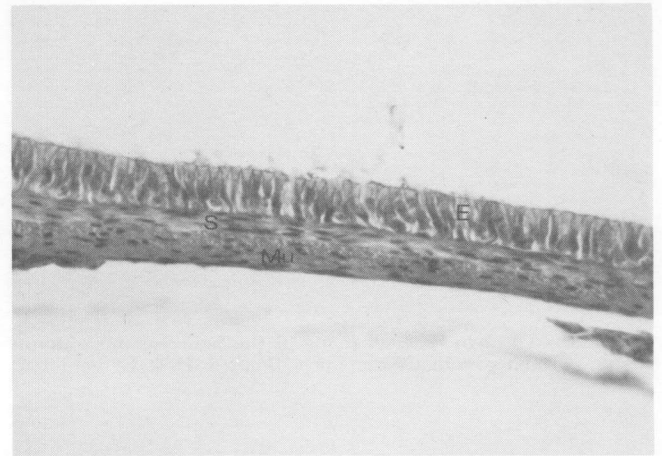


FIG. 47. The thin wall of the gall bladder has a simple columnar epithelium (E) which flattens to cuboidal when stretched. The mucosal epithelial cells have light staining apical portions. The remainder of the wall consists of the submucosa (S) of fibrous connective tissue and the thin muscularis (M) which is usually composed of one layer of smooth muscle. The outer surface is covered by mesothelium. Bouin's; H & E; × 320.
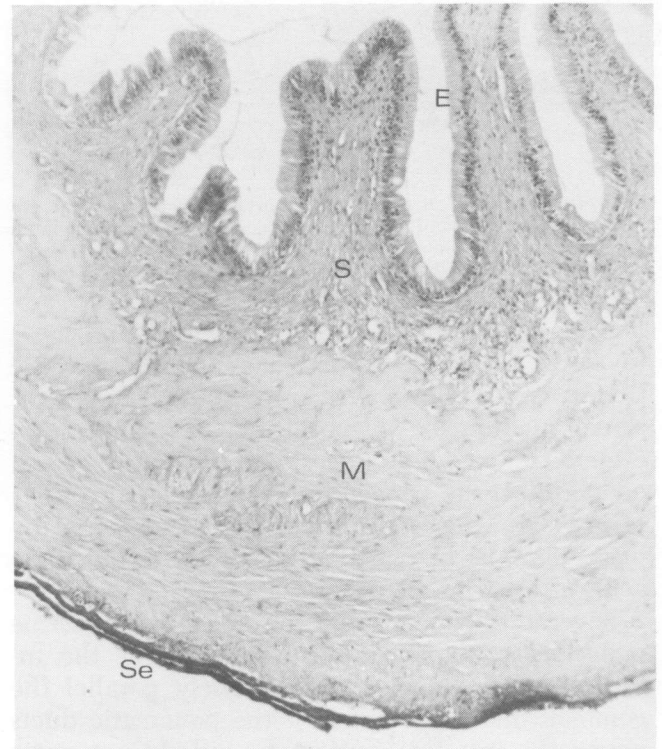


FIG. 48. The common bile duct, connecting the gall bladder to the intestine, has a mucosa of columnar epithelium (E) with basally located nuclei and scattered goblet cells. A submucosa (S), which forms longitudinal folds, lies between the epithelium and the muscularis (M) composed of an irregular layer of smooth muscle. The serosa (Se) covers the outer surface. Bouin's; H & E; × 120.
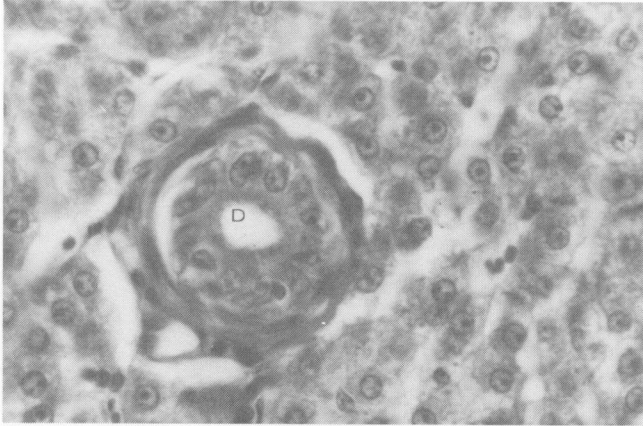
FIG. 49. Bile ducts (D) within the liver receive bile from bile cancaliculi. The duct has columnar epithelium and is surrounded by fibrous connective tissue and a few smooth muscle cells. Bouin's; H & E; × 600.

gall bladder. Other authors have used different terminology for the bile ducts (Chakrabarte et al., 1973).

The walls of the gall bladder (Fig. 47) and common bile duct (Fig. 48) have the basic layers found in the digestive tract, but each layer is re-

duced or simplified. The mucosa has columnar epithelium with basally located nuclei. The common bile duct has scattered goblet cells, and some specimens had columnar cells with a light staining apical region. The mucosal epithelium of the gall bladder flattens to cuboidal when stretched.

The hepatic bile ducts in the liver (Fig. 49) which connect the bile canaliculi to the common bile duct have a columnar epithelium surrounded by fibrous connective tissue. As they approach the common bile duct and emerge from the liver, smooth muscle and serosa are added, and their structure is similar to that of the common bile duct.

## Swim Bladder

The swim bladder (gas bladder) is physostomous with the pneumatic duct connecting the mid-ventral swim bladder to the dorsolateral right side of the esophagus very close to the stomach (Fig. 50). The swim bladder is located retroperitoneally just ventral to the vertebrae and between the head and trunk kidneys (Fig. 29). The walls are white and semi-rigid, and two internal septa
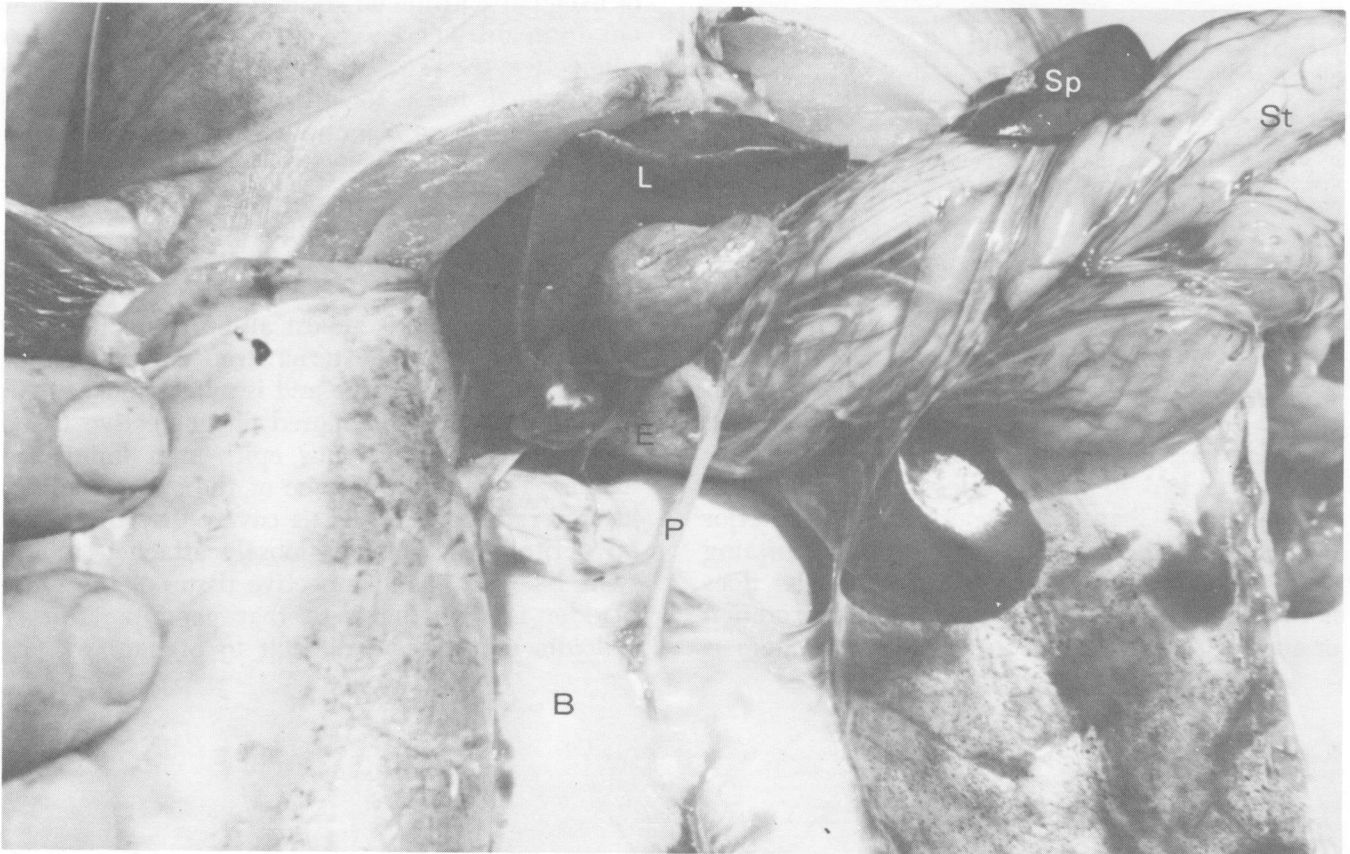


FIG. 50. The pneumatic duct (P) connects the swim bladder (B) to the esophagus (E). St, stomach; Sp, spleen; L, liver. Ventral view of 4 kg channel catfish.
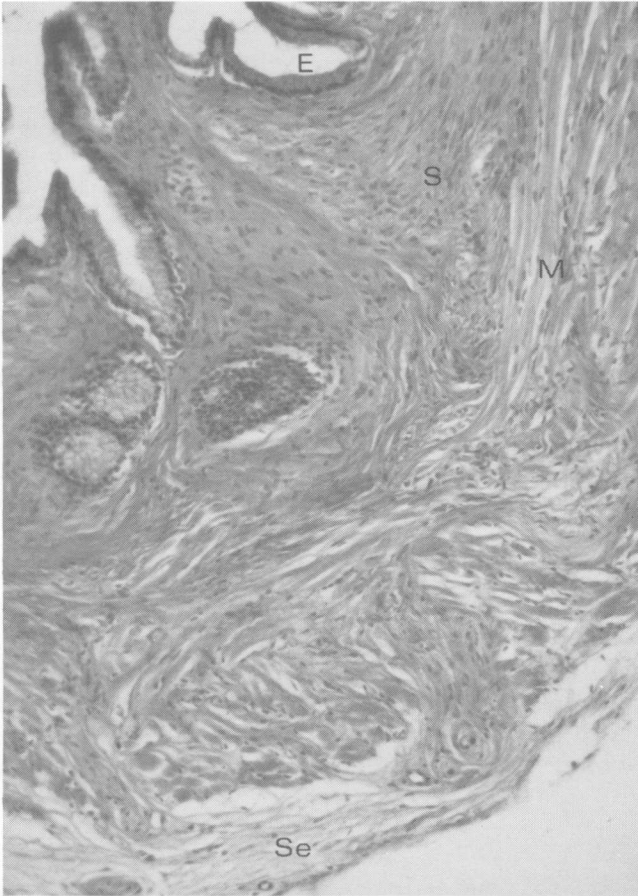
FIG. 51. The pneumatic duct has a mucosa of simple columnar epithelium (E) with basally located nuclei and very light staining apical portion. A submucosa of fibrous connective tissue (S) underlies the epithelium and supports tall longitudinal folds. The discontinuous muscularis (M) is composed of striated muscle and does not form distinct layers. The serosa (Se) has a relatively thick layer of fibrous connective tissue covered by mesothelium. Bouin's; H & E; × 175.



FIG. 52. The swim bladder wall has a tunica externa (E) and a tunica interna (I). The tunica externa is composed of two very dense layers of obliquely situated layers of collagenous fibers. The tunica interna has a thin layer of fibrous connective tissue and a layer of simple squamous epithelium (S) which lines the swim bladder. The epithelium has been pulled away from the connective tissue during sectioning. Bouin's; H & E; × 490.

divide the swim bladder into three chambers. A transverse septum forms an anterior chamber, and a longitudinal septum extending posteriorly from the transverse septum forms two posterior chambers. The transverse septum is incomplete so that each posterior chamber is in communication with the anterior chamber. The anterior chamber is firmly attached to the tripodes of the Weberian ossicle series (Chap. 12). A portion of the anterior chamber is in direct contact with the skin forming a lateral cutaneous area. The swim bladder does not appear to have specialized areas for excretion or absorption of gas from the circulatory system as

found in some teleosts (Jones and Marshall, 1953).

The wall of the pneumatic duct (Fig. 51) has a mucosa of columnar epithelium, a submucosa which supports longitudinal folds, a muscularis of irregularly arranged striated muscle which does not form distinct layers, and a serosa of fibrous connective tissue covered by mesothelium. The longitudinal folds sometime form septa which divide the lumen. The mucosal epithelium has a light staining apical region and basally located nuclei. The submucosa, muscularis, and connective tissue of the serosa intermingle and are often not distinct.

The swim bladder wall (Fig. 52) has only two distinct layers and is almost all fibrous connective tissue. The tunica externa has two layers of fibrous connective tissue and is much thicker than the tunica interna composed of connective tissue and the simple squamous epithelium lining the lumen. The ventral surface of the swim bladder, located retroperitoneally, is covered by the parietal peritoneum which is loosely attached to the swim bladder. The connective tissue of the swim bladder is very dense so that good paraffin or celloidin sections are difficult to prepare.

# CHAPTER FIVE

# ENDOCRINE SYSTEM

Endocrine organs have varied morphology and function but are similar by being ductless glands which depend on the circulatory system to disperse the hormones which they produce. Some endocrine tissues do not form a discrete organ and may be intermingled with other tissues. The gonads contain endocrine tissue but these organs, including the endocrine portion, are described in Chap. 10. The pineal body may have an endocrine function but is an integral part of the brain and is described in Chap. 9. The thymus, sometimes considered an endocrine organ, is important in immunogenesis and is discussed in Chap. 3.

## Head Kidney

Interrenal and chromaffin tissues are found in the head kidney. Hemopoietic tissues are also present in this organ and are discussed in Chap. 3. The head kidney is completely separate from the opisthonephric (trunk) kidney, and is composed of fused bilateral lobes located anterior to the swim bladder (Fig. 29). Kidney tubules are present in young specimens but degenerate as the fish grows and are absent in most fingerlings longer than 4 cm. The posterior cardinal vein passes through the anterior portion of the head kidney and the parietal peritoneum covers the ventral surface. The interrenal and hemopoietic tissues are intermingled throughout most of the organ but are easily distinguished in sections.

### INTERRENAL TISSUE

The interrenal tissue (Fig. 53 and 54), also referred to as adrenal cortical tissue, is homologous to the adrenal cortex of the mammalian adrenal gland (Phillips and Bellamy, 1963), and functions probably include regulation of carbohydrate and protein metabolism, osmoregulation, blood cell movement from hemopoietic tissues, growth, regeneration, and anti-inflammatory reactions (Chester Jones et al., 1969). Interrenal and hemopoietic tissues are found throughout the head kidney of channel catfish. The relative abundance
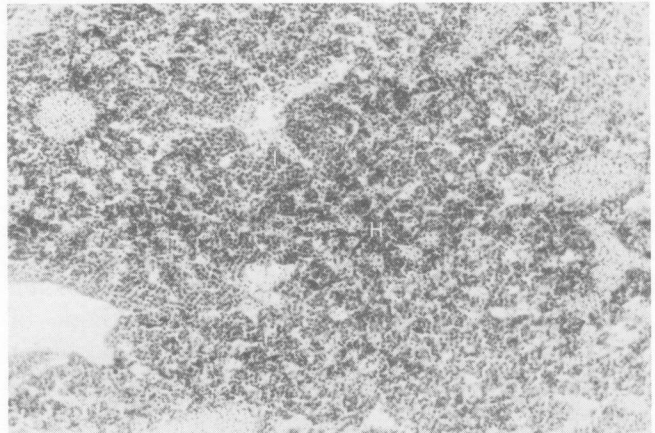


FIG. 53. The head kidney is primarily composed of hemopoietic tissue (H) and interrenal tissue (I). Kidney tubules and renal corpuscles are totally absent except in juveniles less than 40 mm TL. Bouin's; H & E; × 120.
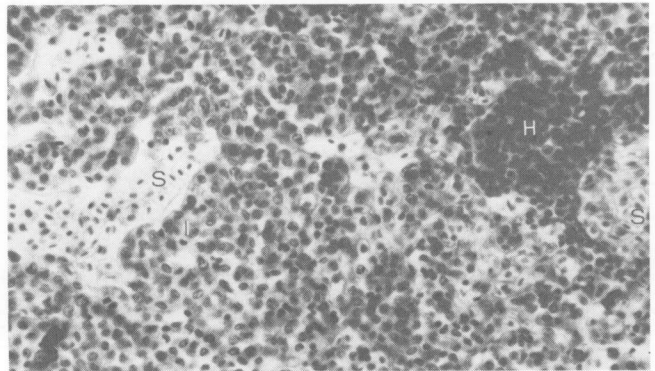


FIG. 54. Interrenal cells (I) have a centrally located nucleus, eosinophilic cytoplasm, somewhat regular cell shape, and often appear to be arranged in cords. Hemopoietic tissue (H) has a generally more basophilic appearance due to the dark nuclei of irregularly arranged cells which often have very little cytoplasm. Both tissue types are found surrounding blood sinuses (S). Zenker's; H & E; × 320.

of these two tissue types varies widely ranging from mostly interrenal to mostly hemopoietic. The interrenal tissue is associated with venous sinuses and fits the type III distributional classification of Nandi (1962).

### CHROMAFFIN TISSUE

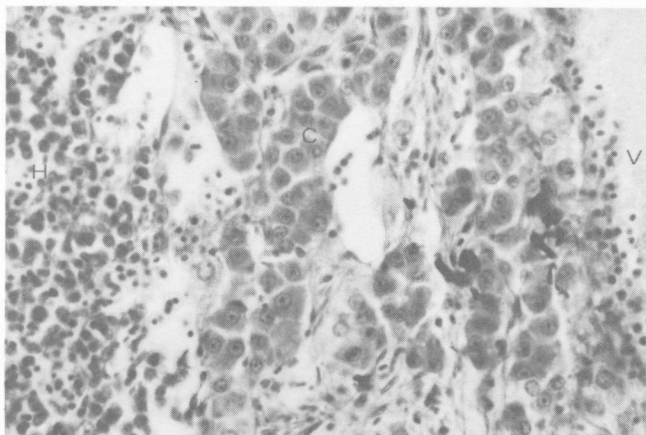The chromaffin tissue (Fig. 55) is homologous to the adrenal medulla of mammals and produces

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FIG. 55. Chromaffin tissue (C) is found only in the wall of the posterior cardinal veins (V) of the head kidney. These large cells have centrally located nuclei and light staining cytoplasm. Some chromaffin cells have a chromaffin reaction when fixed in a potassium dichromate containing fixative but most do not. H, hemopoietic tissue. Helly's; H & E; × 320.

adrenalin and noradrenalin (Euler, 1963) which are sympathomimetic. The chromaffin tissue of channel catfish occurs in the wall of the posterior cardinal vein and its branches and can be classified distributionally as type I (Nandi, 1962). The chromaffin cells sometimes have brown granules (chromaffin reaction) when fixed in potassium dichromate containing fixatives. This chromaffin reaction was not found in *Clarias batrachus* (Dixit, 1970). The absence of the chromaffin reaction in some chromaffin cells may be due to low content of adrenalin (Baecher, 1928).

### Corpuscles of Stannius

The paired corpuscles of Stannius (Fig. 56 and 57) are located on the lateral edges midway between the ends of the posterior or trunk kidney. Each corpuscle is spherical and occasionally multilobed. The various functions which have been
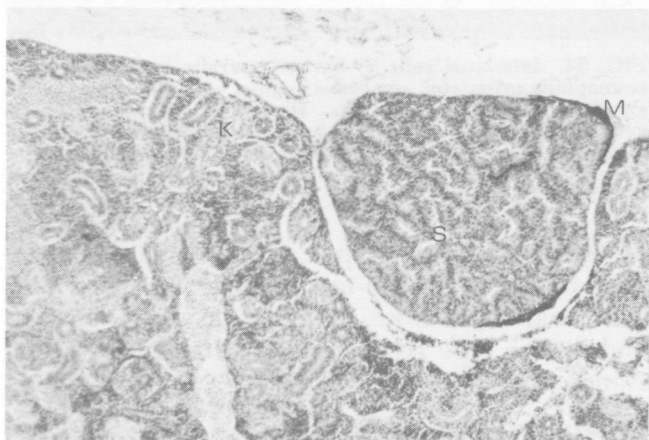


FIG. 56. The corpuscle of Stannius (S) is closely associated with the trunk kidney (K) and has melanophores (M) covering part of its surface. Bouin's; H & E; × 80.

attributed to the corpuscle of Stannius, reviewed by Krishnamurthy (1968) and Chester Jones (1969), include osmoregulation (analogous to the zona glomerulosa of mammalian adrenal cortex), steriod production or storage, and renin production. The corpuscle of Stannius is also important in calcium metabolism (Pang, 1973). A strong rise in the calcium and fall of the phosphate level in the blood of the eel (Fontaine, 1967) and associated changes in bone tissue and mineralization of intercellular substance (Lopez, 1970) have been reported after removal of the corpuscles of Stannius.
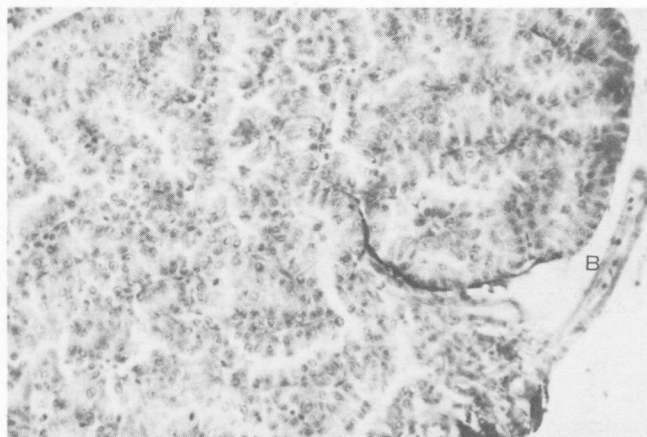


FIG. 57. The cells of the corpuscle of Stannius are arranged in cords which are separated by fibrous connective tissue septa containing capillaries. B, blood vessel. Bouin's; H & E; × 240.

### Pancreatic Islets

The pancreatic islets (islets of Langerhan) (Fig. 41 and 42) are the endocrine portion of the pancreas and are located in the larger nodules (Brockman bodies) found in the mesenteries associated with the bile ducts and anterior hepatic portal vein. These nodules of pancreas containing a large proportion of endocrine tissues are sometimes referred to as "principal islets" (Gorbman and Bern, 1966) although this terminology is confusing (Gammon, 1970; Epple, 1969). Pancreatic islets are surrounded by exocrine pancreas and are not found in association with the pancreas found in the liver or spleen. Some of the smaller nodules of exocrine pancreas in mesenteries also have no endocrine tissue.

Cell types of the pancreatic islets of the channel catfish differentiated by light microscopy include A-cells (alpha cells), B-cells (beta cells), and D-cells (Fig. 58), which have been reported in *I. punctatus* (Brinn, 1971) and *I. catus* (Brinn, 1973). Clear cells found by Bencosme et al. (1965) in *I. nebulosus* may be the result of improper fixation (Brinn, 1973). The A-cells are the probable
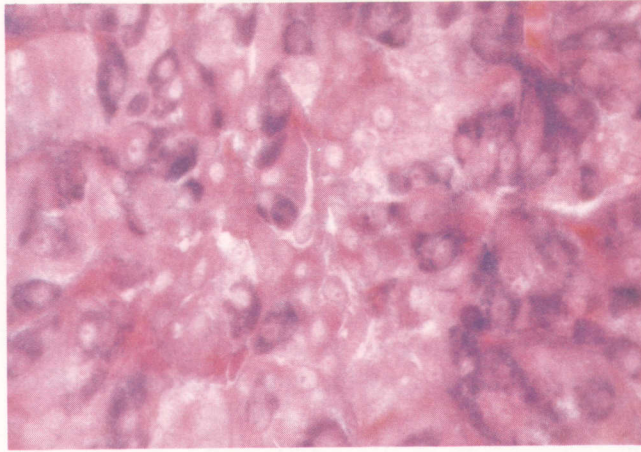
FIG. 58. The pancreatic islet has A-cells (dark pink), B-cells (blue), and D-cells (light pink). Helly's; aldehyde fuchsin trichrome (Epple, 1967); × 600.

source of glucogen and B-cells are the source of insulin (Epple, 1969; Brinn, 1973; Epple and Lewis, 1973). The D-cells probably secrete somatostatin (Johnson et al., 1976). An additional cell type has been described by electron microscopy in *I. catus* (Brinn, 1973).

## Pituitary Gland

The pituitary (Fig. 59) is located ventral to the diencephalon of the brain (Fig. 101 and 102). The gland is composed of the neurohypophysis which develops from the brain and the adenohypophysis which forms from an outpocketing of the oral cavity (Wingstrand, 1966). The saccus vasculosus is located dorsoposterior to the pituitary and may be homologous to the pars nervosa of amniotes (Wingstrand, 1951). This homology has
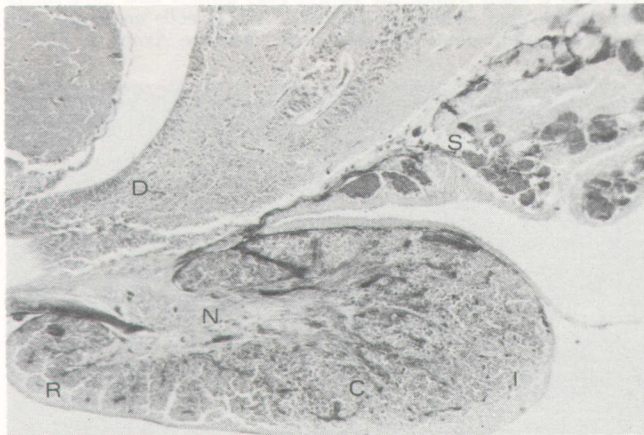


FIG. 59. The pituitary is composed of the neurohypophysis (N) which extends from the diencephalon (D) into the central portion of the gland. Processes of the neurohypophysis extend into all other regions of the pituitary. The adenohypophysis has three regions. The anterior region is the rostral pars distalis (R), the middle region is the caudal pars distalis (C), and the posterior portion is the pars intermedia (I). S, saccus vasculosus. Formalin; Mallory's; × 60.

not been widely accepted and the term pars nervosa is also used for portions of the neurohypophysis in some teleosts (Gorbman and Bern, 1966). The saccus vasculosus is discussed in Chap. 9.

### NEUROHYPOPHYSIS

This part of the pituitary (Fig. 59) consists of nerve fibers which extend from the diencephalon, down a short pituitary stalk, and into the dorsoanterior pituitary. The fibers within the pituitary form a neurohypophysial core with fibers extending into the adenohypophysis.

The neurohypophysis of teleosts has been reviewed by Perks (1969). In the teleost species which have been studied, neurosecretory products are formed in cell bodies in the preoptic nuclei dorsal to the optic chiasma. These neurosecretory products travel down axons to the gland. The axonal fibers are often of two types (Ball and Baker, 1969). Fibers continue into the adenohypophysis which may be controlled by direct nervous action or by liberation of an active agent into the blood from the neurohypophysis. The close contact between fibers of the neurohypophysis and the cells of the adenohypophysis may explain the reduction or absence of the pituitary portal system. Possible roles of the neurohypophysis, besides control of the adenohypophysis, include osmoregulation and control of some phases of reproduction.

### ROSTRAL PARS DISTALIS

The pars distalis of the adenohypophysis has distinct rostral and caudal regions. The pars distalis seems to be the functional equivalent of the pars distalis of tetrapods (Ball and Baker, 1969) so this terminology is preferred to the pro- and meso-adenohypophysis terminology of Pickford and Atz (1957).

*Prolactin cells.* Most of the rostral pars distalis is composed of prolactin cells (Fig. 60 and 61) arranged around prominent blood vessels. These granulated cells typically stain dark red with azocarmine or acid fuchsin although the staining reaction in Figure 60 is weak because of the fixative used. The prolactin cells in channel catfish do not form the follicles found in isospondylous species (Ball and Baker, 1969) but are similar in other characteristics, particularly cell shape.

Prolactin cells are the probable source of prolactin which is important in osmoregulation by limiting the outflow of sodium and chloride ions from the gills, although other functions of prolactin have also been hypothesized (Ball, 1969; Ball and
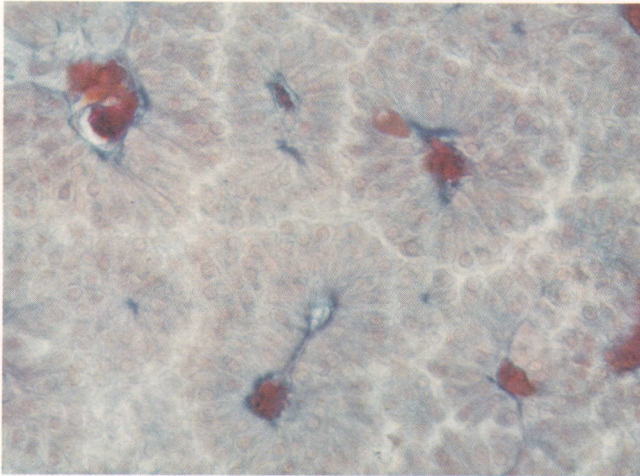
FIG. 60. Prolactin cells of the rostral pars distalis are columnar cells which stain red with azocarmine and are arranged radially around veins. They have nuclei at the end of the cell opposite the vein. Bouin's; Azan; × 320.
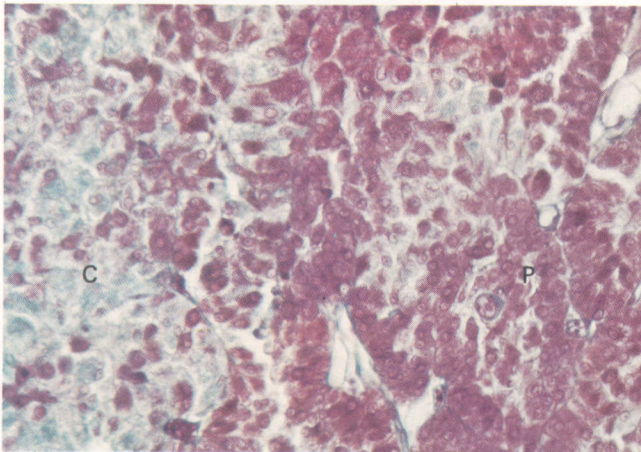


FIG. 61. Prolactin cells stained with acid fuchsin (P) stain similarly to the somatotrops of the caudal pars distalis (C). The blue-green stained cells of the caudal pars distalis are thyrotrops. Bouin's; Masson's; × 240.

Baker, 1969). The appearance of prolactin cells in some species change depending on the salinity of their environment reflecting varying demands on the organism (Schreibman et al., 1973).

*Adrenocorticotropic (ACTH) cells.* ACTH cells (Fig. 62) form a sheet at the interface of the neurohypophysis and caudal pars distalis. These polymorphic cells are generally more spherical and basophilic than prolactin cells. ACTH cells comprise a very small portion of the rostral pars distalis. Adrenocorticotropin effects the release of steroids from interrenal tissue of the head kidney (Ball and Baker, 1969).

## CAUDAL PARS DISTALIS

The caudal pars distalis has been termed the proximal pars distalis and meso-adenohypophysis. This portion of the adenohypophysis is the source

of three hormones and each has been associated with a separate type of cell.

*Somatotrops.* These cells, also termed growth hormone cells, produce a hormone referred to as "growth hormone" (GH) or somatotropin (STH) (Ball and Baker, 1966). These relatively large cells stain orange with azan stain (Fig. 63), and are the only PAS-negative cells in the caudal pars distalis. The staining of these cells with Masson's is very similar to that of prolactin cells (Fig. 61). The growth hormone produced by somatotrops stimulates body growth, and additional actions have been suggested (Ball, 1969).

*Thyrotrops.* These basophilic cells are intermingled with somatotrops in the anteriodorsal region of the caudal pars distalis and stain blue with azan. They are not easily differentiated from
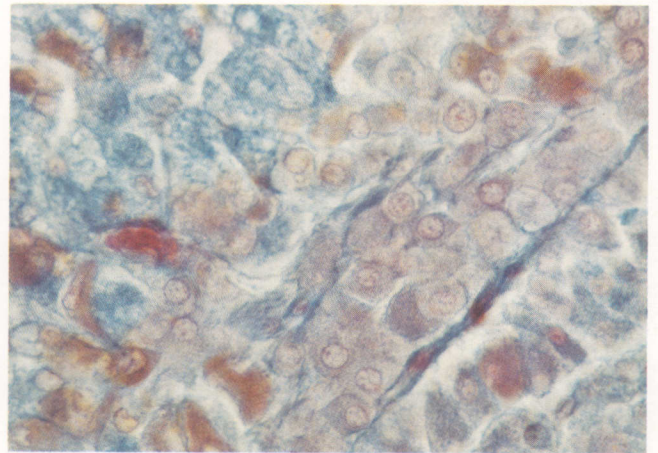


FIG. 62. Adrenocorticotropic (ACTH) cells (center) are located in a band within the rostral pars distalis and adjacent to the caudal pars distalis (upper left). ACTH cells are larger and more basophilic than prolactin cells. Bouin's; Azan; × 600.
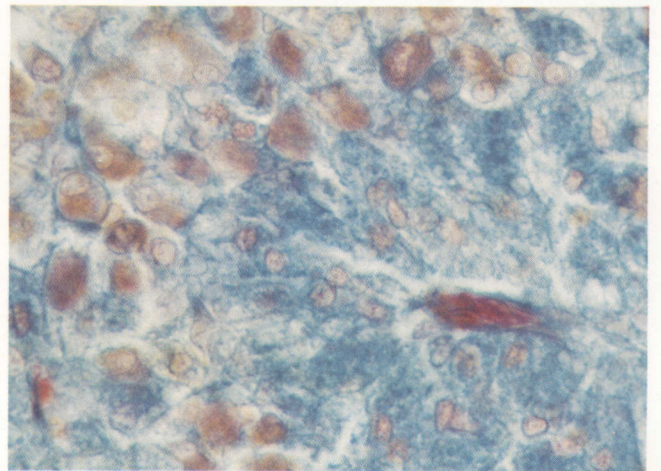


FIG. 63. The caudal pars distalis has orange staining somatotrops and blue staining cells which are thyrotrops and gonadotrops. Bouin's; Azan; × 600.

gonadotrops during some phases of sexual maturation. Both cell types are PAS-positive and basophilic. Gonadotrops are usually found ventrally and are not prominent in juveniles. Thyrotrops are the source of thyrotropin (TSH) which controls thyroid activity (Ball and Baker, 1969).

*Gonadotrops.* Gonadotrops are coarsely granulated basophilic cells (Fig. 63) located ventrally and posteriorly in the caudal pars distalis of sexually mature specimens. Gonadotrops of juveniles stain lightly and are not granulated. These cells produce gonadotropin and are of two types in some species. Different types of gonadotrops have not been demonstrated in channel catfish. Only one gonadotropic hormone has been found in teleosts, and it functions in gonadal maturation and development of secondary sexual characteristics (Ball and Baker, 1969; Hoar, 1969).

## PARS INTERMEDIA

The pars intermedia is the most posterior portion of the pituitary and contains more fibers of the neurohypophysis than other regions of the adenohypophysis. The predominent cell type stains light red with azocarmine of azan stain (Fig. 64) or acid fuchsin of Masson's stain. A few scattered groups of cells which appear identical to gonadotrops (Fig. 64) are also present. The pars intermedia is the probable source of melanophore-stimulating hormone (MSH) which affects the distribution of pigment in melanophores and erythrophores (Ball and Baker, 1969).
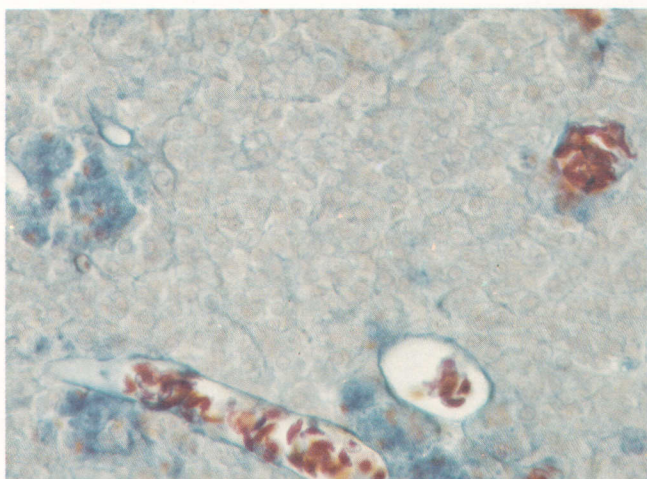


FIG. 64. The pars intermedia is the most posterior part of the adenohypophysis and contains more fibers of the neurohypophysis than other parts of the adenohypophysis. Most of the cells are slightly acidophilic but there are patches of basophilic cells which have large granules. Bouin's; Azan; × 320.
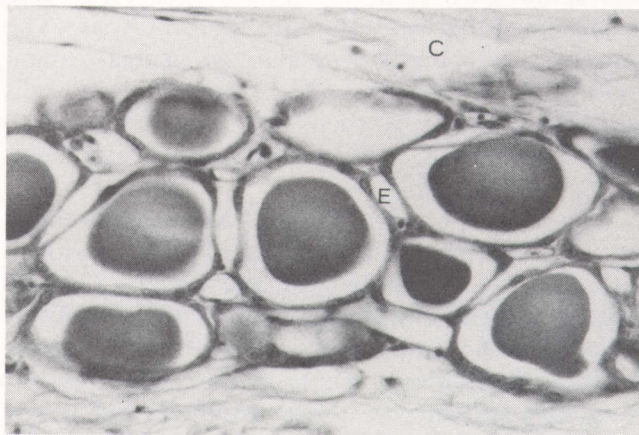


FIG. 65. Thyroid follicles are composed of a layer of epithelium (E) surrounding a colloid filled space. The follicles are found embedded in loose fibrous connective tissue (C) and are not surrounded by a capsule. Bouin's; H & E; × 320.

## Thyroid

Thyroid follicles (Fig. 65) are found along the ventral aorta and afferent branchial arteries ventral to the pharynx. Thyroid tissue is not encapsulated into a distinct organ and is not grossly recognizable. Heterotopic thyroid tissue reported in many teleosts (Baker-Cohen, 1959) has not been reported in channel catfish. The epithelium of thyroid follicles varies in height from cuboidal to squamous depending upon its activity. The colloid within the follicles is eosinophilic and is sometimes vacuolated.

The thyroid produces two hormones, thyroxine and triiodothyronine which have been implicated in almost every aspect of teleost physiology (Sage, 1973). These functions can be grouped into metabolic effects, structural effects, and effects in the central nervous system (Gorbman, 1969).

## Ultimobranchial Gland

These small paired glands are found in the transverse septum between the liver and heart just ventral to the esophagus. These organs are not grossly visible and are often difficult to locate. Each gland consists of cuboidal epithelium surrounding a lumen (Fig. 66). The ultimobranchial glands are the source of calcitonin which probably functions in regulation of calcium levels (Pang, 1973; Copp, 1969) and may be related to osmoregulation (Pang, 1971).

## Caudal Neurosecretory System

The spinal cord dorsal to the most posterior vertebrae has neurosecretory (Dahlgren) cells. These cells have cell bodies which are located in

the spinal cord near the central canal and have axons extending ventrally into the urophysis. The urophysis is a highly vascularized ventral expansion of the spinal cord. The neurosecretory cells are distinguished by their large size compared to adjacent neurons, polymorphic nuclei, and basophilic cytoplasm.

The caudal neurosecretory system of *Ictalurus* sp. (the species was not identified) was examined during a 1-year period (Cucchi, 1969). Seasonal changes in the number of neurosecretory cells or amount of neurosecretory material were not detected. The development of the caudal neurosecretory system was also considered, and it was found that a functional system was established in the third month after hatching.

The function of the caudal neurosecretory system is uncertain, but most evidence indicates osmoregulation or ion balance (Bern, 1969; Berlind, 1973). A role in reproduction has also been indicated by the response of *Gillichthys* sperm duct to a urophysical factor (Berlind, 1972) and the alteration of the neurosecretory cells after

injection of sex hormones into *Clarias batrachus* (Dixit, 1971). However, no seasonal variation in the system was found in *Ictalurus* sp. (Cucchi, 1969).
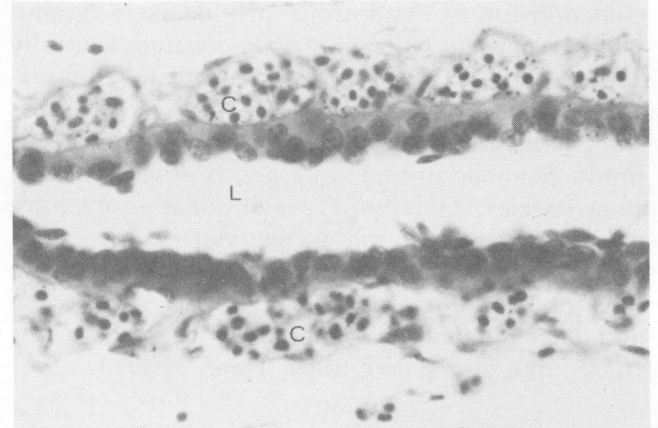


FIG. 66. The ultimobranchial glands are located in the transverse septum which separates the peritoneal cavity from the pericardial cavity. Each gland has an epithelial-lined lumen (L) and numerous capillaries (C). Bouin's; H & E; × 600.

# CHAPTER SIX

# EXCRETORY SYSTEM

Excretion by fish is a function of the kidney and the gills, both of which are also important in osmoregulation. The gills are described in Chap. 11 as respiratory organs. Osmoregulation in freshwater fish consists of the kidney constantly removing water which enters the body through all exposed surfaces and especially the gills. Conservation of ions by the kidney and chloride cells of the gills is also important because of the loss of ions to the hypotonic environment.

## Kidney

The kidney of channel catfish is fused bilaterally but is divided into completely separated anterior and posterior portions (Fig. 29 and 67). The head kidney and trunk kidney of adults and juveniles over 4 cm TL are not connected by any kidney tissues or ducts. The posterior cardinal vein does pass from the trunk kidney to the head kidney. This complete separation of the head kidney was not found in any species examined by Ogawa (1961).

The head kidney is located anterior to the swim bladder and is composed entirely of endocrine and hemopoietic tissue (Chap. 3 and 5). Renal corpuscles and convoluted tubules are present in the head kidney of specimens less than 4 cm TL, but these structures and the duct which runs posteriorly from the head kidney degenerate.

The trunk kidney is located posterior to the swim bladder and extends cranially along the lateral margins of the swim bladder resulting in a U-shaped anterior end. The trunk kidney extends to the posterior end of the body cavity becoming more narrow posteriorly. Corpuscles of Stannius (Chap. 5) are located on the lateral margins of the trunk kidney.

The trunk kidney is composed of nephrons which are the functional units of the kidney. Each nephron is composed of a renal corpuscle and a renal tubule. Hemopoietic tissue, similar to that found in the head kidney, surrounds some of the convoluted tubules and the renal corpuscles. The renal tubules are composed of various segments which have been described by Kendall and Hinton (1974).

## RENAL CORPUSCLE

The renal corpuscle (Fig. 68, 69 and 70) is formed by a glomerulus surrounded by Bowman's capsule. Bowman's capsule is double walled with the parietal epithelium forming an outer wall and the visceral epithelium, which is in direct contact with the glomerulus, forming the inner wall. Bowman's space occurs between the parietal and visceral epithelium and is continuous with the lumen of the renal tubule.



FIG. 67. The head kidney (H) and trunk kidney (T) are completely separate organs. The swim bladder, which has been removed from this figure, lies between the kidneys. The urinary bladder (U) is located in the extreme posterior portion of the body cavity. Ventral view of a 4 kg channel catfish. P, pectoral fin.
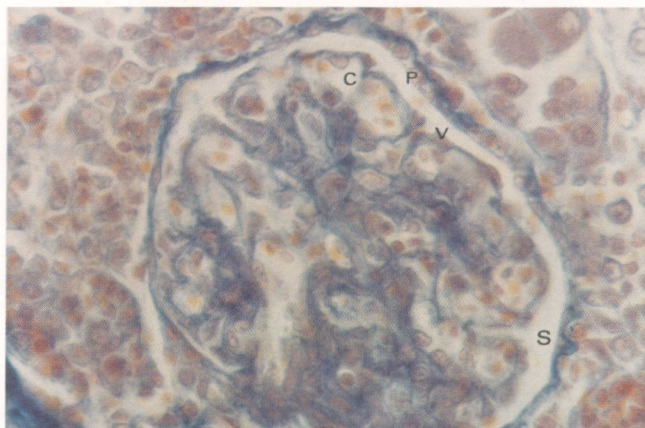
FIG. 68. The renal corpuscle is composed of a glomerulus and the surrounding Bowman's capsule. The glomerulus is a tuft of capillaries (C), composed of endothelial cells, which are separated from the visceral epithelium (V) of Bowman's capsule by the lamina densa which has stained blue. Erythrocytes are present within the capillaries. Bowman's space (S) surrounds the glomerulus and is enclosed by the parietal epithelium (P) of Bowman's capsule which has a basement membrane which has also stained blue. The tissue surrounding the renal corpuscle is hemopoietic tissue and renal tubules. Formalin; Mallory's; × 600.
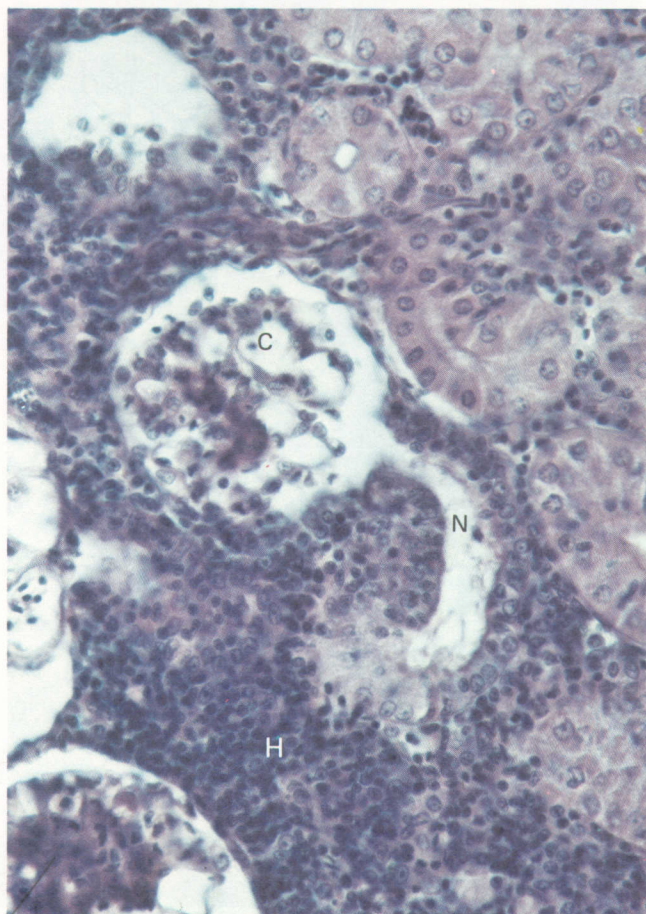
The glomerulus is a tuft of capillaries composed of endothelial cells. The visceral epithelium of Bowman's capsule is separated from the endothelial cells by a lamina densa (basement lamina) which is probably a fusion of the basement membranes of both the endothelial cells and the visceral epithelium (Patt and Patt, 1969).

## RENAL TUBULE

The renal tubules connect the renal corpuscles to collecting ducts which empty into the opisthonephric ducts. Each renal tubule has distinct variations along its length which can be described as segments. These segments vary somewhat in length and appearance between tubules and to a greater extent between specimens.

Leading from the renal corpuscle is a relatively short neck segment (Fig. 70) which has ciliated, cuboidal epithelium which is more basophilic than other segments. A sharp transition occurs between the neck segment and the first proximal segment (Fig. 71). The first proximal segment has columnar epithelium with a prominant striated border and basally located nuclei and is the longest segment in most tubules. The first proximal segment changes gradually into the second proximal segment (Fig. 72) which has lower epithelium, less prominent striated border, and epithelial nuclei located centrally or apically.

An intermediate segment was described by Kendall and Hinton (1974) following the second proximal segment. They state that this segment



FIG. 69. Bowman's space of the renal corpuscle is continuous with the neck segment (N) of the renal tubule. Hemopoietic tissue (H) surrounds most of the renal corpuscle and is much more basophilic than the renal tubules. The capillaries (C) of the glomerulus are much larger than in Fig. 68 because of the difference in fixation. Bouin's; H & E; × 470.
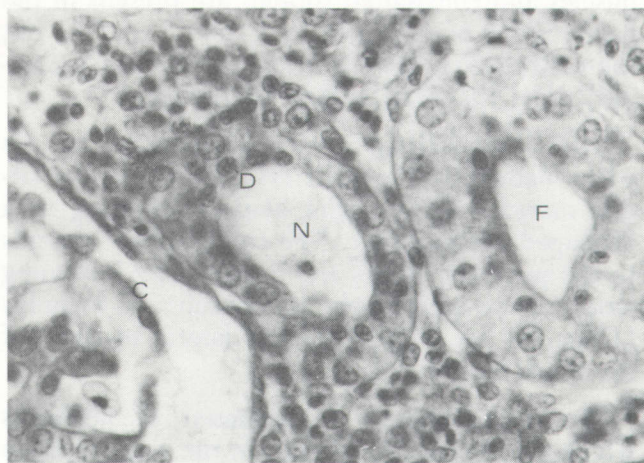


FIG. 70. The neck segment (N) and first proximal segment (F) of a renal tubule and part of a renal corpuscle (C) are surrounded by hemopoietic tissue. The neck segment has ciliated, cuboidal epithelium. The epithelial cells have large, basally located nuclei and are more basophilic than other segments of the tubule. Small, dark staining nuclei (D) are located near the lumen. Bouin's; H & E; × 600.
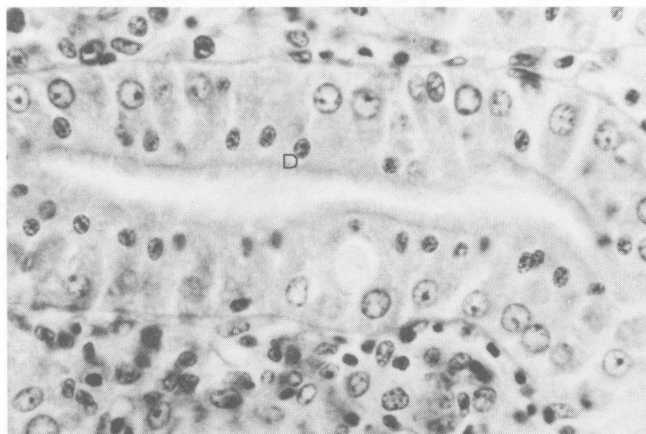
FIG. 71. The first proximal segment of a renal tubule has columnar epithelium with large basally located nuclei. The cytoplasm is frequently more eosinophilic near the lumen. A prominent striated border is present, and small dark staining nuclei (D) are regularly arranged between epithelial cells near the lumen. Cilia extending from the neck segment are sometimes seen in this segment. Transverse sections of the first proximal segment are seen in Fig. 70 and 73. Longitudinal section; Bouin's; H & E; × 600.
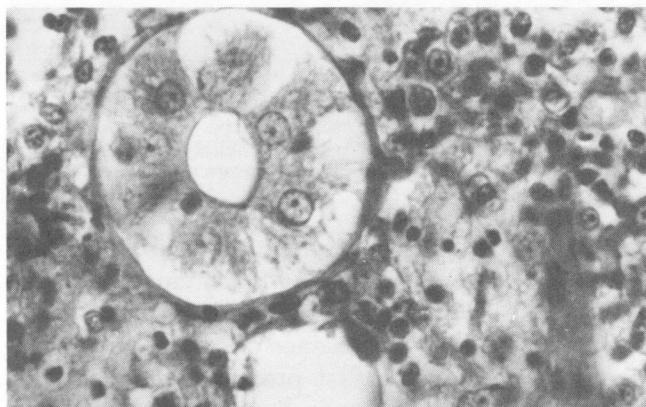


FIG. 72. The second proximal segment of a renal tubule has a smaller diameter than the first proximal segment and little or no striated border. This segment is usually the most variable in appearance. The nuclei may be near the lumen as in this section or centrally located. The staining of the cytoplasm is also variable. The small dark staining nuclei seen in the neck and first proximal segments are present but less abundant. This segment does not have a distinct beginning, and sections of tubules are frequently seen which have characteristics of both first and second proximal segments. Bouin's; H & E; × 650.

may be absent from some tubules and is better differentiated by phosphotungstic acid hematoxylin than by H & E. The intermediate segment is similar to the neck segment by having ciliated cuboidal epithelium but has a smaller lumen and is not as basophilic as the neck segment. This segment was found in some tubules of some specimens, but in tubules which were critically examined in serial sections, it was absent more often than present.

The distal segment (Fig. 73) has low columnar or cuboidal epithelial cells with eosinophilic cyto-

plasm and rounded apical margin. Nuclei are usually located basally but are sometimes located centrally. Basophilic intercalated cells reaching from the basement membrane to the lumen and containing flattened nuclei are located between the epithelial cells. This segment usually shrinks more than other segments during fixation.

The collecting ducts (Fig. 74) change structurally between the distal segment and the opisthonephric duct. Smaller collecting ducts have columnar epithelium surrounded by a thin layer
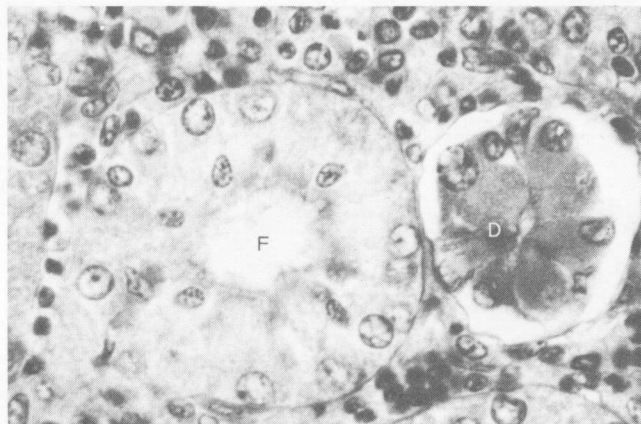


FIG. 73. The distal segment (D) of a renal tubule is easily distinguished from the first proximal segment (F). The diameter of the distal segment is about the same as that of the second proximal segment. The nuclei of the distal segment are basally located, and the very eosinophilic cytoplasm usually shrinks resulting in space around the tubules in sections. The apical cell boundary is rounded, striated border is absent, and the lumen is usually very small. Intercalated cells with flattened nuclei are present between the epithelial cells, and round, dark staining nuclei are occasionally seen. The distal segments sometimes unite before entering the collecting ducts. Bouin's; H & E; × 800.
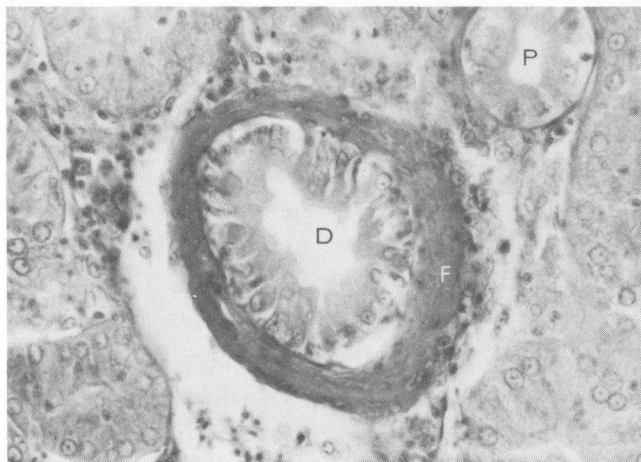


FIG. 74. The collecting ducts of the kidney have epithelium varying from columnar proximally to pseudostratified columnar near the opisthonephric duct. Intercalated cells, similar to those in the distal segments, are present proximally. Fibrous connective tissue (F) surrounds the duct. The connectvie tissue layer is very thin near the distal segment of the convoluted tubule and becomes thick and contains smooth muscle near the opisthonephric duct. P, proximal collecting duct; D, distal collecting duct. Bouin's; H & E; × 320.
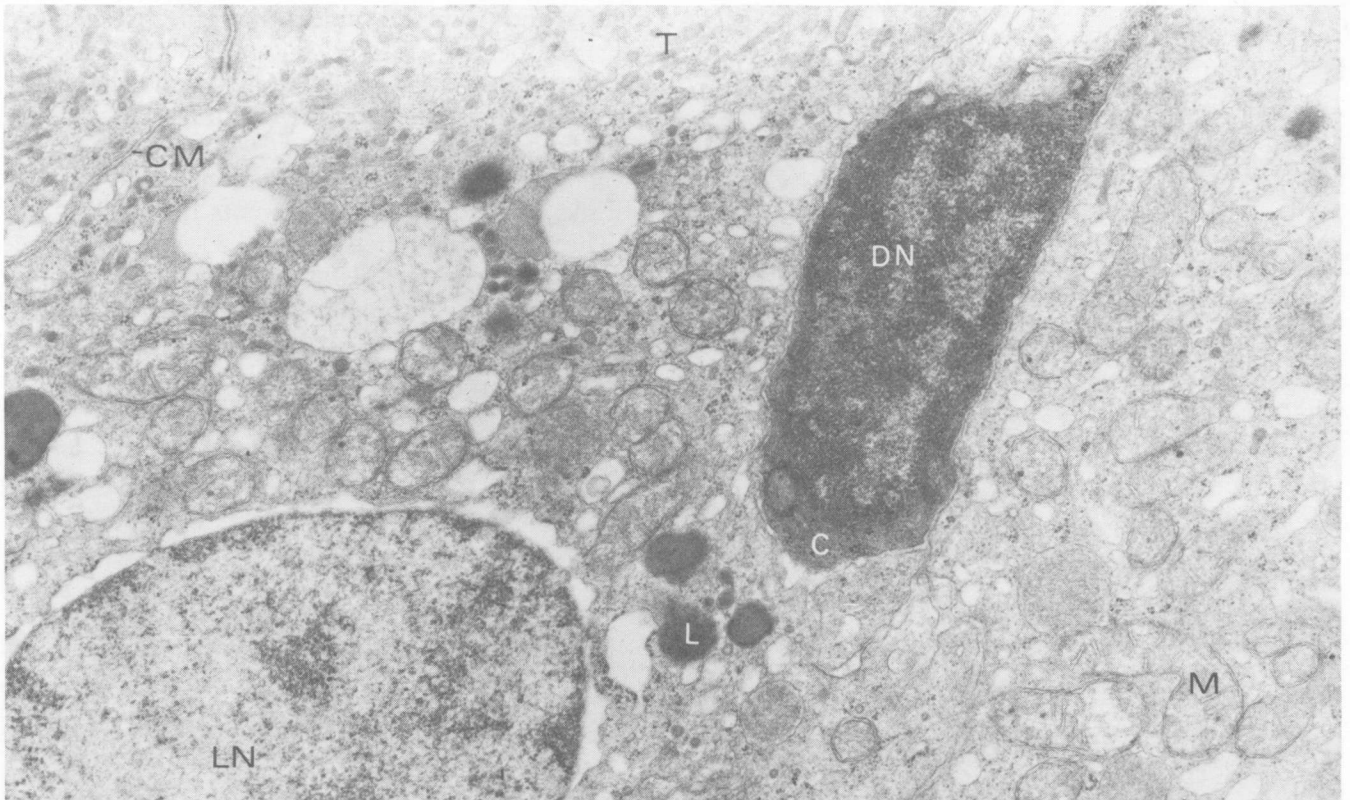
FIG. 75. This electron micrograph of a first proximal segment of a renal tubule has a small, dark staining nucleus (DN) similar to those seen in figures 70, 71, and 73. A larger, light staining nucleus (LN) seen in the basal portion of the epithelium is also present. The cell containing the dark nucleus has very little cytoplasm (C). Structures present in the epithelial cell include mitochondria (M), lipid droplets (L), microtubules (T), and cell membrane (CM). Glutaraldehyde; Uranyl acetate and lead citrate; × 19,500.

of fibrous connective tissue. The collecting ducts join together forming larger ducts before entering the opisthonephric duct. The larger ducts have pseudostratified columnar epithelium and a thick layer of connective tissue which often contains smooth muscle.

All segments of the renal tubule have small, dark nuclei which are spherical or oblong and surrounded by very little cytoplasm (Fig. 75). These are most abundant in the neck and first proximal segment, often being as numerous as the larger nuclei of the tubule cells. The nuclei are often present in drawings (Edwards and Schnitter, 1933) and photographs (Hickman and Trump, 1969) of renal tubules but not discussed. Bulger and Trump (1968) suggested that these were nuclei of wandering blood cells. These nuclei are arranged regularly, especially in the first proximal segment of channel catfish (Fig. 71), indicating that these are a normal part of the tubule. The tubules of small juveniles usually have fewer small nuclei than those of adults.

The nephron of the yellow bullhead, *Ictalurus natalis,* has been described by Hickman and Trump (1969) and is similar to the nephron of the channel catfish except for the presence of numerous eosinophilic droplets in the first proximal segment cells of the bullhead. This may be a result of a variation in the physiological state of the specimens or in specimen preparation.

## Opisthonephric Ducts

Two opisthonephric ducts (also referred to as archinephric or Wolffian ducts) course through most of the length of the kidney and continue to the urogenital pore. The urinary bladder extends anteriodorsally from its connection to the ventral side of the opisthonephric duct posterior to the kidney.

The opisthonephric ducts (Fig. 76) have a pseudostratified columnar epithelial lining without goblet cells. The epithelium is surrounded by a layer of fibrous connective tissue mixed with circularly arranged smooth muscle. The duct posterior to the kidney has a serosa covering the outer surface.

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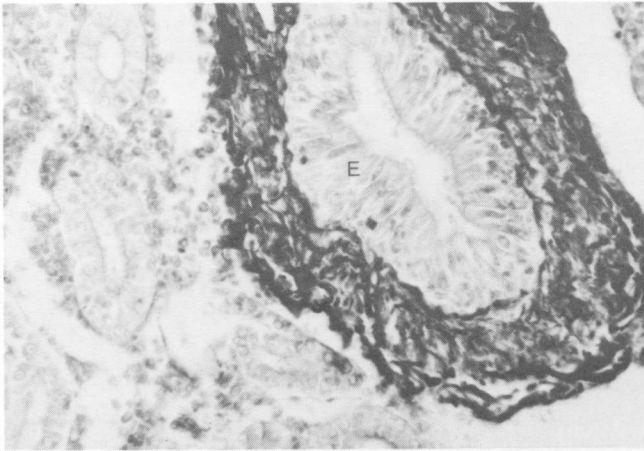
FIG. 76. The paired opisthonephric ducts course through most of the length of the trunk kidney. The pseudostratified epithelial lining (E) is surrounded by a thick layer of fibrous connective tissue with intermingled smooth muscle. Formalin; Mallory's; × 240.
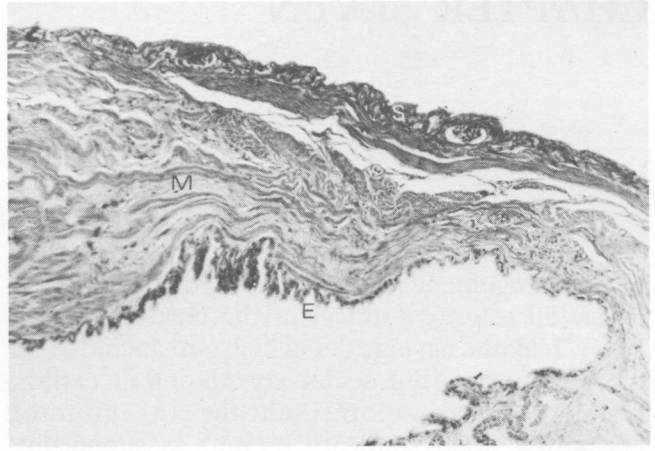


FIG. 77. The wall of the urinary bladder contains irregular bundles of smooth muscle (M) and interfascicular connective tissue. The epithelial lining (E) is somewhat folded when the bladder is contracted. A serosa (S) of fiibrous connective tissue and mesothelium covers the outside. Helly's; H & E; × 80.
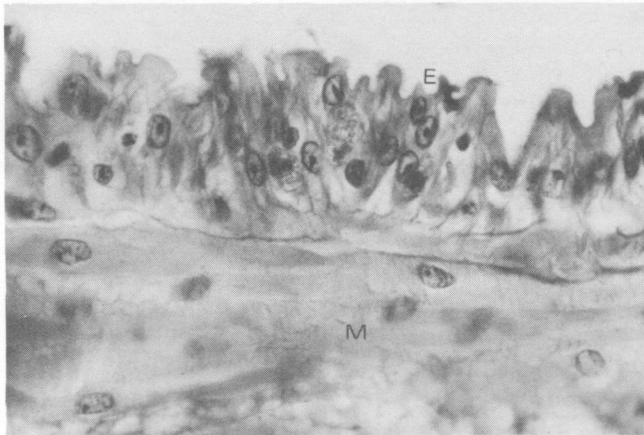


FIG. 78. The epithelium (E) of the urinary bladder is columnar when contracted and has a very irregular distal surface. When stretched, the epithelium is low columnar or cuboidal. A layer of connective tissue mixed with smooth muscle (M) lies beneath the epithelium. Bouin's; H & E; × 600.
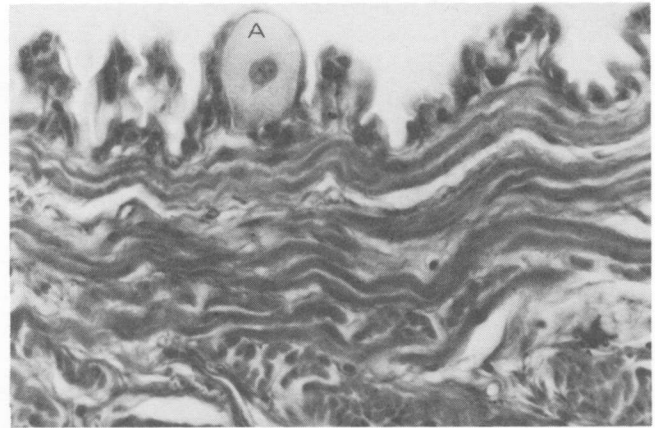


FIG. 79. The epithelium lining the urinary bladder is unusual in the shape of the epithelial cells and because of occasional cells which are similar to the alarm substance cells (A) of the epidermis. These very large cells usually have centrally located double nuclei and a large volume of eosinophilic cytoplasm. Goblet cells are also present in the epithelium of some specimens. Helly's; H & E; × 320.

## Urinary Bladder

The urinary bladder is located in the posterior portion of the body cavity ventral to the trunk kidney (Fig. 67 and 29). The wall (Fig. 77) of the urinary bladder is organized similarly to that of the opisthonephric duct. The lumen is lined with an epithelium (Fig. 78) which is unlike that of any other part of the channel catfish. The epitheliel cells are columnar and sometimes stratified in the relaxed bladder and become cuboidal in the stretched bladder. The apical ends of the cells are irregular resulting in an uneven surface.

Goblet cells and cells which resemble the alarm substance cells of the epidermis (Fig. 79) are present in some specimens. The epithelium is surrounded by a layer of connective tissue and smooth muscle. The smooth muscle of this layer in the urinary bladder is more abundant than in the opisthonephric duct. Smooth muscle fibers are oriented circularly and longitudinally but do not form distinct layers. The external surface has a serosa of fibrous connective tissue covered by mesothelium.

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# CHAPTER SEVEN

# INTEGUMENTARY SYSTEM

The integument is composed of the skin which covers all exterior surfaces of the channel catfish. Many teleosts have scales which are included in the integument, but scales are absent in catfish. Lepidotrichia develop from the integument (Goodrich, 1930) and are present as supporting elements of all the fins except the adipose fin. The skin contains unicellular glands in the epidermis, and axillary glands are present near the pectoral fin. Sense organs are located in the skin and are discussed in Chap. 9.

## Skin

The skin (Fig. 80 and 81) is composed of the epidermis and underlying dermis. The hypodermis or subcutaneous layer lies beneath the dermis of which it is a continuation. The relative thickness of the epidermis and dermis varies in different areas of the body. The thickness of the skin in the head region is generally less than on the trunk.

### EPIDERMIS

The epidermis (Fig. 82) is stratified squamous epithelium with a basal layer of columnar cells (stratum germinativum) which produce addi-



FIG. 81. The epidermis and dermis are easily distinguished using connective tissue stains. The dermis, composed of collagenous connective tissue, has stained green. Alarm substance cells are a prominent part of the epidermis. The lateral-line canal contains a neuromast in which the sensory hair cells have stained darker than adjacent cells. Except for the neuromast, the canal is lined by squamous epithelium. This skin was from a 30 mm TL juvenile and is thinner than that of an adult. Bouin's; Masson's; × 320.

tional epithelium. Cells become squamous in the outer epithelium but are not keratinized. Goblet (mucous) cells are present in all regions of the body but are especially abundant in the oral cavity. Alarm substance or club cells are also present in all areas except on the barbels (Fig. 126), inner surface of the operculum (Fig. 170 and 24) and lips. The term alarm substance cell (*Schreckstoffzellen*) was proposed by Pfeiffer (1962) for the club cells of Ostariophysi because of morphological and functional differences between these cells and club cells of other superorders. The alarm substance cells of channel catfish are large (usually 50 to 60 $\mu$) with a centrally located nucleus which is usually double. Shape is usually spherical or oblong but is sometimes distorted by folds in areas such as around fins. These cells never extend to the surface. The "fright substance" which they contain is released only when the epidermis is injured (Pfeiffer, 1960, 1962, 1963, and 1977). Melanophores are present in some areas of epidermis. Taste buds and pit organs are also located in the epidermis (Chap. 9).

### DERMIS

The dermis is composed of fibrous connective



FIG. 80. Skin from the lateral body wall is composed of epidermis (E) and dermis (D). The hypodermis (H) attaches the skin to the underlying somatic muscles. Sense organs found in the skin include the lateral line (L) and taste buds (T). Goblet cells (G) and alarm substance cells (A) are unicellular glands located in the epidermis. Melanophores (M) are usually located in the hypodermis or a superficial layer of the dermis but may also be found in the epidermis. Bouin's; H & E; × 140.

tissue. A compact layer is located beneath the epidermis; and the hypodermis, composed of loose connective tissue, lies between the compact layer and underlying tissue. Some regions of the hypodermis contain adipose tissue. Melanophores are located above and below the compact layer of the dermis except in ventral (white) portions of the skin. The melanophores immediately beneath the epidermis sometimes appear to lie in a thin layer of loose connective tissue superficial to the compact layer. The hypodermis is thin over most of the body but is thick in some regions such as parts of the head and fins. The lateral line is located in the dermis (Chap. 9).

## Fins

The fins are covered by skin and supported by lepidotrichia except for the adipose fin. The pectoral fins (Fig. 83) and dorsal fin have a hard ray or spine which is quite unlike the unmodified lepidotrichia but which develops from lepidothrichia (Reed, 1924a). The caudal, pelvic, and anal fins are similar to the pectoral and dorsal fins except no spine is present.

The fins, except for the adipose fin, have epidermis with a reduced number of alarm substance cells (Fig. 84). The compact layer of the dermis is reduced and the hypodermis is expanded to fill the space between lepidotrichia. The lepidotrichia are composed of bilateral bony elements which have nerves and blood vessels between them.

The adipose fin (Fig. 85) is composed of a medial layer of loose fibrous connective tissue covered by skin. The dermis of some portions of the fin has additional connective tissue arranged



FIG. 83. Tranverse section of pectoral fin showing the spine (S) and lepidotrichia (L) which are formed from bilateral elements. The epidermis (E) has fewer alarm substance cells and goblet cells than the skin of the body. The dermis consists of a very thin compact layer supporting the epidermis and loose areolar tissue surrounding the lepidotrichia. Bouin's; H & E; × 25.
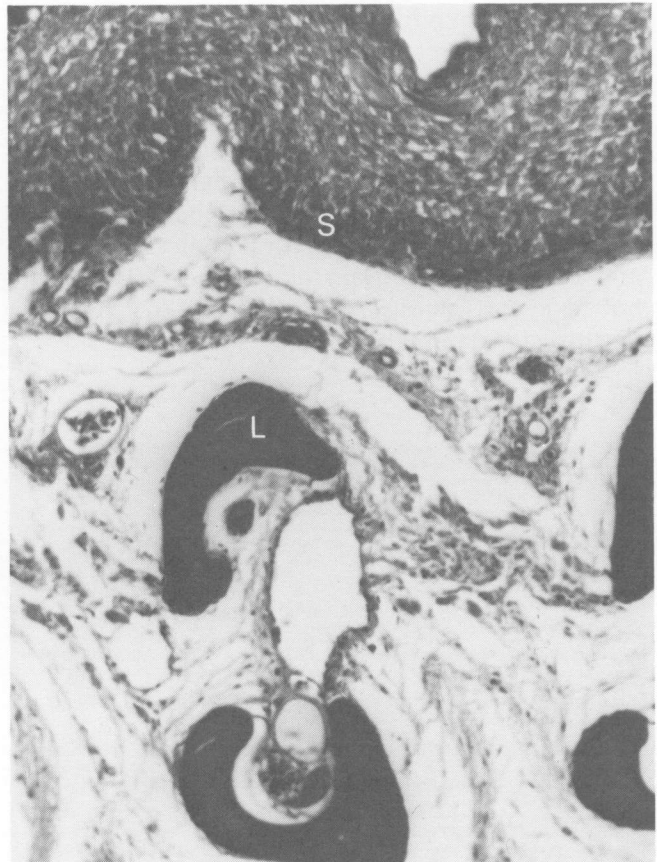


FIG. 84. An enlargement of the skin (S) and lepidotrichia (L) seen in Fig. 83. Bouin's; Masson's; × 175.



FIG. 82. The epidermis is stratified squamous epithelium. The basal layer is the stratum germinativum (S), and the cells become flattened distally. Goblet cells (G) have vacuolated cytoplasm and a flattened, basally located nucleus. The alarm substance cells (A) are very large and have a double nucleus. Bouin's; H & E; × 600.

in distinct bundles. Adipose tissue, which is not an important constituent of this fin, is sometimes present within the central connective tissue layer near the fin base. The epidermis of this fin is similar to that of the body.

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## Axillary Glands

Multicellular axillary glands (Fig. 86 and 87) are located beneath the skin dorsal to the pectoral fin. Axillary glands seem best developed in fingerlings and were not found in large adults. The structure of these glands in other species has been described by Reed (1924b).

The axillary gland is surrounded by a thin sheath of fibrous connective tissue, and a small pore opens near the base of the pectoral spine. The lumen is filled with vacuoles of a clear staining substance divided by thin septa. Large cells which are similar to the alarm substance cells of the epidermis are associated with the septa and gland wall. Thicker septa divide the gland into lobes. Epithelial cells and large cells with fine granules line the gland wall and interlobular septa.

The function of the axillary gland has been associated with the production of toxins which could be injected by the spines of the fins (Reed, 1907). This hypothesis seems tenuous for several reasons. No duct or other means of transferring the contents of the gland to the spine tip exists. The spine and surrounding epithelium of some species is toxic, at least to other fish (Birkhead, 1967), without the contents of the axillary gland, and the dorsal fin spine which has no axillary gland is as toxic as the pectoral spines. The spine and covering epithelium of channel catfish were not toxic to *Gambusia* (Birkhead, 1967) but may be toxic to mammals.



FIG. 86. The axillary gland (A) has a pore (P) dorsal to the pectoral fin (F). Tranverse section of a fingerling. Bouin's; H & E; × 70.
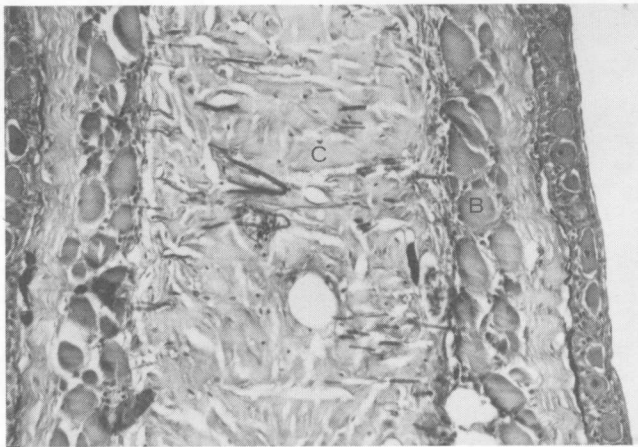


FIG. 85. The adipose fin has a medial layer of fibrous connective tissue (C) covered by skin. The dermis has distinct bundles of connective tissue (B) in addition to the usual fibrous connective tissue. The epidermis is similar to that of the body. Adipose tissue is sometimes present in the central layer of the fin. Bouin's; H & E; × 120.
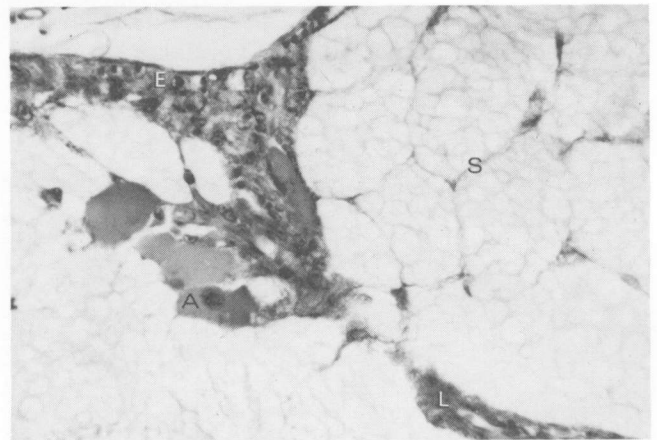


FIG. 87. The axillary gland is filled with clear staining vacuoles. Thin, irregular septa (S) divide the vacuoles, and large cells resembling alarm substance cells (A) are associated with the septa. Larger septa (L) divide the gland into lobes. The wall of the gland is lined with epithelial cells (E). Bouin's; H & E; × 240.

# CHAPTER EIGHT

# MUSCULAR SYSTEM

Muscles are of three basic types: skeletal, smooth, and cardiac. The skeletal or striated muscles (Fig. 88 and 89) are usually located so that they move elements of the skeleton, and these muscles will be described grossly in this chapter. Smooth muscle (Fig. 90 and 91) is found in visceral organs and blood vessels and may form distinct layers or be mixed with other tissues. Its location is described in the discussions of the organs in which it is found. Cardiac muscle is found only in the heart and is described in Chap. 3.



FIG. 88. Skeletal muscle is composed of longitudinally oriented parallel fibers which have cross striations. Each fiber has several nuclei located peripherally. Bouin's; H & E; × 800.
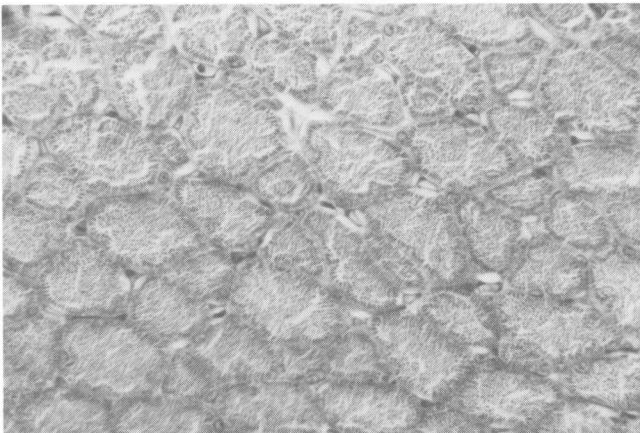


FIG. 89. The peripherally located nuclei and large size of skeletal muscle fibers are seen in this transverse section. Each fiber is composed of numerous myofibrils which appear as dots at this magnification. Bouin's; H & E; × 320.
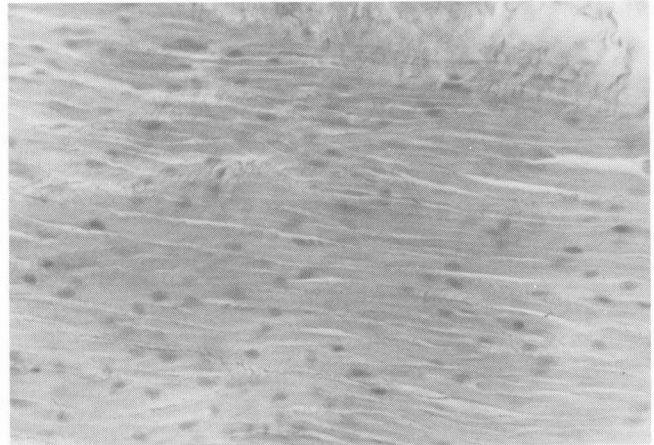


FIG. 90. Smooth muscle fibers are not striated and have centrally located nuclei. Each cell is much smaller than striated muscle fibers. Urinary bladder; Helly's; H & E; × 320.
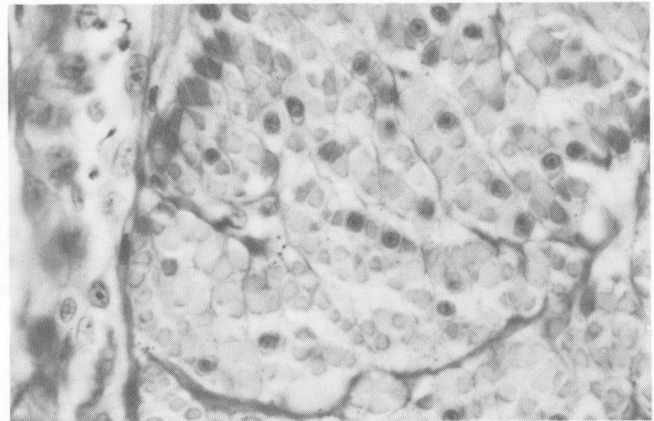


FIG. 91. This transverse section of smooth muscle demonstrates the small size and centrally located nuclei characteristic of this tissue type. Myofibrils seen in skeletal muscle are not visible. Urinary bladder; Bouin's; H & E; × 600.

The musculature of *I. nebulosus*, described by McMurrich (1884a), is nearly identical with that of *I. punctatus*. However, some of the terminology used by McMurrich is no longer used; therefore, it has been modified to agree with more recent authors such as Greene and Greene (1913) or Edgeworth (1935).

The muscles were examined grossly in fresh, formalin-preserved, and boiled specimens. Although boiling destroys the connective tissue attaching the muscle to bone, this method was found to be very useful. Fresh or frozen speci-

mens were placed in water which was then heated and boiled briefly. Overcooking resulted in the muscles falling from the skeleton in which case the bones were used in the study of the skeletal system. Superficial connective tissue, which obscures details of the musculature on fresh specimens, was easily removed from properly cooked specimens, and the muscles were easily dissected.

Histological sections of fingerlings were useful in determining the origin and insertion of some smaller muscles. The use of sections for examination of muscles of the branchial arches was particularly beneficial since these muscles were difficult to examine grossly without disturbing their normal relationships. The innervation of some muscles were also confirmed from sections.

## Myomeres of the Trunk and Tail

The myomeres are segmentally arranged along the body posterior to the head (Fig. 92). Each myomere is composed of muscle fibers arranged parallel to the longitudinal axis of the body. Myocommata (myosepta) are sheets of fibrous connective tissue (Fig. 93 and 94) which separate adjacent myomeres and attach to vertebrae. Most of the muscle fibers of the myomeres attach to the myocommata and thus indirectly to the vertebrae. These muscles form the largest portion of the muscular system and are the most important muscles in locomotion.

The myomeres are separated bilaterally in the tail by median dorsal and ventral septa containing the neural and hemal spines respectively. In the
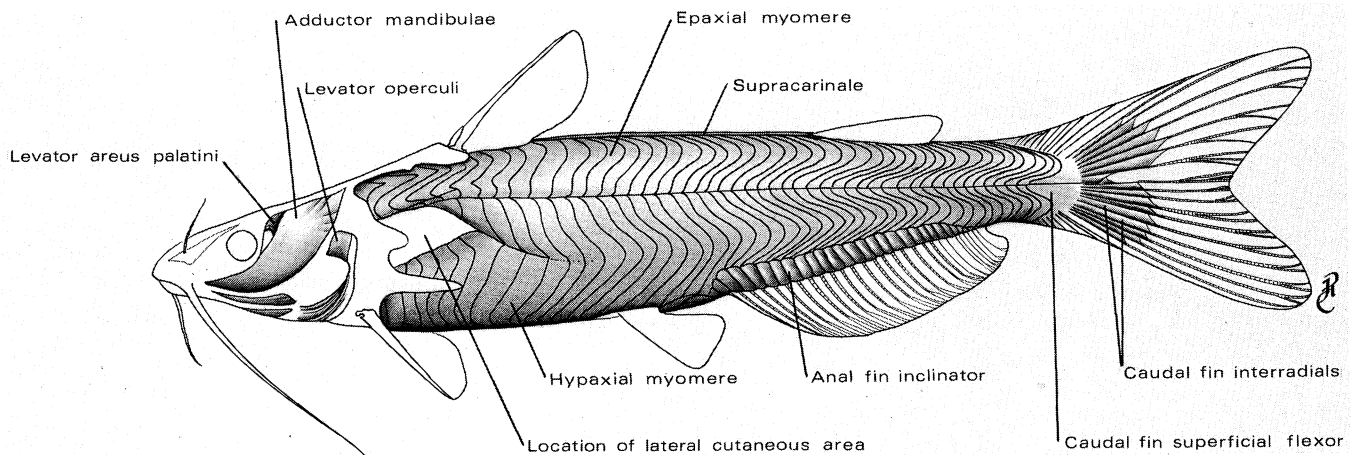


FIG. 92. Lateral view of the superficial muscles.
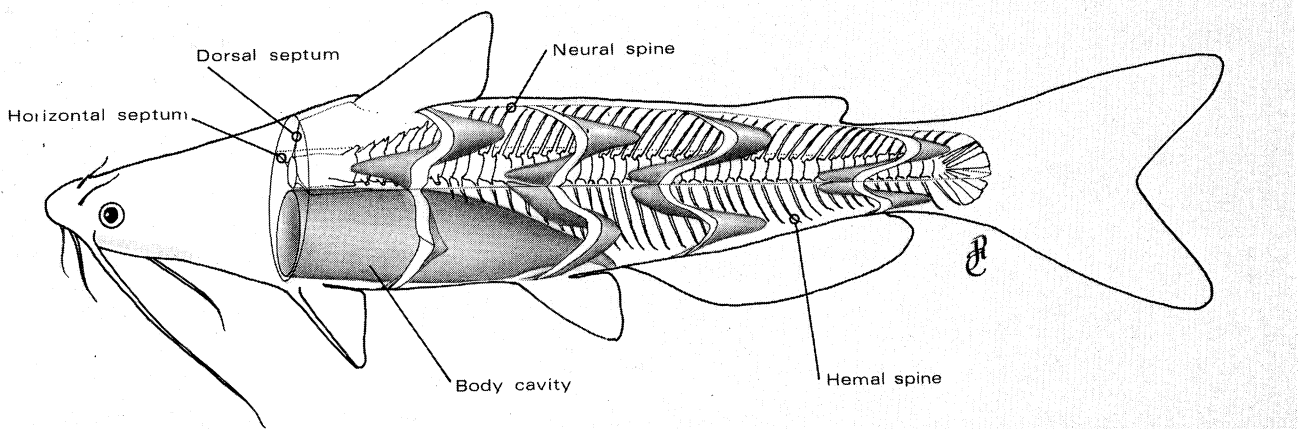


FIG. 93. Myomeres from different regions of the body vary in shape with the anterior region being particularly modified. The septa dividing the myomeres are composed of fibrous connective tissue, and some are supported by neural or hemal spines.

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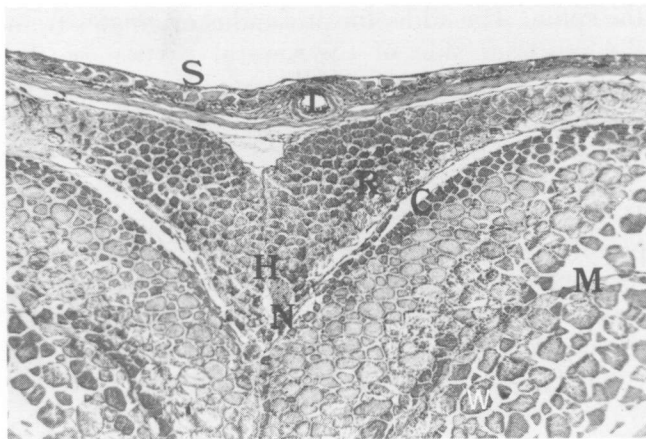
FIG. 94. Transverse section of lateral region of the tail of a fingerling. The white muscle (W) of this region is covered with red muscle (R). M, myocommata; S, skin; L, lateral line; H, horizontal septum; C, connective tissue septum between red and white muscle; N, lateral-line nerve. Bouin's; H & E; × 60.

trunk region, the myomeres are separated by the median dorsal septum and the body cavity. A horizontal septum (Fig. 94) extends from the centra of the vertebrae to the lateral line and divides the myomeres into epaxial and hypaxial components.

Each myomere has a superficial "W" shape with the center point oriented anteriorly. The myocommata at the horizontal septum extend anteriorly as they approach the vertebrae while extending posteriorly from the dorsal and ventral portions of the myomere. This results in a rather complex three-dimensional shape (Fig. 93).

The superficial fibers of each myomere have a darker color grossly than the deeper muscle from which they are separated by a septum of fibrous connective tissue (Fig. 94). This muscle is often referred to as red muscle (LeDanois, 1958) and was termed musculus lateralis superficialis by Greene (1913) who termed the underlying muscle of the myomeres the musculus lateralis profundus. Red muscle is thickest at the lateral line and becomes very thin dorsally and ventrally. The lateral line nerve is located in the horizontal septum separating the epaxial and hypaxial red muscle. The superficial or red muscle of the myomeres is distinct histologically from the deeper white muscles (Fig. 94). The fibers of the red muscle are smaller in diameter and have an increase in vascularity.

## Muscles of the Fins

### ANAL FIN

Three types of bilaterally paired muscles are inserted on each ray of the fin. The inclinator muscles (Fig. 92 and 95) originate from the fascia covering the ventral surface of the myomere and insert on the lateral surface of the rays. The inclinators produce the sinuous motion of the fin. The erector muscle and depressor muscle directly oppose each other with the erector inserting on the anterior surface of the ray and the depressor inserting on the posterior surface. The erectors and depressors originate from the pterygiophores supporting the rays.

The infracarinales are bilaterally paired muscles located midventrally and oriented parallel to the body axis. The median infracarinales (retractor ischii) reach from the posterior pelvic girdle to the anterior pterygiophore of the anal fin. The posterior infracarinales extend from the posterior pterygiophore to the hemal spines supporting the caudal fin. The infracarinales act to spread the fin rays and may also flex the body ventrally.

### DORSAL FIN

The muscles are arranged as opposing erectors and depressors as in the anal fin, although the origins and shapes of the muscles of the two anterior modified rays are altered. The erector and depressor of the defensive spine are especially enlarged while those of the first ray, which serves as a locked device, lock the ray in the erected position by sliding it over the dorsal extremity of the pterygiophore. Inclinator muscles are absent except for the pair which insert on the most anterior unmodified ray and originate from the posterior edge of the horizontal plate supporting the spine.

The supracarinales are paired, longitudinal muscle bundles in the middorsum. They extend from
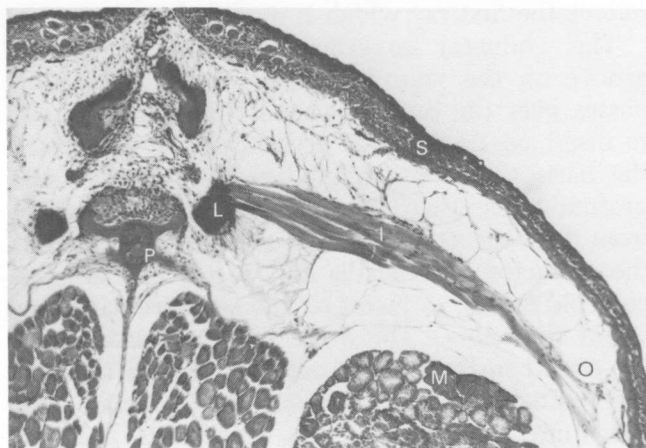


FIG. 95. Transverse section of anal fin and adjacent body. An inclinator (I) of the anal fin originates (O) from the fascia between the skin and myomeres and inserts on the base of the lepidotrichia (L). S, skin; P, pterygiophore; M, myomere. Bouin's; H & E; × 80.

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the adipose fin to the pterygiophores of the posterior rays of the dorsal fin. These muscles retract the dorsal fin and flex the body dorsoventrally.

## CAUDAL FIN

Terminology of the caudal musculature is that of Nursall (1963).

The superficial flexor (Fig. 92) is formed from the posterior myomere of the tail. The muscle inserts on the fin rays by a broad fascia which covers the underlying muscles.

The hypochordal longitudinal muscles (upper division of ventral portion of deep caudal muscle in McMurrich, 1884a) originates from the upper hypurals and inserts by long tendons on the dorsal principle rays. The deep dorsal flexor (dorsal portion of deep caudal muscle in McMurrich) originates from the neural spines of the posterior vertebrae and inserts on the dorsal rays. The deep ventral flexor (lower division of ventral portion of deep caudal muscles in McMurrich) is thin and fan-shaped. It originates on the lower hypurals and inserts on the ventral rays.

Interradial muscles (Fig. 92) (intrinsic muscles of McMurrich) obliquely connect the rays. Two layers of fibers are present between the central rays with the superficial fibers almost perpendicular to the deeper fibers.

## PECTORAL FIN

The muscles which move the pectoral fins are the adductors and abductors, each of which has separate superficial and deep portions. These muscles are located in the grooves of the cleithrum and coracoid, and some pass through tunnels in these bones. The actions of these muscles not only adduct and abduct the fin but also lock and unlock the first ray which is modified into a spine.

The abductor superficialis originates in the groove on the ventral surface of the cleithrum, passes over the bridge formed from the coracoid to insert on the inferior process of the spine and the basis of the unmodified rays. The abductor profundus has two separate parts. One originates from the ventral surface of the cleithrum beneath the abductor superficialis and passes beneath the coracoid bridge to insert on the semicircular process of the spine. The other part originates from the dorsal surface of the coracoid, passes through the tunnel formed between the coracoid and cleithrum and inserts on the spine with the first part of this muscle.

The adductor superficialis originates from the inner surface of the ascending portion of the coracoid and inserts on the base of all rays except

the spine. The adductor profundus originates from the posterior side of the ventral portion of the coracoid, passes beneath a bridge-like spiculum of bone on the coracoid and inserts on the spine of the fin.

The cucullaris (trapezius of McMurrich, 1884a) originates from the lower surface to the pterotic, just posterior to the origin of the adductor hyomandibularis. It inserts on the dorsal process of the cleithrum near its articulation with the posttemporal. Numerous fibers from this muscle attach to the membrane forming the posterior wall of branchial cavity.

## PELVIC FIN

As in the pectoral fin, this fin has abductors and adductors with each having two parts. The abductor superficialis and abductor profundus originate from the ventral surface of the basipterygia and insert on the fin rays. The adductor superficialis and adductor profundus originate from the dorsal surface of the basipterygia and insert on the dorsal side of the rays. Both superficial muscles are more laterally oriented than the deep portions.

The arrector dorsalis and arrector ventralis muscles originate from the external process of the basipterygium and insert on the lateral fin ray. The arrector ventralis is small and easily overlooked, but the arrector dorsalis is easily located on the lateral edge of the pelvic girdle. These muscles were omitted by McMurrich (1884a) but are described in *I. nebulosus* by Shelden (1937).

The infracarinales insert on both the anterior and posterior margins of the pelvic girdle. The anterior portion of the infracarinales (protractor ischii) and the median portion (retractor ischii) can move the pelvic girdle or flex the body dorsoventrally. The retractor ischii extends lateral to the anus to insert on the anterior pterygiophores of the anal fin.

## Muscles of the Head

The head musculature is distinct from the myomeres by a loss of obvious segmentation and by innervation, in most instances, by cranial nerves. The hypobranchial muscles are an exception which are innervated by spinal nerves reflecting their derivation from anterior myomeres (Romer, 1955). The innervation by cranial nerves and the association of the head musculature with the visceral arches suggests that these muscles are closely allied with the smooth muscles of the gut which are also innervated by cranial nerves.

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The innervation of the cranial muscles was used to divide them into groups. The information on the innervation of cranial muscles given by Mc-Murrich (1884a) was used in most cases. When McMurrich's description was questionable, verification was by serial sections or information given by Edgeworth (1935), Singh and Munshi (1968), and Le Danois (1958).

## EYE MUSCLES

Although these muscles are innervated by cranial nerves, they develop from somites of the head and are considered somatic muscles. Six muscles are inserted on each eye (Fig. 100) and are innervated by cranial nerves III, IV, and VI (Chap. 9). Two oblique muscles originate from the anterior orbit. The superior oblique inserts on the dorsal margin of the eye and the inferior oblique inserts on the ventral margin. Four recti muscles originate from the posterior part of the orbit. The superior rectus inserts dorsally, the inferior rectus ventrally, posterior (lateral, external) rectus inserts on the posterior margin, and the anterior (medial, internal) rectus inserts near the anterior margin.

## MANDIBULAR MUSCLES

These muscles are innervated by the trigeminal nerve (Cr.N.V). The adductor mandibulae (Fig. 92) is the largest muscle of the head and fills the large depression on the side of the skull posterior to the orbit. It originates from the hyomandibular and the bones just dorsal to it, and it inserts on the articular and dentary. Many teleosts have three or four subdivisions of the adductor mandibulae (Edgeworth, 1935), but these are not distinct in channel catfish.

The retractor tentaculi is a specialized muscle which originates from the pterygoid and inserts by a long tendon on the base of the maxilla which supports the maxillary barbel. This muscle is probably a specialized part of the adductor mandibulae (Eaton, 1948; McMurrich, 1884a). The muscles involved in moving the maxillary barbels are simple in the channel catfish compared to some other siluroids such as *Rita rita* in which several muscles are involved (Singh and Munshi, 1968).

The levator arcus palatini (Fig. 92) originates from the posterior edge of the parethmoid and lateral edges of the frontal and sphenotic, and it inserts on the transverse ridge of the hyomandibular. The anterior portion of this muscle lies immediately beneath the skin while the posterior portion and the insertion of the entire muscle lies beneath the adductor mandibulae.

The dilator operculi originates from the frontal, sphenotic, and hyomandibular, passes over the hyomandibular, and inserts on the dorsal process of the opercular. The anterior portion of the dilator operculi is covered by the levator arcus palatini, and the posterior portion is covered by the adductor mandibulae.

The intermandibularis anterior is located on the ventral side of the head and connects the median sides of the dentaries. The intermandibularis anterior is near the symphysis of the dentaries and is rather short. The intermandibularis posterior (geniohyoideus of McMurrich, 1884a) (Fig. 96), also located on the ventrum of the head, originates from the outer, ventral surface of the ceratohyal and inserts on the dentary near the insertion of the intermandibularis anterior. Two strips of pseudocartilage like that supporting the barbels cross the ventral surface of this muscle from anterior to posterior with the mental and mandibulary barbels originating from the anterior portion of the strips.

## HYOID MUSCLES

These muscles are innervated by the facial nerve (Cr.N. VII). The levator operculi (Fig. 92) originates from the posterior ridge of the hyomandibular and edge of the pterotic, and it inserts on the upper border of the opercular. The levator operculi lies immediately beneath the skin. The adductor operculi originates from the pterotic and inserts on the inner surface of the opercular and is sometimes diffiicult to separate from the levator operculi.

The adductor arcus palatini has separate anterior and posterior portions which lie beneath the skin covering the roof of the mouth. Both por-
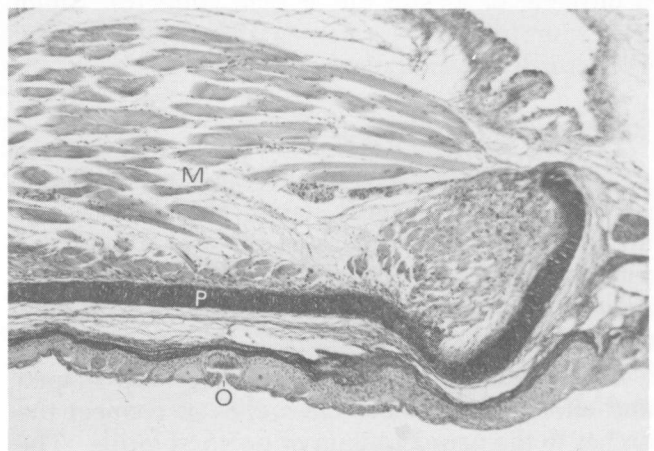


FIG. 96. The intermandibularis posterior muscle (M) has strips of pseudocartilage (P) crossing the ventral surface. The mental and mandibulary barbels are attached to these strips. Sagittal section of fingerling; O, small pit organ. Bouin's; H & E; × 60.

tions are broad, flat muscles. The anterior portion originates from the parasphenoid and orbitosphenoid and inserts on the inner surface of the posterior portion of the palatine. Eaton (1948) refers to this muscle as the abductor tentaculi because of its indirect action on the maxillary barbel. The posterior portion originates from the posterior parasphenoid and the prootic, and it inserts on the inner surface of the pterygoid and anterior hyomandibular.

The interhyoideus is on the ventral side of the head. It originates from the ceratohyal and hypohyal, and it inserts on an aponeurosis at the midline. The insertion of the interhyoideus is immediately beneath the skin, but the origin is covered by the intermandibularis posterior. This muscle was called the anterior portion of the hyohyoideus by McMurrich (1884a).

The hyohyoideus is the constrictor of the branchiostegal rays and has three portions. The pars dorsalis is between the opercular, interopercular, and the enlarged first branchiostegal ray. The pars medialis interconnects the remaining branchiostegal rays. The pars ventralis extends from the last ray to the midline. The hyohyoideus was termed the posterior portion of the hyohyoideus by McMurrich (1884a) and is sometimes separated into hyohyoideus superior consisting of the pars dorsalis and pars medialis and hyohyoideus inferior consisting of the pars ventralis (Singh and Munshi, 1968).

The adductor hyomandibularis originates from the lower surface of the pterotic and inserts on the lower surface of the hyomandibular. McMurrich (1884a) states that this muscle aids the adductor arcus platini in adducting the hyomandibular, but Allis (1908) states that this muscle is a retractor or levator rather than adductor. Singh and Munshi (1968) refer to this muscle as the retractor hyomandibularis.

## BRANCHIAL MUSCLES

These are innervated by the vagus nerve (Cr.N. X) or glossopharyngeal nerve (Cr.N. IX) and are used to move the four gill arches and the pharyngeal teeth. Branchial muscles are often difficult to locate in dissections because of their small size and deep location.

Most of the branchial muscles are strap shaped and either interconnect the arches or connect the arches to the neurocranium or pectoral girdle. The muscles inserting on the dorsal part of the arches and on the upper pharyngeals will be described separately from the ventral muscles.

One muscle, the attractor arcus branchialis (Fig. 97), connects the epibranchial and ceratobranchial of the fourth arch and can not be classified as either dorsal or ventral. This muscle was omitted by McMurrich (1884a).

*Dorsal muscles.* A series of seven levatores arcuum branchialia are found dorsal to the branchial arches. These originate from the pterotic and sphenotic and insert on the three anterior epibranchials and the upper pharyngeal which bears the dorsal pharyngeal teeth. These are described in detail by McMurrich (1884a).

Two transversi dorsales are present connecting branchial arches of opposite sides of the pharynx. These muscles and a similar muscle on the ventral side of the pharynx are some of the few unpaired muscles present in the channel catfish. The transversus dorsalis anterior connects the first and second epibranchials and the pharyngobranchials of the left and right sides, and the transversus dorsalis
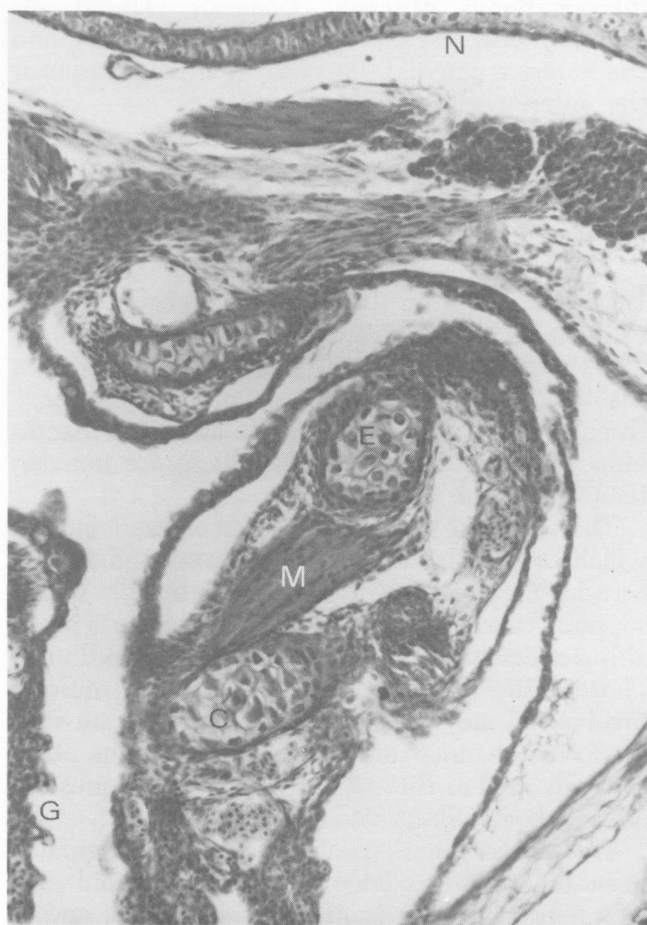


FIG. 97. Sagittal section of pharynx of a channel catfish 4 days after hatching. The epibranchial (E) and ceratobranchial (C) of the fourth gill arch are formed by cartilage and are connected by the attractor arcus branchialis muscle (M). This muscle is also present in adults, but the gill arch cartilage is replaced by bone. N, neurocranium, G, gill. Bouin's; H & E; × 180.
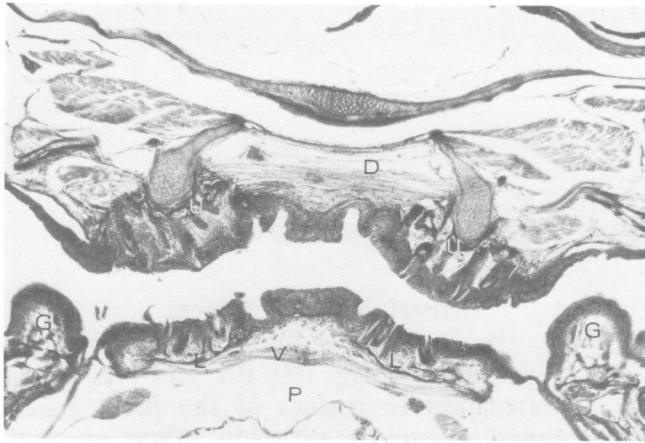
FIG. 98. Transverse section of the pharynx of a fingerling. The transversus dorsalis posterior muscle (D) connects the upper pharyngeals (U), and the transversus ventralis posterior muscle (V) connects the lower pharyngeals (L). The upper and lower pharyngeals are the bones which bear the pharyngeal teeth. G, gill arch; P, pericardial cavity. Bouin's; H & E; × 32.

posterior (Fig. 98) connects the upper pharyngeals.

Obliqui dorsales (interarculales dorsales obliqui) interconnect some of the branchial arches. One muscle connects the first epibranchial to the dorsal process of the third epibranchial. A second muscle connects the second epibranchial to the process of the third epibranchial. A third muscle connects the pharyngobranchial between the third and fourth epibranchials to the fourth epibranchial.

*Ventral muscles.* The subarcualis rectus communis (hypobranchialis of McMurrich, 1884a) lies ventral to the branchial arches just lateral to the midline (Fig. 99). It originates from the hypohyal and passes posteriorly. Insertion is by four slips to the second, third, fourth, and fifth ceratobranchials.

The transversus ventralis anterior and transversus ventralis posterior (Fig. 98) connect the fourth and fifth ceratobranchials of the right and left sides. The anterior muscle was found to connect the third ceratobranchials instead of the fourth in some specimens. The anterior muscle crosses the midline and is unpaired, but the posterior muscle inserts on a midventral aponeurosis and is paired.

An obliquus ventralis (interarcualis ventralis obliquus) is present on the surface of each of the anterior three branchial arches (Fig. 99). These muscles lie dorsal to the subarcualis rectus communis. Each muscle originates near the midline and inserts on the ceratobranchial.

The cleithropharyngeus superficialis and profundus connect the anterior process of the fifth ceratobranchial (lower pharyngeal) to the cleithrum of the pectoral girdle. Both muscles proceed laterally and ventrally from their insertion. The cleithropharyngeus superficialis originates further posterior and is larger than the profundus. These muscles were termed pharyngo-clavicularis externus and internus by McMurrich (1884a) while cleithropharyngeus was the term used by Eastman (1971) for similar muscles in *Cyprinus carpio*. These muscles are similar to the coracobranchialis muscles of other teleosts (Edgeworth, 1935), but since the homology is uncertain the more accurate terms cleithropharyngeus is preferred.

## HYPOBRANCHIAL MUSCLES

The only hypobranchial muscle present is the rectus cervicis. It originates from the dorsal surface of the cleithrum and extends anteriorly to insert on the urohyal. This muscle was termed the hypopectoralis by McMurrich (1884a), and coracohyoid by Branson (1966). The name rectus cervicis is preferred by Edgeworth (1935) because this muscle seems homologous to the same muscle in tetrapods. It develops from the ventral portion of the anterior myomeres and is innervated by spinal nerves. The development of this muscle from myomeres is indicated by its segmentation and the presence of myocommata (Fig. 99).
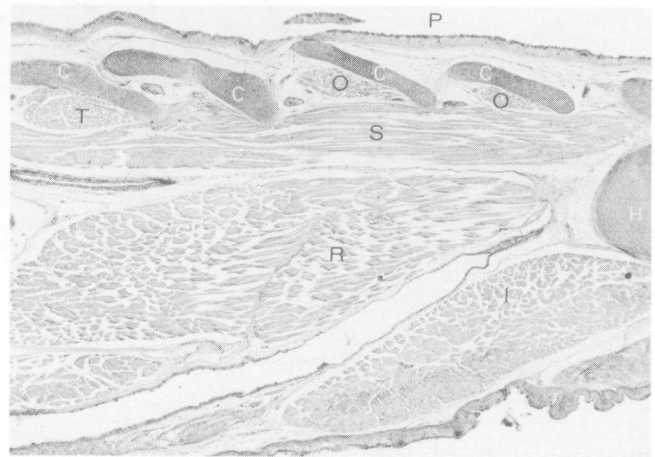


FIG. 99 Sagittal section of the ventral pharynx of a fingerling. The subarcualis rectus communis muscle (S) lies just ventral to the ceratobranchials, (C). Its origin from the hypohyal (H) and three of its four insertions are seen in this figure. The obliqui ventrales muscles (O) are present between the subarcualis rectus communis muscle and the ceratobranchials of the anterior three branchial arches. The transversus ventralis anterior (T) connects the two fourth ceratobranchia. R, rectus cervicis; I, interhyoideus; P, pharynx. Bouin's; H & E; × 25.

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# NERVOUS SYSTEM

The brain and spinal cord form the central nervous system which has cranial and spinal nerves extending to all portions of the body. The autonomic nervous system is composed of elements of both cranial and spinal nerves, and literature on this portion of the nervous system of fishes has been reviewed by Cambell (1970). Sense organs include the eyes, ears, olfactory organs, taste buds, and lateral-line organs. These organs are connected to the central nervous system by cranial nerves.

**Central Nervous System**

The external surface of the brain is molded in several lobes seen in Fig. 100, 101, and 102. Some lobes correspond to regions of the brain based on embryonic development while others are portions of a region. Brain anatomy is more clearly described using the five regions determined from embryology, but familiarity with the various lobes is useful for orientation and reference.

Tracts are bundles of nerve fibers connecting discrete centers, often termed nuclei, in the brain
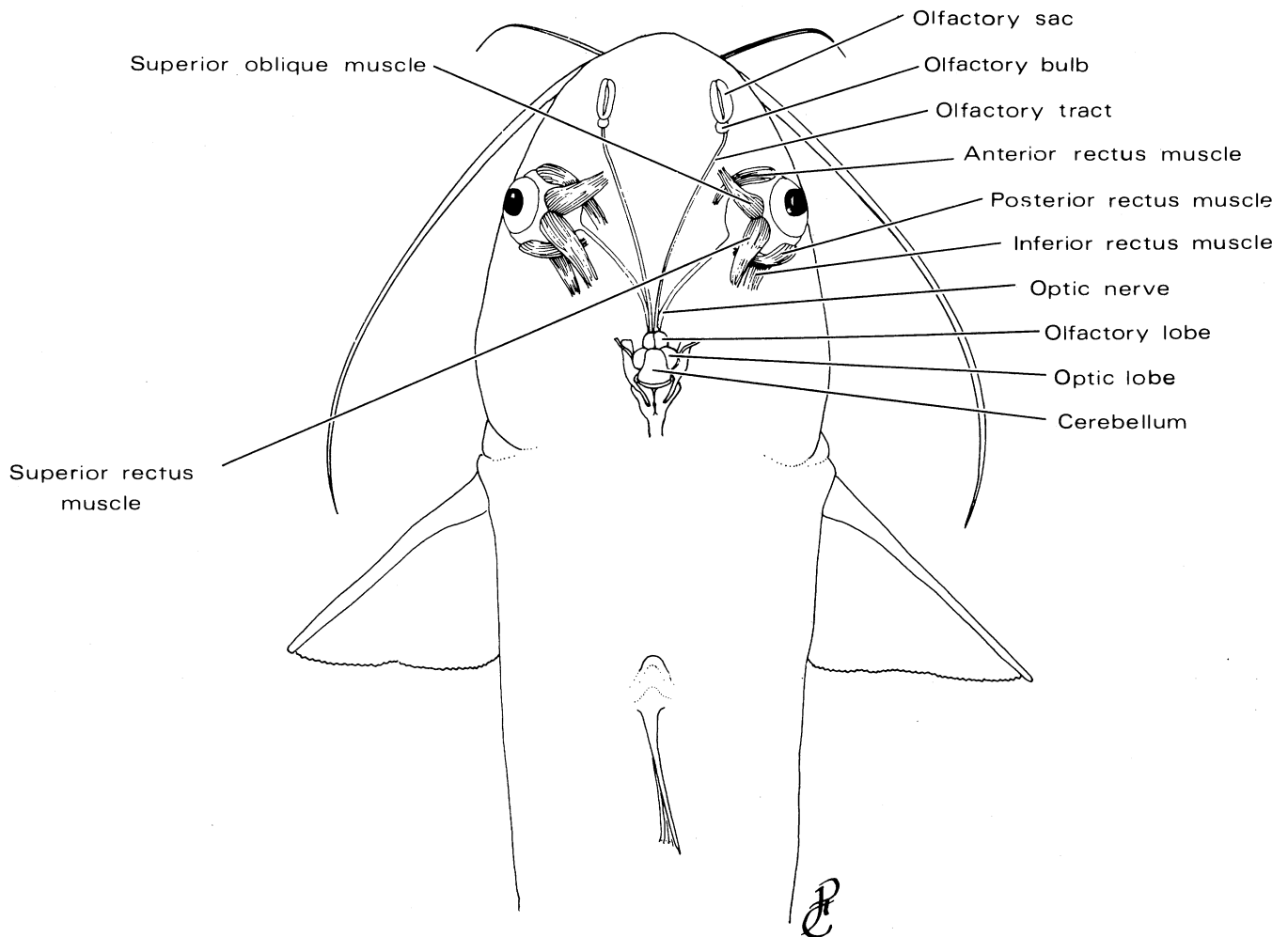


FIG. 100. This dorsal view of the head indicates the location of the brain, eyes, eye muscles, and olfactory organs. The brain extends anteriorly to the olfactory bulbs by way of the olfactory tracts. The first cranial nerve is very short and located between the olfactory sac and bulb. The eye is connected to the brain by the second cranial nerve.

Corpus cerebelli

Lateral accessory branch ( VII )

Optic lobe

Acousticolateralis lobe

Olfactory lobe

Vagal lobe

Olfactory tract

Spinal cord

Optic (II)

Inferior lobe

Vagus (X)

Pituitary gland

Glossopharyngeal (IX)

Trigeminofacial complex
( V and VII )

Medulla oblongata
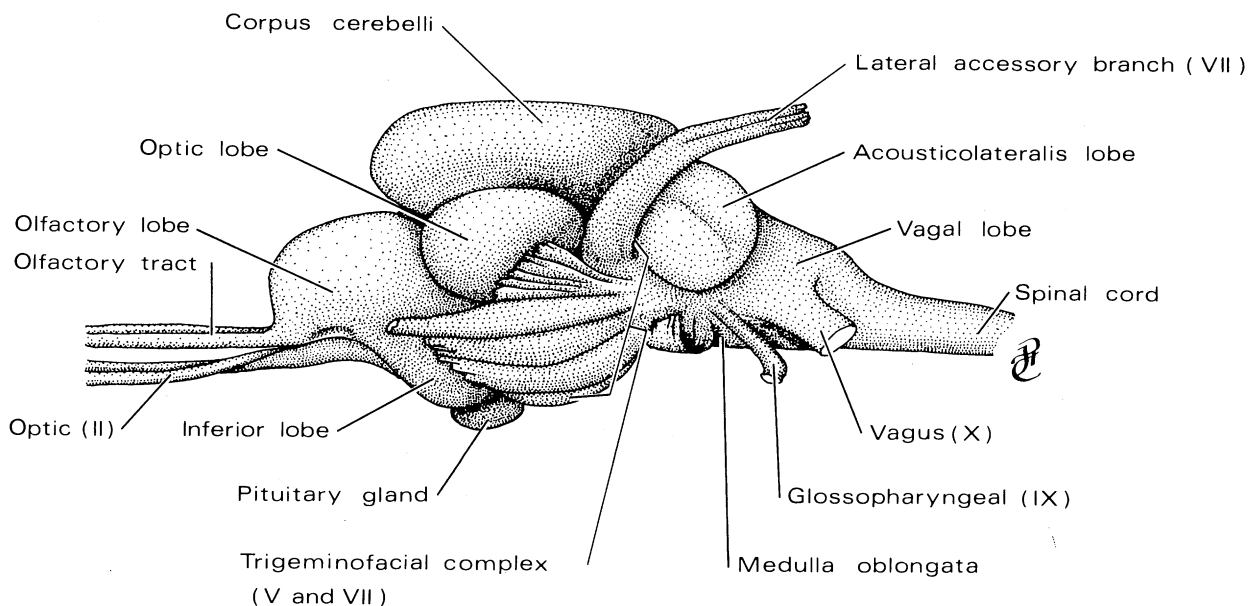
**FIG. 101.** The lateral view of the brain and several cranial nerves. The anteriorly located olfactory bulbs have been omitted.



Olfactory tract

Optic (II)

Optic chiasma

Olfactory lobe

Pituitary gland

Oculomotor (III)

Trochlear ( IV )

Saccus vasculosus

Optic lobe

Inferior lobe

Trigeminofacial complex
( V and VII )

Anterior portion of
acoustic ( VIII )

Abducens (VI)

Posterior portion of
acoustic ( VIII )

Medulla oblongata

Glossopharyngeal ( IX )

Vagus ( X )
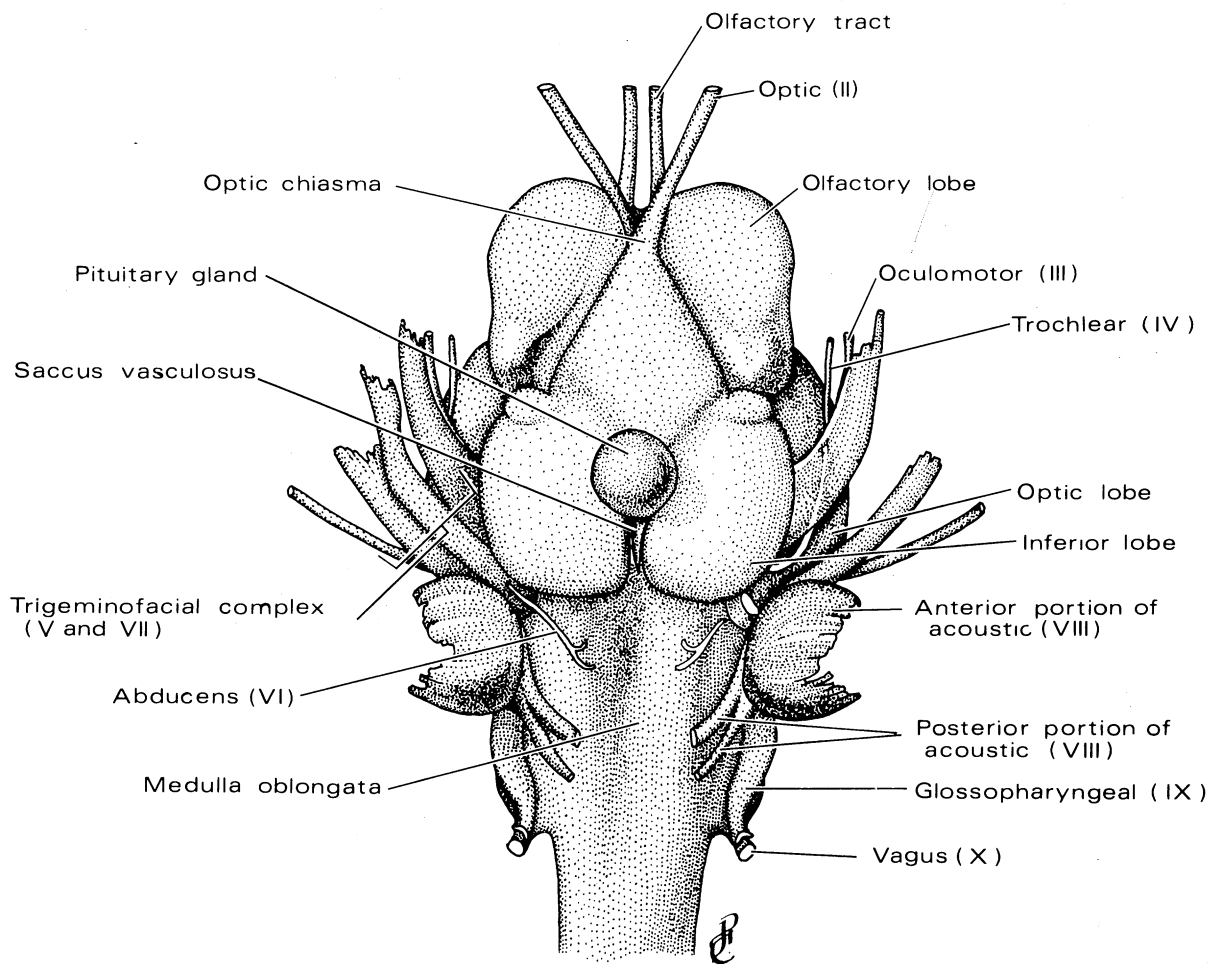
**FIG. 102.** The ventral view of the brain except for the olfactory bulbs shows emergence of all cranial nerves except Cr.N.I.

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and spinal cord. The general paths of tracts have been described in several species of fish and have been summarized by Ariens Kappers (1906), Ariens Kappers et al. (1936), and Lagler et al. (1962). The gustatory tracts have been described in ictalurids including channel catfish (Herrick, 1905).

The meninx primitiva (Fig. 103) covers the brain and spinal cord. This membrane is a single layer of fibrous connective tissue. In most areas the meninx primitiva is thin, but a few areas have additional areolar connective tissue. Blood vessels are frequently found in the meninx primitiva which forms the vascular supporting layer of the telae choroideae.

Ependymal cells (Fig. 104) are interstitial cells of the nervous system which line the brain ventricles and neural canal of the spinal cord, and form a portion of the telae choroideae. When lining a cavity, ependymal cells are usually ciliated columnar cells with tapered bases which become fibrous and extend into the underlying nervous tissue.

## TELENCEPHALON

The telencephalon forms the paired olfactory lobes and olfactory bulbs (Fig. 100). The olfactory bulbs located adjacent to the olfactory sac are connected to the olfactory lobes by long olfactory tracts (Fig. 100). The telencephalon seems most important in reception and transmission of olfactory impulses but is also involved in reproductive behavior, color vision and learning (Bernstein, 1970).

The telencephalon is everted (Bernstein, 1970) so that the olfactory lobes are thickenings of the floor of a sac, the ventriculus communis, which



FIG. 104. Ependymal cells (E) with cilia line the ventricles of the brain. Bouin's; H & E; × 470.

has an extremely thin roof and walls (Fig. 105).

Each olfactory lobe is solid, and except for the most anterior portion, the two lobes are connected ventrally. Ependymal cells are found on the outer surface of the olfactory lobe, and the periphery has a higher density of neurons than the central region. The optic chiasma is the point at which the optic nerves cross and is located ventral to the olfactory lobes.

## DIENCEPHALON

The dorsal side of this region is covered by the cerebellum and the ventral side forms the inferior lobes (Fig. 102 and 106). The pineal organ extends from the dorsum of the diencephalon, and the pituitary gland (Chap. 5) and saccus vasculosus are associated with the ventrum.

The diencephalon can be divided into three zones. The dorsal zone is the epithalamus which includes the pineal complex. The thalamus is the middle zone and is sometimes divided into dorsal and ventral portions. The hypothalamus is ventral and has efferent tracts leading to other parts of



FIG. 103. Meninx primitiva (M) covers the outer surface of the brain and spinal cord. Optic tectum; Bouin's; H & E; × 320.

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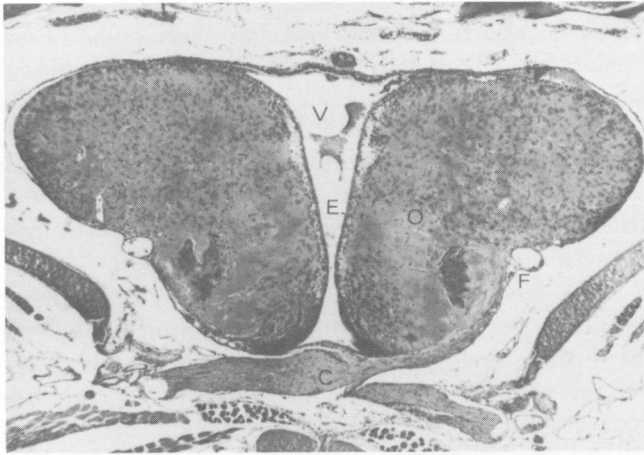
FIG. 105. The olfactory lobes (O) of the telencephalon are partially surrounded by the thin walled ventriculus communis (V) which is usually disrupted when the brain is removed from the cranium. This transverse section was made of the intact head of a 35 mm TL specimen. C, optic chiasma; F, endorhinal fissure; E, ependyma. Bouin's; H & E; × 50.

the brain and the neurohypophysis of the pituitary. The diencephalon serves to connect and integrate various parts of the brain and pituitary.

A tela choroidae (Fig. 107) is formed from the roof of the diencephalon covering the third ventricle and extends anteriorly to the posterior portion of the telencephalon. The tela choroidea is composed of the lamina epithelialis of modified ependymal cells and the choroid plexis formed from the meninx primitiva. The pineal stalk is adjacent to the tela choroidea which is covered by the cerebellum. Cerebrospinal fluid which fills the brain ventricles, neural canal of the spinal cord, and the space immediately surrounding the brain is produced by the tela choroidea (Patt and Patt, 1969).

*Pineal organ.* A long stalk connects the pineal organ to the diencephalon. The flattened pineal organ (Fig. 108) and tubular stalk (Fig. 109) are hollow with columnar cells surrounding the lumen. The stalk begins beneath the forward edge of the cerebellum and extends anteriorly to the pineal located dorsal to the telencephalon just anterior to the level of the optic chiasma. Most of the stalk is in contact with the thin roof of the ventriculus communis of the telencephalon.
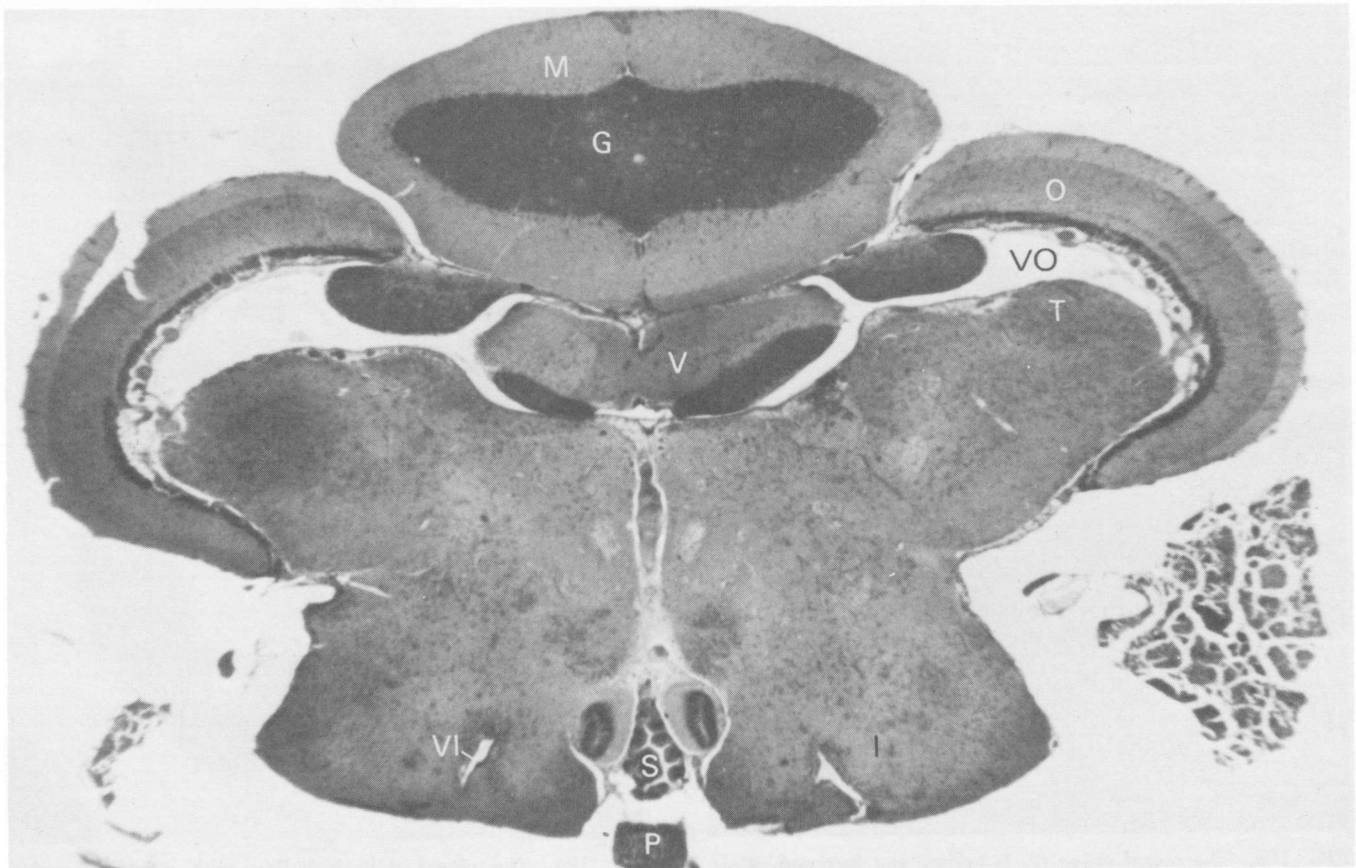


FIG. 106. This transverse section of the brain has portions of the diencephalon, mesencephalon, and cerebellum. The saccus vasculosus (S) lies between the inferior lobes (I) of the diencephalon, and the pituitary gland (P) is ventral to them. The corpus cerebelli of the cerebellum, with molecular (M) and granular (G) layers, covers the central portion of the optic tecta (O) and the valvula cerebelli (V). VO, ventricle of optic lobe (mesocoel); T, tegmentum of optic lobe; VI, ventricle of inferior lobe. Bouin's; H & E; × 32.

The cells surrounding the lumen have been described in several species and are usually sensory
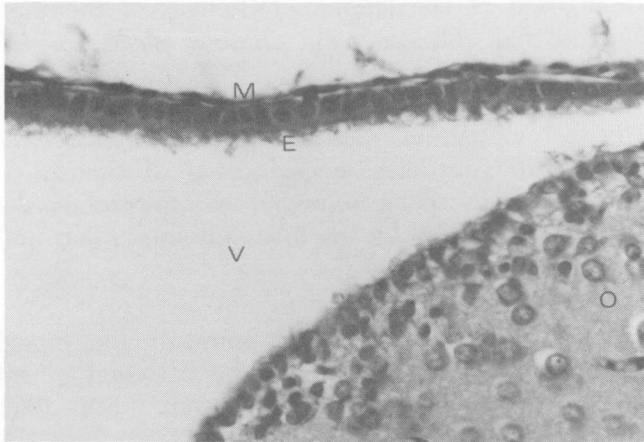


FIG. 107. The tela choroidea consists of the meninx primitiva (M) and the ependymal cells (E). It covers the third ventricle (V) of the diencephalon. The tela choroidea is very similar to the thin roof of the ventriculus communis of the telenecephalon except for a slight increase in vascularity. O, olfactory lobe; Bouin's; H & E; × 320.

cells, supporting cells, and ganglion cells (Fenwick, 1970a). It has been reported that the pineal of *Clarias lazera* has only glandular epithelial cells with sensory cells being absent (Rizkalla 1970). Another member of the Siluriformes, *Corydoras aneus,* has few sensory cell outer segments, and the pineal organ seems specialized for a secretory function (Hafeez, 1971).

The precise function of the pineal is not known. Some hypotheses regarding its function are that it is a photosensory structure serving as a dosimeter of incident light, a detector of pressurë or chemical composition of the cerebrospinal fluid, or a gland which is either endocrine or related to the composition of the cerebrospinal fluid (Fenwick, 1970a). These hypotheses are not exclusive and it is likely that some or all of these functions are involved. The pineal organ of the goldfish serves as an endocrine organ, producing melatonin which seems to inhibit gonadal formation by inhibiting



FIG. 108. The pineal organ (P) is hollow and flattened. Columnar cells surround the lumen which contains an eosinophilic material. The pineal organ is located directly beneath the dermis (D) and dorsal to the telencephalon (T) in this 30 mm TL specimen. A very thin roof composed of meninx primitiva and ependymal cells covers the ventricle (V) of the telencephalon. E, epidermis. Bouin's; H & E; × 350.



FIG. 109. The pineal stalk is hollow with ciliated pseudostratified columnar epithelium (E) lining the lumen. A layer of nerve fibers (N) surround the epithelial cells, and several capillaries are usually found beneath the simple squamous epithelium covering the organ. The tela choroidea of the diencephalon (T) is closely associated with the base of the stalk. Bouin's; H & E; × 350.

the release of hormones from gonadotrophic cells of the pituitary (Fenwick, 1970b). In the same species, both eyes and the pineal organ are necessary for normal phototactic response (Fenwick, 1970c).

The function of the pineal organ may vary in different species of fish. Hafeez (1971) found pronounced variation in cell types of the pineal organ. Some species seemed specialized for a sensory function while others were specialized for secretion. A secretory function may be predominant in Siluriformes since both *Corydoras aneus* (Hafeez, 1971) and *Clarias lazera* (Rizkalla, 1970) have pineal organs that are specialized for secretion.

*Saccus vasculosus.* This organ lies between the inferior lobes (Fig. 102 and 106) with the anterior end dorsal to the pituitary. It can usually be seen grossly as a vascular area between the inferior lobes. The lumen is continuous with the third ventricle with the opening located in the anterior portion of the saccus vasculosus.

The folded wall (Fig. 110) has large blood sinuses located in the folds and two epithelial cell types (Fig. 111). Coronet (crown) cells are large, with basally located nuclei and a knobbed process which extends into the lumen. Ciliary processes with globular expansions at the tips extend from the apical portion of each crown cell. Supporting cells located between crown cells have nuclei located in the middle or apical portion of the cell. Apically located nuclei are often triangular in shape.

The function of the saccus vasculosus in fish is uncertain. The sensing of changes in water or ventricular pressure (Dammermann, 1910; Kurotaki, 1961) and secretion of acid mucopolysaccharides (Khanna and Singh, 1967) have been suggested.

## MESENCEPHALON

This region is composed of the optic tectum which forms the superior border of the third ventricle (mesocoel) and the tegmentum which forms the inferior border (Fig. 106). The optic tecta are the optic lobes (Fig. 100 and 101) which are partially covered dorsally by the cerebellum. The wall of the optic tecta have several layers (Fig. 112) which vary in the type of fibers present and density of cell nuclei. The layers of teleost optic tecta have been described by Ariens Kappers et al. (1936), and Schwassimann and Kruger (1968).

The function of the mesencephalon involves the reception and integration of visual stimuli re-

ceived from the eyes. The optic nerves of channel catfish are completely decussated so that each optic tectum receives stimuli only from the retina on the opposite side of the body.
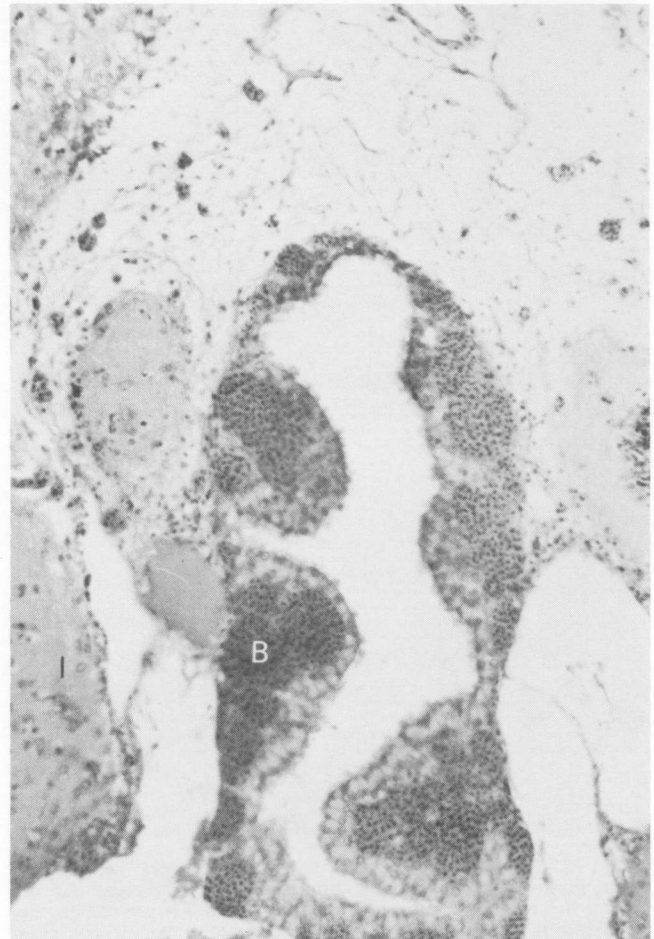


FIG. 110. The saccus vasculosus has a folded wall with large blood sinuses (B). Inferior lobes (I) of the brain are on either side of this transverse section. Bouin's; H & E; × 175.
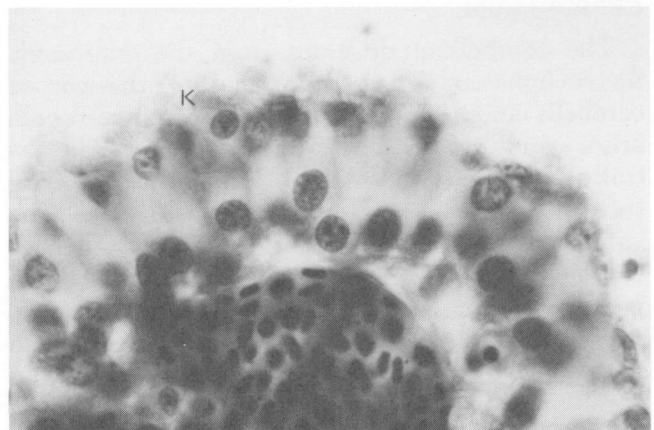


FIG. 111. The wall of the saccus vasculosus has two cell types. The coronet cells have basal nuclei and ciliary structures located on knobbed processes (K) extending into the lumen. Supporting cells have apically located nuclei. Bouin's; H & E; × 800.
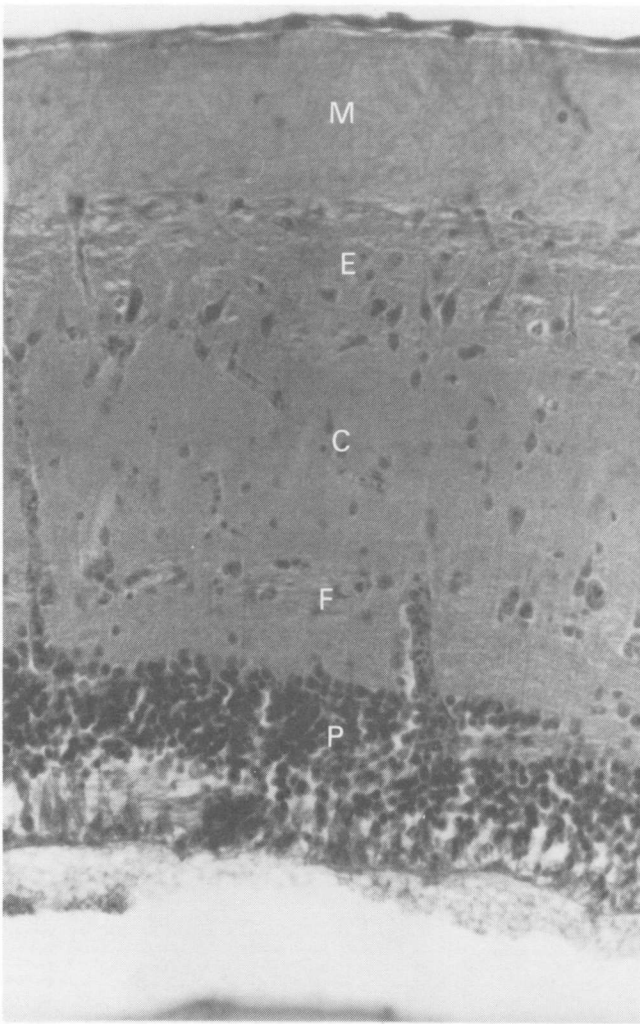
FIG. 112. The optic tectum has several layers which have been divided and named in various ways by different authors. Using the terminology of Schwassmann and Kruger (1968), five principle layers are present. Starting at the outer surface, these are the stratum fibrosum marginate (M), stratum plexiform et fibrosum externum (E), stratum griseum centrate (C), stratum fibrosum profundum (F), and stratum griseum periventriculare (P). Bouin's; H & E; × 253.

## CEREBELLUM

The cerebellum develops from the embryonic metencephalon and is composed of the corpus cerebelli and the valvula. The corpus cerebelli arises caudal to the optic lobes and proceeds rostrally forming a prominent lobe on the dorsal surface of the brain (Fig. 100 and 101). The valvula cerebelli projects rostrally from the base of the corpus cerebelli into the mesencephalic ventricle (Fig. 106). The corpus cerebelli (Fig. 106, 113, and 114) has a very small ventricle which is lined by ependymal cells surrounded by a granular layer composed of small dark staining nuclei. The outer portion of the corpus cerebelli is composed of the molecular layer consisting of fibers and few nuclei. Purkinje cells (Fig. 114) are located between these layers. The valvula has

similar granular and molecular layers. The anterior medullary velum continues rostrally from the valvula. The dorsocaudal margin of the corpus cerebelli forms the interauricular granular band (Fig. 113) with a large number of small nuclei interspersed with fibers. A tela choroidea (Fig. 113) consisting of a layer of cuboidal ependymal cells covered by the meninx primitiva extends from the interauricular granular band to the facial lobe posterior to the corpus cerebelli.

The cerebellum seems to function in maintenance of muscle tone, postural reflexes, and integration of stimuli from the eyes and acoustico-lateralis organs (Bernstein, 1970). Direct stimulation of the cerebellum through implanted electrodes has been used in determination of function in *Ictalurus* (Clark et al., 1960). Stimulation usually resulted in flexion of the body or tail and
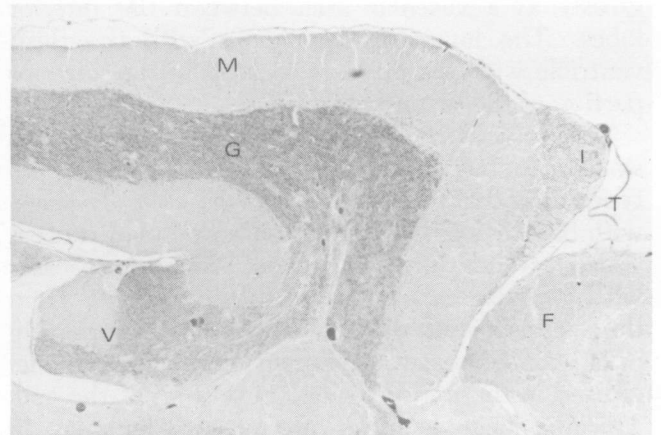


FIG. 113. The corpus cerebelli of the cerebellum has distinct granular (G) and molecular (M) layers. These layers continue into the valvula cerebelli (V). The interauricular granular band (I) is located on the posterior edge of the cerebellum. The facial lobe (F) is posterior to the cerebellum. T, tela choroidea; midsagittal section. Formalin; H & E; × 35.
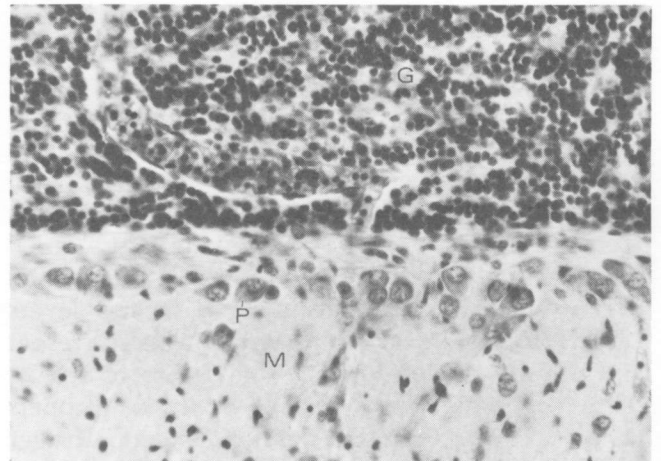


FIG. 114. Purkinje cells (P) are located between the granular (G) and molecular (M) layers of the cerebellum. Bouin's; H & E; × 320.

retraction of maxillary barbels. "Stimulus-rebound", consisting of movement during the stimulation followed by movement in the opposite direction after cessation of stimulation, occurred under some circumstances.

## MEDULLA OBLONGATA

This region is formed from the myelenchephalon. The paired facial and vagal lobes (Fig. 100 and 101) are dorsal enlargements, and the acousticolateralis lobes are lateral enlargements of the medulla. The facial lobes (Fig. 115) are separated by the fourth ventricle lined by ciliated ependymal cells. The ventricle has a thin dorsal covering and flexes to the side as it proceeds ventrally. The vagal lobes are also separated by the fourth ventricle, but the ventricle in this region is straight rather than curved (Fig. 116). The medulla

oblongata extends caudally from beneath the vagal lobes and blends into the spinal cord.

Several cranial nerves emerge from the medulla oblongata. Columns of nerve fibers connect these cranial nerves and the spinal cords to other regions of the brain. The medulla oblongata is especially important in the functioning of the reticulomotor system, taste, and audition (Bernstein, 1970).

## SPINAL CORD

The spinal cord (Fig. 117) has a small central canal surrounded by ependymal cells. Gray matter of non-myelinated fibers is concentrated around the central canal with a single dorsal horn and paired ventral horns of gray matter extending toward the periphery. White matter of myelinated fibers is located between the horns.

The spinal cord is protected by neural arches of the vertebrae and extends to the caudal peduncle. A filum terminale is formed from the posterior end of the spinal cord. It extends dorsoposteriorly parallel to the uroneural and tapers to a point. Melanophores are located in the areolar connective tissue surrounding the meninx primitiva. Spinal nerves branch from the spinal cord.

### Cranial Nerves

Ten cranial nerves (Fig. 100, 101, and 102) were found in channel catfish. These nerves are similar in origin and appearance to cranial nerves found in other fish (Lagler et al., 1962; Romer, 1955; Hyman, 1942). Cranial nerves have been described in other ictalurids by Wright (1884), Workman (1900) and Herrick (1901), and these seemed identical to those of channel catfish. Func-



FIG. 115. The facial lobes (F) are dorsal enlargements and the acousticolateralis lobes (A) are lateral enlargements of the medulla oblongata (M). The ventricle (V) between the facial lobes has a distinctive shape. 8, eighth cranial (auditory) nerve. Bouin's; H & E; × 12.



FIG. 116. The vagal lobes (V) are located posterior to the facial lobes and are dorsal enlargements of the medulla oblongata (M). X, tenth cranial (vagus) nerve; IV, fourth ventricle. Bouin's; H & E; × 20.



FIG. 117. The spinal cord has a central canal (C) and horns of gray matter (D, dorsal horn; V, ventral horn) located between white matter. Areolar connective tissue (A) with numerous melanophores fills the space between the spinal cord and neural arch (N) of the vertebrae. Bouin's; H & E; × 60.

tions attributed to the cranial nerves in this chapter are those suggested by the above authors.

The terminal cranial nerve (CR.N.0) was not found in dissections or histological sections of the region between the olfactory lobes and the olfactory bulb. If present, it is fused into the olfactory tract and is not distinguishable from it. The terminal nerve of carp is within the olfactory tract but can be distinguished from it in sections (Ariens Kappers et al., 1936).

## OLFACTORY (I)

This short nerve connects the olfactory sac to the olfactory bulb (Fig. 100, 123) and should not be confused with the longer and more prominent olfactory tracts. The olfactory nerves are too short to be easily located. It is a special sensory nerve and is unusual since the nerve fibers are formed from the sensory epithelium in the olfactory sac instead of from separate neurons with cell bodies forming ganglia.

## OPTIC (II)

These nerves connect each retina to the optic tectum on the opposite side of the brain. The optic chiasma (Fig. 105) is formed where the optic nerves cross ventral to the olfactory lobes. They enter the ventral side of the brain at the hypothalamus and continue directly to the optic tecta.

The optic nerves are special sensory nerves and are similar to a brain tract which results because of the formation of the retina from the brain tube. The fibers originate in the ganglion cell layer of the retina.

## OCULOMOTOR (III)

The oculomotor nerve leaves the brain between the inferior lobes and medulla oblongata dorsal to the saccus vasculosus. The nerve is both somatic motor and automatic in function. It innervates four of the eye muscles which rotate the eye (Chap. 8). The muscles innervated are the superior rectus, inferior rectus, anterior rectus, and inferior oblique. The autonomic function involves pupillary dilation in certain teleosts (Young, 1931), although in most teleosts the pupil is immobile (Munz, 1971).

## TROCHLEAR (IV)

This nerve is small and is often difficult to locate grossly. In sections it was found to leave the medulla just ventroposteriorly to the optic lobe. This location is dorsal and slightly posterior to the origin of the oculomoter nerve. The trochlear is

in close contact with the ganglionic complex of the fifth and seventh cranial nerves after leaving the brain. It then follows the superficial ophthalmic branch of the fifth nerve until it reaches the superior oblique eye muscle which it innervates.

## TRIGEMINAL (V)

The fifth and seventh cranial nerves are united as they leave the brain. This complex originates from the anterior lateral portion of the medulla and just posterior to the level of the optic lobe. These nerves proceed anteriorly briefly after leaving the brain and then branch. These branches have been described in detail in *I. melas* (Herrick, 1901).

The trigeminal nerve is a branchial nerve with both somatic sensory and visceral motor functions, and innervates the anterior portion of the head, especially the upper and lower jaws. Taste buds and lateral-line elements are not innervated by the trigeminal.

## ABDUCENS (VI)

The roots of this nerve are located on the ventral surface of the medulla oblongata posterior to the inferior lobe. This small somatic motor nerve innervates one eye muscle, the posterior rectus.

## FACIAL (VII)

The facial is closely associated with the trigeminal nerve. The branches of this nerve in *I. melas* have been described by Herrick (1901). Visceral motor, visceral sensory, and lateral-line elements are contained in this nerve which serves muscles of the hyoid arch, lateral-line components of the head, and taste buds including those in the outer skin. Taste buds of the skin posterior to the head are innervated by the lateral accessory branch (Fig. 128) which proceeds dorsally from the trigeminofacial complex to the dorsum of the brain. It continues posteriorly from the cranium and through the epaxial muscles.

## ACOUSTIC (VIII)

This special sensory nerve is fan-shaped as it leaves the lateral surface of the medulla (Fig. 115) immediately posterior to the trigeminofacial complex and proceeds directly to the ear. The anterior portion of the nerve goes to the pars superior of the ear. The posterior portion of the nerve, separated from the anterior portion and directed ventrally, innervates the pars inferior of the ear.

## GLOSSOPHARYNGEAL (IX)

This nerve leaves the lateral surface of the medulla just posterior to the acoustic nerve. The glossopharyngeal has visceral motor, visceral sensory, and lateral-line components. It innervates muscles surrounding the first gill slit, taste buds in the pharynx, and lateral-line organs on the posterior head.

## VAGUS (X)

The vagus nerve originates from the lateral surface of the vagal lobe (Fig. 116). Visceral and somatic sensory, lateral-line, and visceral motor components are present. Muscles of the posterior gill slits and anterior visceral organs of the body cavity are innervated by the vagus. Lateral-line organs of the posterior head and the body, taste buds of the pharynx, and other sense receptors of the posterior head are connected to the brain through the vagus. A visceral branch with motor and sensory function innervates the heart and organs of the anterior body cavity.

The vagus nerve is important in the parasympathetic automatic nervous system. Increase in branchial vascular resistance, reduction in heart rate, contraction of the stomach, and possibly control of swim bladder inflation are attributed to parasympathetic stimulation (Cambell, 1970).

### Sense Organs

## EYE

The general organization of the channel catfish eye is similar to that of other teleosts (Fig 118). Six oculomotor muscles are inserted on the periph-

ery of the eye (Chap. 8). The choroid gland found in many teleosts is absent.
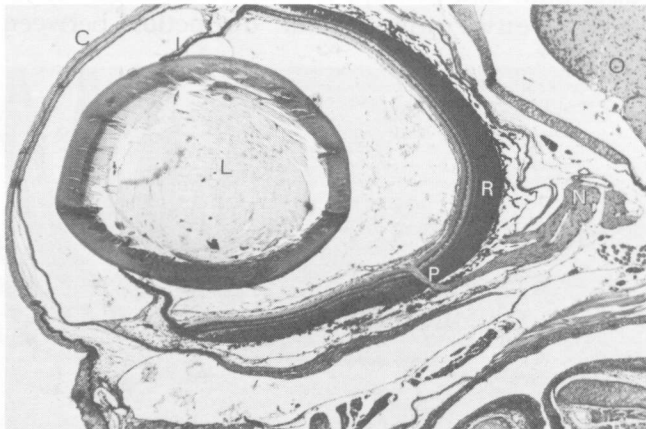
Except for the lateral surface, the eye is covered by a partially cartilaginous sclera and a heavily pigmented choroid (Fig. 119). The spherical lens (Fig. 118 and 120), which is held in place by a suspensory ligament and retractor lentis muscle, is covered by the cornea (Fig. 120). The iris (Fig. 119) is a continuation of the choroid. The optic nerve connects the retina to the mesencephalon.

Retinal structure of the channel catfish has been described by Arott et al. (1974) and Naka and Carraway (1975). Rods and cones are present in about equal numbers, and twin cones are absent. These photoreceptor cells are located in an outer layer of the retina (Fig. 121 and 122). The outer
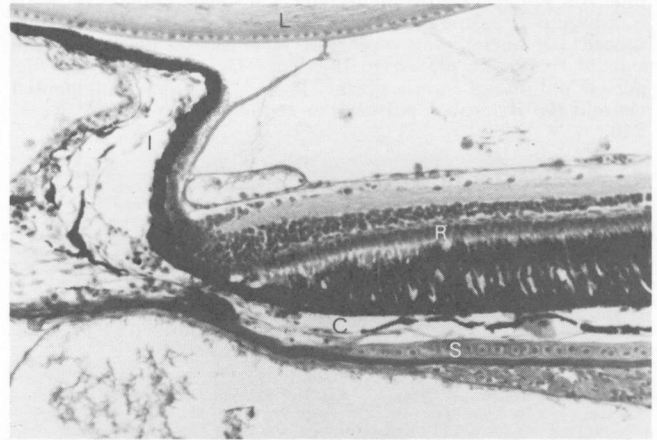


FIG. 119. The iris (I) is a continuation of the choroid (C) and is heavily pigmented. The cartilaginous sclera (S) covers the choroid. The retina (R) contains the receptor cells which sense light focused by the lens (L). Bouin's; H & E; × 160.
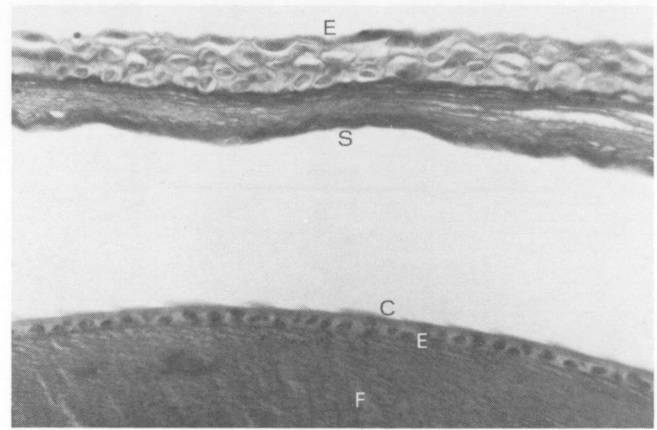


FIG. 120. The cornea covers the outer surface of the eye. The outer layer of the cornea is composed of stratified squamous corneal epithelium (E) which is continuous with the epidermis of the surrounding skin. The other layer is the stroma or substantia propria (S) which is composed of collagenous connective tissue. The outer portion of the stroma is continuous with the dermis of the skin and the inner part is continuous with the sclera. The lens has an outer noncellular capsule (C) covering the lens epithelium (E) of cuboidal cells. The bulk of the lens is composed of lens fibers (F). Bouin's; H & E; × 320.



FIG. 118. This portion of a transverse section of the head of a 30 mm TL specimen has the olfactory lobe of the brain (O), optic nerve (N), and eye. The eye is slightly compressed dorsoventrally and the lens (L) is not sectioned well. P, optic papilla; R, retina; I, iris; C, cornea. Bouin's; H & E; × 35.
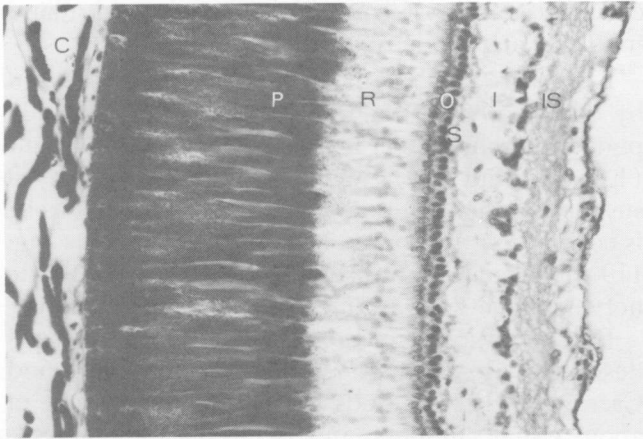
FIG. 121. The retina is composed of several layers. The largest layer contains the outer segments of rods and cones (R) as well as pigment (P). Two layers of nuclei compose the outer nuclear layer (O). The outer synaptic layer (S) is very thin and not readily distinguished. The inner nuclear layer (I) is composed primarily of horizontal cell fibers and widely spaced cell nuclei. Inner synaptic layer (IS) is located on the side of the retina closest to the lens. Ganglion cells are dispersed and do not form a distinct layer. The heavily pigmented choroid (C) is located outside the retina. Bouin's; H & E; × 240.
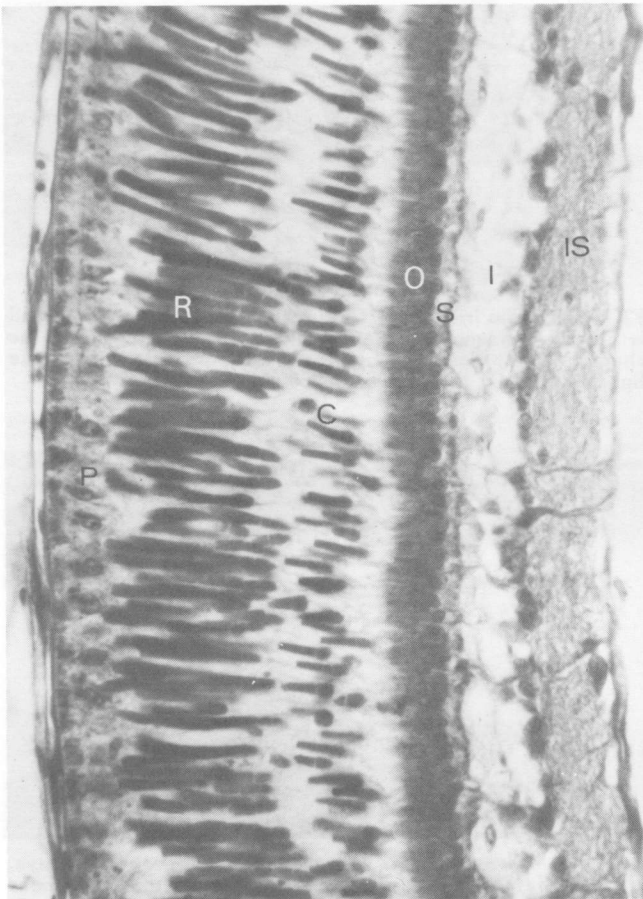


FIG. 122. Bleaching of the retina (1:1000 Chlorox solution) removes the melanin and tapetum lucidum so that rods (R) and cones (C) are clearly visible. This retina was light adapted so that the rods are located deeper in the retina than the cones. Nuclei of pigment cells (P) are also visible after bleaching. O, outer nuclear layer; S, outer synaptic layer; I, inner nuclear layer; IS, inner synatic layer. Bouin's; H & E; × 350.

segments of these cells are mobile with their position determined by light intensity. The migration of pigment from the pigment epithelium accompanies the movement of the outer segments of the photoreceptor cells resulting in adaption for various light intensities. The pigment layer has a tapetal pigment, which forms a tapetum lucidum, and melanin. Both types of pigment must be removed for clear examination of the rods and cones (Fig. 122). The nuclei of the rods and cones are stationary and are located in the outer nuclear layer.

The photoreceptor cells synapse with bipolar and horizontal cells in the very thin outer synaptic (plexiform) layer. Cell bodies of the bipolar and horizontal cells as well as amacrine cells and displaced ganglion cells are located in the inner nuclear layer (Naka and Carraway, 1975). Most of this layer is composed of horizontal cell fibers with cell bodies of the various cell types widely dispersed.

The inner synaptic (plexiform) layer contains synapses between cells of the inner nuclear layer and ganglion cells. Numerous myelinated fibers are present.

Ganglion cells are scattered and do not form the distinct layer found in most vertebrate retinas. Fibers of the ganglion cells form bundles which proceed along the inner surface of the retina to optic papillae (Fig. 118). Nine to twelve optic papillae are present (Naka and Carraway, 1975) and several bundles of nerve fibers exit through each papillae. These nerve bundles join to form the optic nerve.

## OLFACTORY ORGAN

Chemoreception in fish is by olfactory organs, taste buds and perhaps free nerve endings. In an aquatic environment, the distinction between



FIG. 123. The olfactory epithelium (E) is connected to the olfactory bulb (B) by the first cranial (olfactory) nerve (I). Sagittal section of 65 mm TL specimen. Bouin's; H & E; × 60.
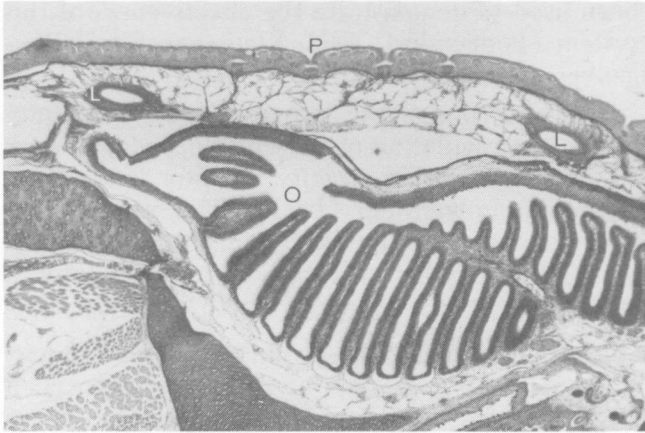
FIG. 124. The olfactory sac (O) has lamellae of epithelium. The epidermis dorsal to the olfactory organs has several small pit organs (P). Two lateral-line canals (L) are present beneath the epidermis. The break in the dorsal wall of the olfactory sac is an artifact. Bouin's; H & E; × 32.

"smell" and "taste" is unclear since both are mediated by dilute aqueous solutions (Hara, 1971), Behavioral experiments with *I. natalis* and *I. nebulosus* indicate that in these species the taste buds are used to locate food, and olfactory organs are used to detect chemical signals (pheromones) as a type of intraspecific communication (Bardach et al., 1967; Todd et al., 1967).

The olfactory organs (Fig. 100) are located in olfactory sacs which have anterior and posterior nares. The receptor cells are located in sensory epithelium which forms lamellae (Fig. 123 and 124). Nerve fibers from the receptor cells form the first cranial nerve which enters the olfactory bulb (Fig. 123).

The epithelium covering the olfactory folds (Fig. 125) has four cell types, receptor cells, supporting (sustentacular) cells, basal cells, and non-sensory ciliated cells. Epithelium covering the dorsal and lateral sides of the olfactory sac has the same four cell types and also has numerous goblet cells. The receptor cells have elongated nuclei and an eosinophilic process reaching to the surface of the epithelium. Two types of receptor cells are found in *Phoxinus* differing in the structure of their distal tips (Bannister, 1965). The non-sensory ciliated cells have oval nuclei closer to the surface than nuclei of other cells. Supporting cells have oval nuclei which are less basophilic than the nuclei of receptor cells. Basal cell nuclei lie beneath those of the other cell types. Caprio and Raderman-Little (1978) examined channel catfish olfactory lamellae with a scanning electron microscope.
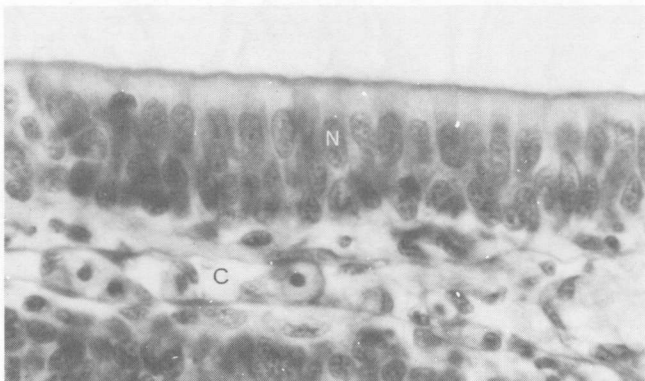
## TASTE BUDS

These gustatory organs are found over the entire external surface of channel catfish as well as inside the mouth, pharynx (Fig. 30), and anterior esophagus. The gill arches and barbels (Fig. 126) have especially numerous taste buds. The taste buds have essentially the same structure regardless of location and are innervated by cranial nerves VII, IX, and X (Herrick, 1901).

Taste buds are located in the epidermis except for those located in the esophagus where they are in the mucosa (Chap. 4). In regions where the epidermis is thick, the apical portion of the taste bud is flush with the surface and the dermis forms a papilla which reaches to the base of the organ. In thin epidermis the base rests on the dermis and the taste bud projects above the surface of the epithelial cells.

Taste buds have a characteristic flask shape (Fig. 127) with centrally located nuclei near the base. Three cell types are present: receptor cells, supporting cells, and basal cells. Various types of receptor cells have been described from electron microscope studies (Desgranges, 1965; Storch and



FIG. 125. The olfactory epithelium is primarily composed of nonsensory ciliated columnar cells with superficially located nuclei (N). Other types of cells discussed in the text are not seen clearly in this figure. The center of each lamellae has numerous capillaries (C). Bouin's; H & E; × 800.
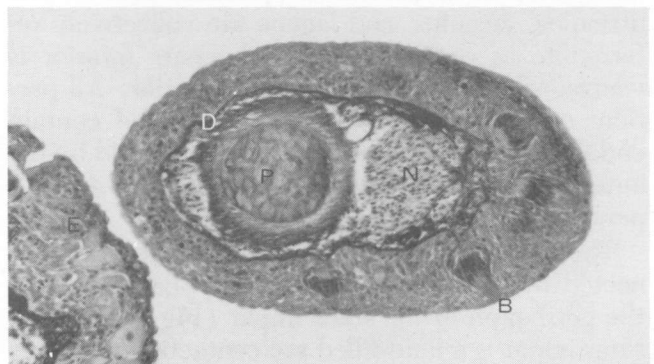


FIG. 126. The barbels are composed of a central core of pseudocartilage (P) and nerves (N). Skin with a thin dermis (D) forms the outer surface. Numerous taste buds (B) are located in the epidermis. The epidermis does not have the alarm substance cells found in the epidermis covering most of the body (E). Bouin's; H & E; × 120.
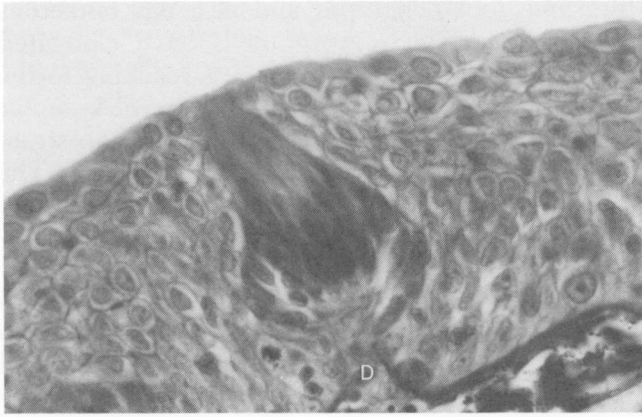
FIG. 127. Taste buds are located in the epidermis and have a characteristic shape. Nuclei are located basally with cell processes extending to the surface. Cell types are discussed in the text. The epidermis of the barbel is stratified with surface cells cuboidal or slightly flattened. Dermis (D), containing nerve fibers, forms a papilla reaching the base of the taste bud. Bouin's; H & E; × 600.

Welsch, 1970). The elongated sensory cells are located in the center of the organ and have long processes which form the apical portion of the taste bud. Supporting cells are located peripherally between the sensory cells and the surrounding epithelial cells. Oval basal cells are located at the base of the taste bud. The ultrastructure of the channel catfish taste bud has been described by Grover-Johnson and Farbman (1976).

## EAR

The ears consist of membranous labyrinths embedded in the otic region of the brain case lateral to the medulla. The labyrinths are part of the acousticolateralis system which has several types of sense organs with structurally similar sense cells. Each labyrinth (Fig. 128) has a pars superior consisting of the utriculus and three semi-circular canals and a pars inferior consisting of the sacculus and lagena. The sacculus and lagena of *I. nebulosus* have been described (Jenkins, 1977). The utriculus, sacculus, and lagena are collectively referred to as otolith organs. The pars inferior is ventral and posterior to the pars superior. All portions of the labyrinth are connected and contain endolymph. The pars superior is innervated by the anterior portion of the eighth cranial nerve and the pars inferior by the posterior portion.

The par inferior and the swim bladder are connected by the Weberian ossicles (Chap. 12) and the perilymph of the sinus impar (Fig. 129). The sinus impar is a fluid-filled sac contacting the sinus endolymphaticus (Fig. 128) which is continuous with the cavity of the labyrinth. This connection increases the sensitivity to sound and raises the upper frequency threshold. Interrupting this connection and destruction of the swim bladder have

been used to demonstrate the effectiveness of this system (Poggendorf, 1952; Kleerekoper and Roggenkamp, 1959).

The functions of the labyrinth include maintenance and regulation of muscle tone, receptor for angular acceleration, gravity receptor, and sound receptor (Lowenstein, 1971). The semicircular canals and their ampullae are involved with detection of angular acceleration and the otolith organs detect gravity and sound.

*Semicircular canals and ampullae.* Three semicircular canals are present at right angles to each other. Two are vertical and one is horizontal. These canals are surrounded by bone and cartilage and are composed of dense collagenous connective tissue lined by simple squamous epithelium. Near the utriculus, each semicircular canal has an en-



FIG. 128. Transverse section of a 50 mm TL juvenile through the posterior ear region. The pars inferior of the labyrinth is composed of the lagena (L) and the sacculus (S). The cavity of the labyrinth is continuous with the sinus endolymphaticus (SE) which is surrounded by the sinus impar (SI). A, asteriscus (otolith); M, medulla oblongata; C, semicircular canals; N, lateral accessory branch of Cr.N. VII; G, ganglia of Cr.N. X; E, esophagus; H, head kidney. Bouin's; H & E; × 15.
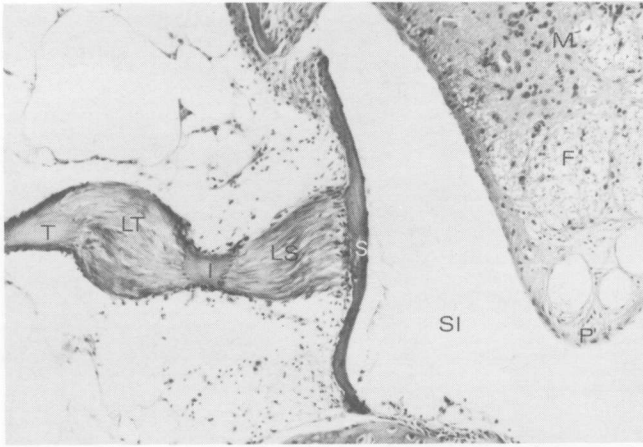
FIG. 129. The functional connection between the swim bladder and ear consists of the Weberian apparatus and the perilymph of the sinus impar (SI). This transverse section through the posterior head shows the scaphium (S) of the Weberian chain bordering the sinus impar. The scaphium is connected to the intercalarium (I) by the ligamentum scaphium (LS). The ligamentum tripus (LT) connects the intercalarium to the tripus (T) which is connected to the swim bladder. The other Weberian ossicle, the claustrum, forms a portion of the wall of the sinus impar and is not driectly involved in the connection between the swim bladder and ear. The meninx primitiva (P) is thickened ventrally, and slightly posterior to the level of this section it extends to the vertebrae ventral to it forming separate atria sinus impar. M, Mauthner cells of spinal cord; F, myelinated fibers of spinal cord white matter. Bouin's; H & E; × 120.

largement called an ampulla. A crista (Fig. 130), which is the sense organ of the semicircular canal, is located on an elevated stalk of connective tissue within the ampulla.

The epithelium of the cristae is composed of sensory hair cells and supporting cells. The sensory cells are tall columnar with an oval nucleus in the midportion of the cell. Electron microscopy studies indicate that the sensory hair cells of cristae and other acousticolateralis system sense organs are homologous (Lowenstein, 1971). All have several stereocilia and a single kinocilium arranged in a characteristic pattern. Stereocilia are hair-like processes with a uniformly dispersed longitudinal fibrillae, while kinocilia are true cilia with the typical tubule arrangement of cilia.

The sensory hairs are embedded in a cupula composed of a jelly-like substance which in life reaches to the opposite side of the ampulla (Lowenstein, 1971). The cupula shrinks during fixation but is usually not lost during specimen preparation as it is from neuromasts of the lateral line. Deflections of the cupula due to angular acceleration bend the sensory hairs resulting in stimulation of the sensory cells.

*Otolith organs.* Three sacs are present in the labyrinth. Each contains an area of sensory epithelium, a macula (Fig. 131), which is associated with an otolith. An additional area of sensory

epithelium, the macula neglecta, is located near the junction of the pars superior and pars inferior. The wall of these organs is composed of dense collagenous connective tissue lined by simple squamous epithelium.

The utriculus is the most anterior sac and is part of the pars superior. This organ seems most important in gravity responses in most species (Lowenstein, 1971). A large horizontal macula covers the ventral surface of much of the utriculus and an otolith lies above the macula.

The medially located sacculus and lateral lagena compose the pars inferior (Fig. 128). Each chamber contains a macula and otolith and is continuous with the sinus endolyphaticus. These organs of the pars inferior function in sound detection and possibly detection of positional changes (Lowenstein, 1971).

The otoliths are calcareous deposits associated
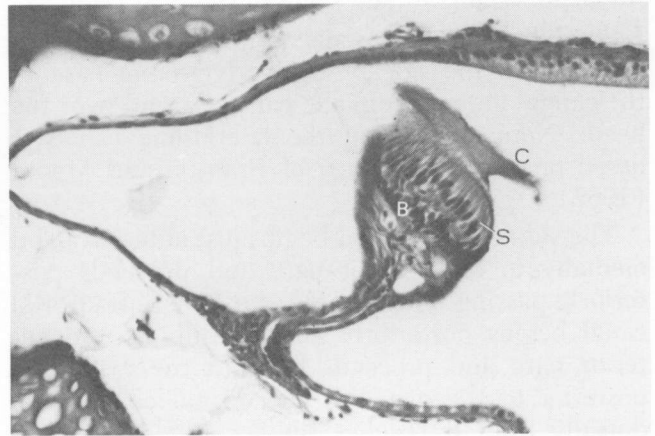


FIG. 130. The cristae are located on a stalk of connective tissue within the ampullae. The sensory cells (S) of the cristae are tall columnar with apical sensory hairs embedded in a cupula (C). Supporting cells (B) have basally located nuclei. Bouin's; H & E; × 250.



FIG. 131. The maculae of the various otolith origins are histologically similar. The macula of the sacculus is composed of sensory hair cells (H) and supporting cells (S). The sagitta (O) is the otolith of this chamber. Bouin's; H & E; × 240.

with each macula. These solid deposits are non-cellular and functionally replace the cupulae of cristae and neuromasts. Each otolith is named according to the chamber in which it is located. The utriculus contains the lapillus, the sacculus contains the sagitta, and the lagena contains the asteriscus.

The sensory epithelium of the maculae is very similar to that of the cristae except that the maculae are much larger in surface area. The sensory epithelium is located on the wall of each chamber replacing the simple squamous epithelium lining other areas.

## LATERAL-LINE SYSTEM

Three types of lateral-line sense organs are present in the skin of channel catfish. Canal neuromasts are found in lateral-line canals located in the dermis, superficial (free) neuromasts in the epidermis (large pit organs of Herrick, 1901), and small pit organs in the epidermis.

*Lateral line.* The lateralis (Fig. 80 and 81) extends down the side of the body to the base of the caudal fin, and cephalic canals extend over the head. Nomenclature of the lateral-line canals is based on the terminology of Branson and Moore (1962).

The supraorbital canal begins just anteriorly and medially to an anterior nare and proceeds posteriorly passing dorsal to the eye. The infraorbital canal begins posteriorly and laterally to the anterior nare and proceeds beneath the eye. Just posterior to the eye, the infraorbital canal turns dorsally until it reaches the level of the supraorbital canal. The infraorbital and supraorbital canals join to form the postocular commissure which proceeds posteriorly.

The preoperculomandibular canal starts on the lower jaw just anteriorly and laterally to the mandibulary barbel and proceeds posteriorly on the lower jaw and then dorsoposteriorly in the preopercular bone and over the posterior edge of the hyomandibular bone until it joins the postocular commissure to form the cephalic lateralis which continues posteriorly. The lateralis proper begins immediately posterior to the posttemporal bone. The cephalic lateral lines of channel catfish were partially described by Herrick (1901) and are similar to those of other silurids.

The lateral-line canal opens to the surface by pores which are regularly spaced. Accessory ossicles (Fig. 132) surround the lateralis in the region of each neuromast. On the head, these ossicles are often fused in other bones but are separate in the lateral body. Each ossicle is cylin-
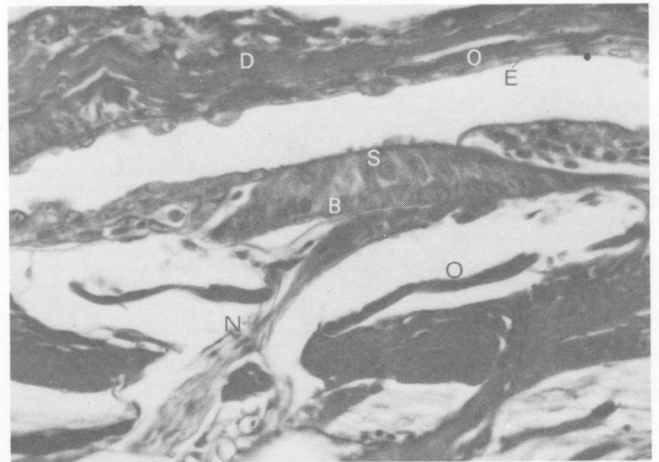


FIG. 132. This longitudinal section of the lateral line of an adult has an accessory ossicle (O) surrounding the canal. The neuromast has dark staining, pear-shaped sensory cells (S) and supporting cells with basally located nuclei (B). D, dermis; E, stratified squamous epithelium lining canal; N, nerve. Bouin's; H & E; × 320.

drical with an opening for the nerve which connects the neuromast to the lateral line nerve. Accessory ossicles begin developing in the anterior portion of the fish first and are not found in juveniles less than 60 mm TL.

The sense organs of the lateral line are neuromasts (Fig. 132 and 81) and are generally distributed so that one neuromast is found between adjacent lateral-line pores. The sensory cells are pear-shaped and located in the upper portion of the neuromasts. Nuclei of the supporting (sustentacular) cells are located basally with the cell extending between sensory cells. Cupulae were usually not present, but these were probably lost during fixation or sectioning. Dijkgraaf (1962) indicates that the loss of cupulae from neuromasts during preparation is common and that many reports of the absence of cupulae are in error. The ultrastructure of lateral-line sense organism is similar to the sense organs of the ear (Lowenstein, 1971).

The lateral-line canal (Fig. 80, 81, and 132) is located in the dermis, and where accessory ossicles are present, bone surrounds the canal. A layer of loose areolar connective tissue separates these surrounding tissues from the very thin stratified squamous epithelium which lines the canal. Neuromasts are elongated and replace the stratified squamous epithelium lining other parts of the canal.

The lateral-line neuromasts are stimulated when water movement bends the cupulae causing a stimulation of the sense hairs. Possible water movements involved include currents, sound waves, and water disturbance caused by moving

objects. Dijkgraaf (1962) concludes that detection of the later type of water movement is the most important function of the lateral-line organs which serve as distant touch receptors. Other authors have concluded that the lateral-line is also important as a near-field acoustic detector (Harris and van Bergeijk, 1962; Tavolga, 1971).

*Superficial neuromasts.* These differ from the neuromasts of the lateral-line canals primarily by being located singly in the epidermis. The structure and function of these organs in most·species seem to be similar to the neuromasts of the lateral-line canals (Herrick, 1901; Dijkgraaf, 1962; Flock, 1971). These organs can be seen grossly as a small depression often surrounded by a small unpigmented area. They occur in distinct rows which sometimes continue the path of lateral-line canals.

While superficial neuromasts were often grossly observed, their locations were highly variable. The most frequent locations were on the head but no attempt was made to determine their precise location due to the variability between specimens.

Histology of superficial neuromasts has been described in *I. melas* (Herrick, 1901) and in *I. nebulosus* (Bailey, 1937). These authors refer to these structures as large pit organs and describe them as extending from the dermis to the surface of the epithelium. The organ is composed of sensory and supporting cells which are sometimes separated from the epidermis by a groove and are wider at the apex than taste buds.

*Small pit organs (ampullary organs).* These organs, described in *I. melas* by Herrick (1901), are found on all external surfaces of the body of channel catfish but are most abundant on the head (Fig. 124). The structure of the sense organs is similar to that of both canal and superficial neuromasts, but they are located in a depression of the epidermis (Fig. 133 and 134). The cupulae and sensory hairs of receptor cells of neuromasts are absent. The ultrastructure of small pit organs has been described by Mullinger (1964).

The relationship of these organs to other lateral-line organs is seen in the similarity in structure

and by the connection to the central nervous system. Small pit organs are innervated by the same cranial nerve branches as other lateral-line organs (Herrick, 1901). However, the function of these organs is probably different than other lateral-line organs. Dijkgraaf (1962) concludes that small pit



FIG. 133. Small pit organs are located at the bottom of depressions of the epidermis. In regions of thick epidermis, a pore (P) leads to the surface. T, tangential section of taste bud; G, goblet cells; A, alarm substance cells; D, dermis; C, melanophores; S, stratum germinativum. Celloidin section; Kolmer's; H & E; × 175.
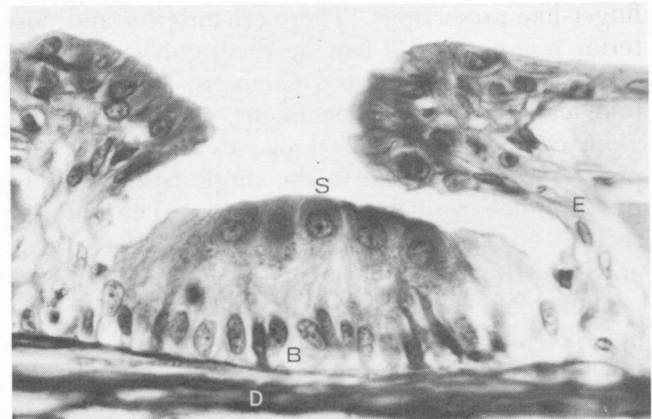


FIG. 134. A small pit organ has dark staining sensory cells (S) and supporting cells with basally located nuclei (B). Sensory hairs and cupula are absent. D, dermis; E, epidermis. Bouin's; H & E; × 600.

organs, as well as ampullary lateral-line organs of other species, are electroreceptors which sense weak potentials or potential changes.

# CHAPTER TEN

# REPRODUCTIVE SYSTEM

The gonads are located in the posterior body cavity immediately ventral to the trunk kidney and swim bladder (Fig. 29) and are attached by mesenteries to the parietal peritoneum covering the kidney and swim bladder. Short ducts extend from the posterior end of the gonads to the genital pore. In addition to the production of gametes, the gonads also produce hormones from endocrine tissue. Spawning behavior has been described by Clemens and Sneed (1957). The sexing of channel catfish based on secondary sex characteristics is discussed in Chapter 2. Morphology of channel catfish spermatozoa was described by Jaspers et al. (1976).

## Male Reproductive System

The testes are lobate, consisting of numerous finger-like projections. There are anterior and posterior regions which can be distinguished grossly (See Fig. 1 of Sneed and Clemens, 1963) or histologically. In fresh specimens, the anterior region, composed of paired masses of lobules, appears white compared to the single fused mass of pink lobules of the posterior region. The anterior region, comprising at least three-fourths of the entire testes, has longer, thicker lobules than the posterior region. These distinctions are more pronounced in sexually mature specimens than in juveniles.

### ANTERIOR REGION OF THE TESTES

The anterior portion of the testes is composed of coiled, branched seminiferous tubules with spermatogenesis occurring along the length of all tubules (Fig. 135). Each lobule is surrounded by a thin tunica albuginea composed of fibrous connective tissue which is continuous with the septa which separate the seminiferous tubules. Formation of spermatozoa from the germinal epithelium appears similar to that in other vertebrates (Patt and Patt, 1969). Spermatocytes and spermatotids are clamped in small cysts of equal maturity (Fig. 135 and 136). Sertoli cells (follicle or companion cells) with flattened, irregularly shaped nuclei and slightly eosinophilic cytoplasm can often be seen enveloping the cysts of spermatogenic cells. Apparently mature spermatozoa and abundant
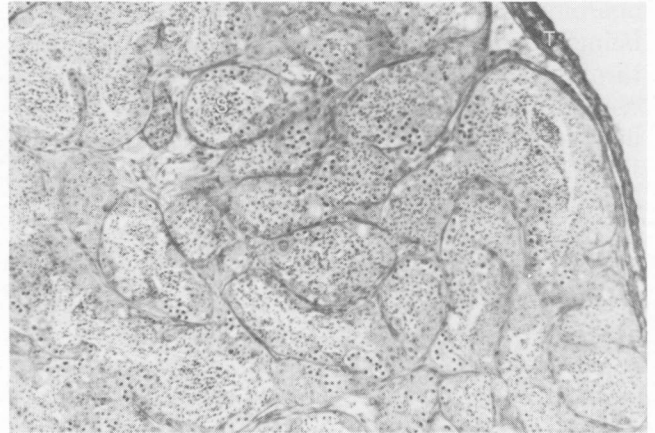


FIG. 135. The anterior portion of the testes is composed of seminiferous tubules with spermatozoa (S) filling the lumen of each tubule. The tunica albuginea (T) surrounds each lobule. Numerous mitotic figures are found in the epithelium of the tubules of this testis which was collected in November. Bouin's; H & E; × 130.
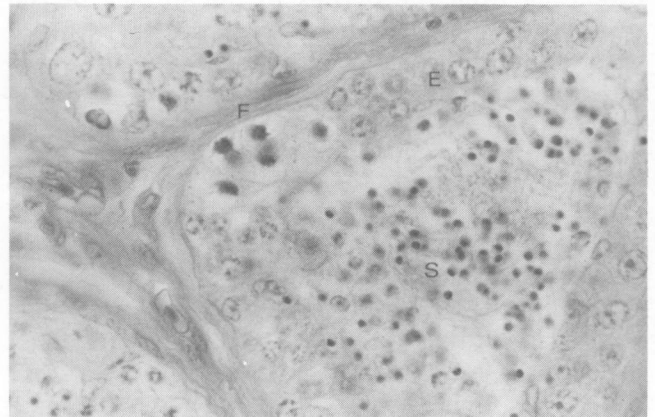


FIG. 136. The seminiferous tubule is lined with epithelium (E) composed of spermatogenic cells and Sertoli cells. Spermatogenic cells of equal maturity are often grouped together. Fibrous connective tissue (F) surrounds the tubule. Spermatozoa (S) are found in the lumen during all seasons. Testis collected in November. Bouin's; H & E; × 600.

mitotic figures are present in the seminiferous tubules of adults during all seasons. As spawning nears, the size of the seminiferous tubules and the quantity of spermatozoa increases greatly (Fig. 137) resulting in an increase in the overall size of the organ. An increase in mitosis is noticeable during winter and spring before spawning. A decrease in the thickness of the wall can be seen immediately after spawning, and a considerable
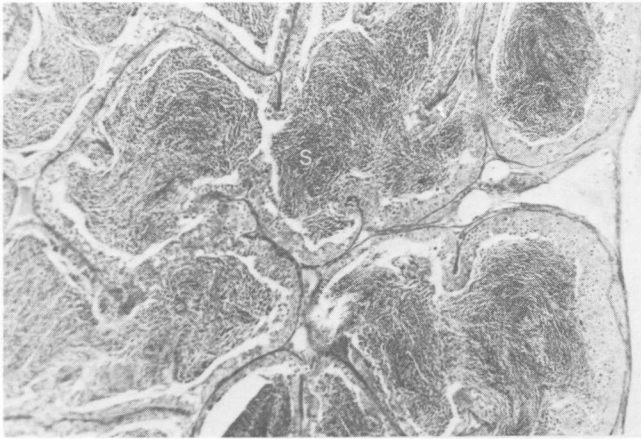
FIG. 137. The seminiferous tubules of this testis collected during April, approximately 1 month before spawning, are swollen with spermatozoa (S) (compare to Fig. 135). Bouin's; H & E; × 60.

number of spermatozoa remain in the tubules. Sertoli cells become more prominent after spawning, perhaps because of increased phagocytosis of unused sperm.

## POSTERIOR REGION OF THE TESTES

The posterior region of the testes is composed of branched, coiled tubes, but the cells of the tubule wall are very different from those of the anterior region (Fig. 138 and 139). Spermatozoa are usually not present in the posterior region, although they were found in some specimens after spawning. Seasonal changes are minimal, although Sneed and Clemens (1963) report that the epithelial cells increase in size as spawning season approaches. The function of the posterior region is unknown. A similar region is associated with the testes of *Gillichthys* and has been referred to as a seminal
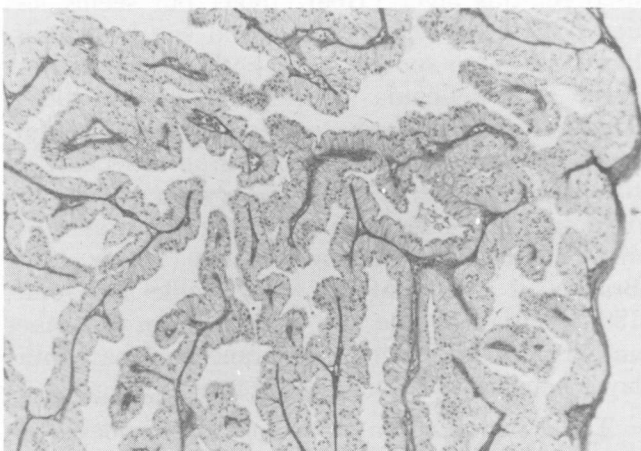


FIG. 138. The posterior lobe of the testis is composed of coiled tubules lined with simple columnar epithelium with very light staining cytoplasm. Spermatogenic cells and Sertoli cells are absent. The tubules are more highly branched than in the anterior region. Bouin's; H & E; × 60.
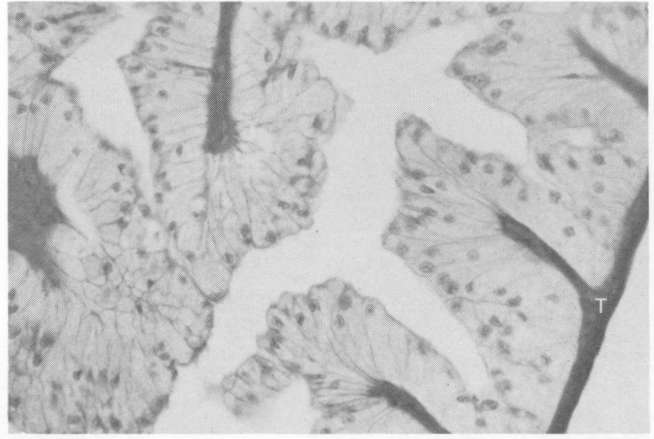


FIG. 139. The simple columnar epithelium lining the tubules of the posterior region of the testes has apically located nuclei and very light staining cytoplasm. The tunica albuginea (T) and septa between tubules are composed of fibrous connective tissue. Bouin's; H & E; × 240.

vesicle (Weisel, 1949). Sneed and Clemens (1963) found that fertilization and hatching were successful without the addition of any substance from the posterior region.

## ENDOCRINE FUNCTION OF THE TESTES

The testes of teleosts are thought to be the source of androgens important in regulation of reproduction, secondary sex characteristics, and reproductive behavior (Hoar, 1969; Liley, 1969). Testicular hormones are thought to originate in interstitial cells (Leydig cells) found between seminiferous tubules (Gottfried and van Mullem, 1967) or in boundary cells located in the wall of the tubules (Marshall and Lofts, 1956). Neither of these cell types were found in the channel catfish; however, more extensive histochemical tests might demonstrate the presence of these cells. Alternative sources of androgen within the testes are the Sertoli cells (Hoar, 1969) and possibly the posterior region of the testes which at present has no known function.

## Female Reproductive System

The paired ovaries are tubular in shape and enclosed in a tunica albuginea of fibrous connective tissue covered by mesothelium. Large amounts of smooth muscle are found in the wall of mature ovaries (Fig. 140). The tunica albuginea of juveniles is poorly developed (Fig. 141). Ovigerous lamellae composed of two layers of oocytes supported by fibrous connective tissue and covered by simple squamous epithelium project toward the center from the tunica albuginea. This lamellar structure is seen in longitudinal sections of
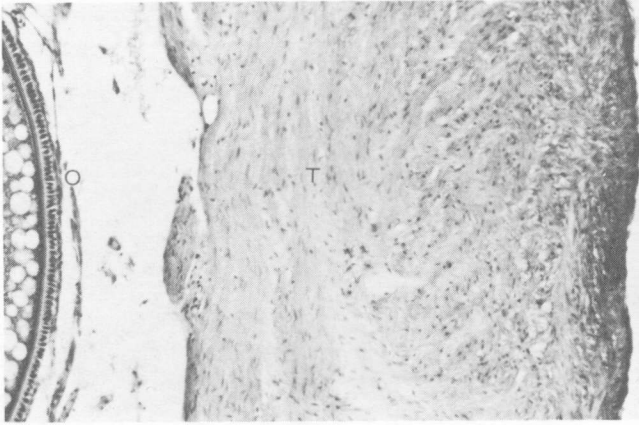
FIG. 140. The outer wall of the ovary is the tunica albuginea (T) and contains smooth muscle in adults. Mesothelium covers the outer surface. O, oocyte. Bouin's; H & E; × 120.



FIG. 142. The ovigerous lamellae are seen in this longitudinal section of a juvenile ovary. Numerous primary follicles (F) supported by fibrous connective tissue compose the lamellae. A lumen (L) remains in the center of the ovary and is lined by simple squamous epithelium. The tunica albuginea (T) surrounds the ovary. Helly's; H & E; × 120.

juvenile ovaries (Fig. 142). A space remains in the center of the ovary which is continuous with the short oviduct leading to the genital pore.

### OOGENESIS

Oogenesis involves the proliferation of oogonia by mitosis and the development of oocytes which develop from the oogonia. Oogonia (Fig. 143) are found in groups or "nests" in the ovigerous lamellae and are most abundant during the summer and fall. Oogonia appear similar to undifferentiated germ cells of embryos (Hann, 1927).

Oogonia become oocytes when meiosis begins. Specialized cells surround the developing oocyte forming a follicle. Considerable changes in structure as well as an increase in size occur in the follicles as spawning approaches. These changes



FIG. 141. This transverse section of a juvenile ovary shows the mesentery (M) attaching it to the peritoneum covering the swim bladder (S). The ovary is filled with primary follicles (F) containing oocytes which have a large, light staining nucleus and strongly basophilic cytoplasm. The tunica albuginea surrounding the ovary is very thin. The visceral peritoneum covers the external surface and is continuous with the mesentery. Bouin's; H & E; × 70.

have been described in many species and are often described in terms of artitrary stages (James, 1946; Cooper, 1952; Braekevelt and McMillan, 1967; Combs, 1969; Moser, 1967; Shelton, 1964; See Hoar, 1955, 1957, 1965 for further references).

The terminology of the structures of the follicle has varied among authors. Most confusion has involved the noncellular, striated layer termed zona radiata in this chapter. This descriptive term has been used by numerous authors studying both histology and ultrastructure of species in which this layer is striated. Hurley and Fischer (1966), using electron microscopy, found the striations of the zona radiata of brook trout to be pores penetrated by microvilli formed by the underlying plasma membrane which they termed vitelline membrane. The term zona pellucida has been used for this layer (Hoar, 1969) but seems less descriptive than zona radiata and can be confusing since some species have both a zona radiata and a zona pellucida (Hurley and Fisher, 1966). This layer has also been termed the chorion (Mattews, 1938) which seems undesirable because of the use of this term for an embryonic membrane of amniotes. The term vitelline membrane has also been used for the zona radiata (Moser, 1967; Braekevelt and McMillan, 1967; Jollie and Jollie, 1967), although the use of this term by other authors for the plasma membrane or a basophilic layer beneath the zona radiata is confusing.

The transformation from oogonia to oocyte involves an increase in the size of the cell and nucleus. The chromatin of the nucleus forms a reticulum, and the nucleolus moves to one side of the nucleus after which multiple nucleoli are seen.

Soon after the oocyte begins to differentiate, a layer of squamous cells can be seen surrounding it. The cytoplasm of these oocytes becomes strongly basophilic and the nucleus stains lightly. Growth and differentiation of the primary follicles often stops at this stage when the diameter is 50 to 80 $\mu$. Only primary follicles are found in ovaries of juveniles (Fig. 141 and 142), and they are found in adult ovaries during all seasons.

Maturation of the oocyte in preparation for spawning involves the nucleus, cytoplasm, and surrounding tissues (Fig. 143, 144, and 145). The nucleus enlarges and the nuclear membrane becomes irregular. The cytoplasm becomes vacuolated, especially near the plasma membrane, and yolk is deposited. The cytoplasm becomes less basophilic than in primary oocytes and becomes eosinophilic as yolk is deposited. An eosinophilic zona radiata develops around the oocyte and a basophilic layer, possibly the plasma membrane, can be seen beneath it in more mature oocytes. Distinct striations are present in the zona radiata during the late development. A layer of follicular cells (granulosa) develops from the squamous cells surrounding the primary oocytes. These cells become cuboidal and later columnar. A thin theca of vascular connective tissue forms the outer layer of the follicle. The epithelium lining the ovary covers part of the follicle. The oocytes reach a diameter of 3 to 4 mm before spawning. The follicular cells become granular and separate from the zona radiata as spawning approaches.
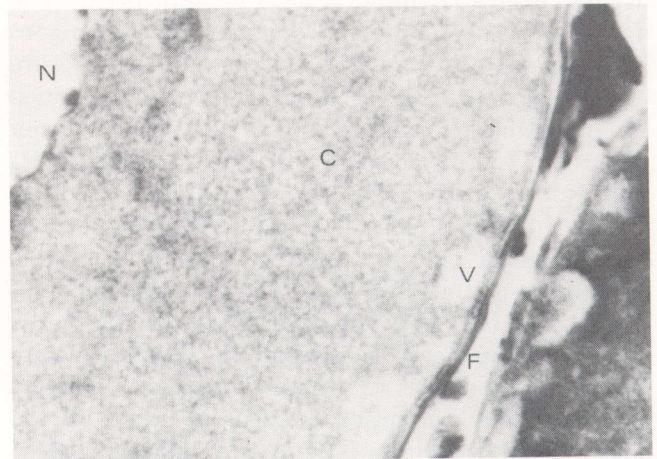


FIG. 144. This oocyte is slightly more mature than the primary oocytes seen in figures 141 and 142. The cytoplasm (C) and nucleus (N) are enlarging, and vacuoles (V) are seen in the periphery of the cytoplasm. The follicular cells (F) surround the oocyte. Bouin's; H & E; × 800.



FIG. 143. Oogonia are found in groups (G) associated with the epithelial lining (germinal epithelium) of the ovary. The group of oognia results from repeated mitotic division. The oogonia have 4 to 5 $\mu$ diameter nuclei with a centrally located nucleolus and eosinophilic cytoplasm. Cell margins are indistinct and no follicular cells are present. A maturing oocyte has clear vacuoles (V) in the cytoplasm, an irregular nuclear membrance and several nucleoli. This oocyte is surrounded by a dark staining zona radiata which is not yet striated, a layer of cubodial follicular cells, and a thin theca. Bouin's; Masson's; × 240.



FIG. 145. The zona radiata (Z), a single layer of columnar follicular cells (F), and theca (T) surround the oocyte. Vacuoles (V) of yolk are located in the periphery of the cytoplasm. A thin basophilic layer occurs between the zona radiata and cytoplasm. Faint, radial striations are present in the zona radiata. Bouin's; H & E; × 1200.

## SPENT OVARIES

Atretic follicles were not found before spawning but were common in some specimens for a few weeks after spawning (Fig. 146 and 147). The follicular cells enlarge and phagocytize the oocytes which were not spawned. The resulting structure during phagocytosis resembles the corpora atretica or preovulatory corpora lutea reported in other teleosts (Lambert and von Oordt, 1965; Bretschneider and Duyvene de Wit, 1947).

The follicular cells of empty follicles in spent ovaries often enlarge, and the connective tissue surrounding the follicle thickens and becomes more vascular (Fig. 146 and 148). Although the follicular cells become vacuolated, the changes are not as pronounced as in post ovulatory corpora lutea reported in other teleosts (Samuel, 1943) and elasmobranchs (Hisaw and Albert, 1947). The use of the term corpora lutea is questionable but has been defended by Hoar (1957, 1965, 1969).

## ENDOCRINE FUNCTION OF THE OVARY

Estrogens and progesterone have been found in the ovaries of many teleosts and may be produced by the ovarian follicles and corpora lutea as they



FIG. 147. Atretic follicles were only found in spent ovaries. The follicular cells (F) become tall columnar cells with apical nuclei and have vacuolated cytoplasm. Remains of the oocyte (O) are present in the follicle. Bouin's; H & E; × 240.

are in higher vertebrates (Hoar, 1969). These hormones are important in the control of reproductive cycles, secondary sexual characteristics, and behavior (Hoar, 1969; Liley, 1969). The follicular cells of follicles and corpora lutea-like structures are present in channel catfish and seem to be likely sources of hormones from the ovaries.



FIG. 146. An ovary 2 days after spawning contains atretic follicles (A), empty follicles (E), and young follicles. Primary follicles (F) appear identical to those in juveniles. Bouin's; H & E; × 25.
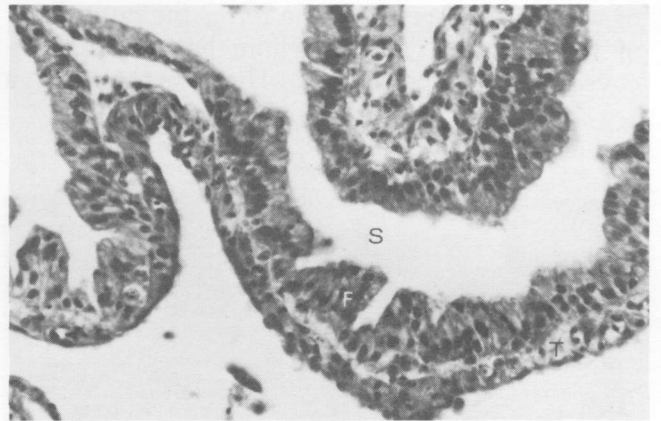


FIG. 148. The empty follicles of spent ovaries are collapsed with a space (S) remaining in the location once occupied by the oocyte. The vacuolated follicular cells (F) are tall columnar with basal nuclei, and the theca (T) is thickened and highly vascularized. Bouin's; H & E; × 240.

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# CHAPTER ELEVEN

# RESPIRATORY SYSTEM

The gills are used for gas exchange between the blood and water. Accessory respiratory organs and pseudobranchs are absent in the channel catfish. The gills are important in osmoregulation because water can easily enter the blood at the gills and because of chloride cells located on the gills which may transport monovalent ions into the blood (Philpott and Copeland, 1963). The gills are also important in the excretion of nitrogenous wastes in the form of ammonia (Smith, 1929; Forster and Goldstein, 1969).

## Pharynx

Four pairs of gills are present in the pharynx (Fig. 29). The gills are covered by the operculum so that only one external opening is present on each side. The opercular covering forms a cavity in which the respiratory surfaces of the gills are located. Water flows through the gill slits, which are guarded by rakers, and then over the gills. Unidirectional water flow is maintained by the oral valve (Fig. 149) and branchiostegal membrane. The oral valve consists of flaps of skin just posterior to the upper and lower jaws which prevents water from exiting through the mouth. The opercular membrane is supported by branchiostegal rays (Chapter 12) and prevents water from entering through the opercular opening.

## Gills

Each gill consists of a gill arch, gill filaments, and gill lamellae (Fig. 150). The gill arch is supported by the branchial arches of the branchiocranium (Chapter 12). In juveniles, varying amounts of cartilage are present supporting the arch because these bones are preformed in cartilage. Two rows of gill rakers and filaments are present on each arch, and the lamellae (secondary lamellae) branch from the filaments. The lamellae are the actual respiratory surfaces. Electron microscopy has been useful in understanding the structure of lamellae (Hughes and Grimstone, 1965; Newstead, 1967).

The gill filaments (Fig. 151, 152, and 153) are supported by cartilage which is unlike the hyaline cartilage of other parts of the body (Chap. 12; Fig. 169). The filaments are flattened in cross section with the cartilage located near one side. The afferent arteriole is located near the cartilage and the efferent arteriole is located on the opposite side of the filament. Stratified squamous epithelium covers the filament. Goblet cells are most abundant on the margins near the arterioles, and alarm substance cells are absent. The gill lamellae project from the sides of the filaments.

The gill lamellae (Fig. 154 and 155) are com-



FIG. 149. The oral valve consists of folds of skin (V) immediately posterior to the oral teeth (T). Sagittal section of fingerling. Bouin's; H & E; × 60.
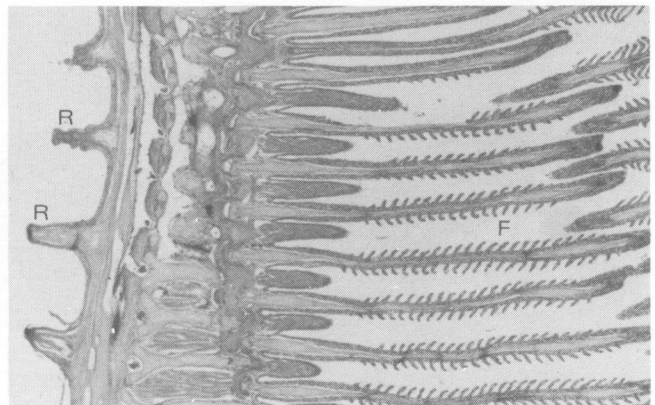


FIG. 150. Each gill arch has two rows of filaments (F) which project into the opercular cavity. Two rows of gill rakers (R) project from the inner surface of each arch. Lamellae, the actual site of gas exchange with the water, project from both sides of each filament. Formalin; H & E; × 25.
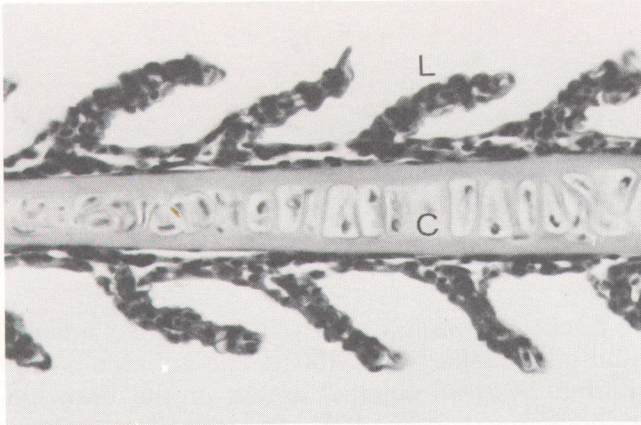
FIG. 151. Lamellae (L) project from both sides of the gill filament sectioned longitudinally. Gill-filament cartilage (C) supporting the filament is seen in this section. Formlin; H & E; × 240.



FIG. 154. Chloride cells (C) are more eosinophilic than other cells of the gill epithelium and are abundant between lamellae. The lamellae have pillar cells (P) which separate the walls of squamous epithelium. Bouin's; H & E; × 600.
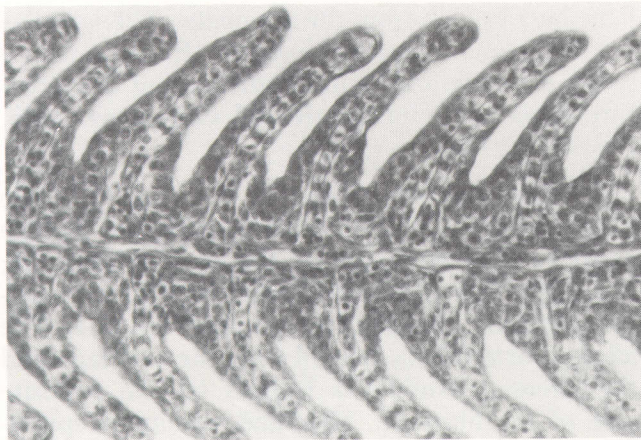


FIG. 152. This longitudinal section of gill filament is near the center of the filament where cartilage is absent and lamellae are their maximum length. The epithelial cells appear different than those in Fig. 151 because of the difference in fixation. Bouin's; H & E; × 240.
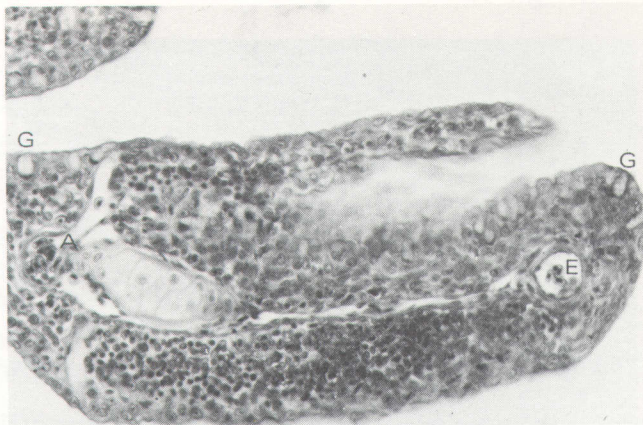


FIG. 153. Transverse section of a gill filament. The supporting cartilage is located on the side of the filament just internal to the afferent arteriole (A). Blood flows from the lamellae through the efferent arteriole (E). Goblet cells (G) are most abundant toward the margins of the filaments. Bouin's; H & E; × 240.



FIG. 155. An electron micrograph of a gill lamella. Pillar cells (P) support the lamellae and flanges of these cells (F) surround the blood sinusoids (S). A basement membrane underlies the epithelium (E) which is usually two cells thick. R, erythrocyte. Glutaraldehyde; uranyl acetate and lead citrate; × 8,000.

posed of a thin epithelium covering pillar cells. The pillar cells support the lamellae and have flanges which surround the blood sinusoids. The lamellae are open except for the pillar cells which

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connect the sides. Blood enters the lamellae from the afferent arterioles of the filaments and exits into the efferent atreriole. Chloride cells (acidophilic cells) (Fig. 156) are located near the base of the lamellae and in the trough between lamellae.

The effectiveness of the gill lamellae for gas exchange is increased because of counter current exchange (Lagler et al., 1962). The blood flows through the lamellae in the direction opposite of that in which water flows over the lamellae, and exchange may be efficient enough so that only passive diffusion is necessary to supply oxygen to the blood (Hughes, 1966).



FIG. 156. Electron micrograph of a chloride cell near the base of a lamella. Mitochondria (M) and endoplasmic reticulum are the most abundant elements of the cytoplasm. The nucleus of the chloride cell is not present in this section. E, epithelial cell. Glutaraldehyde; uranyl acetate and lead citrate; × 14,600.

# CHAPTER TWELVE

## SKELETAL SYSTEM

The skeletal system (Fig. 157) consists primarily of bone and hyaline cartilage. Larval specimens have a predominantly cartilaginous skeleton with bone becoming more prominent with increasing age until the skeleton is almost entirely bone in the adult. Several of the bones become tightly fused so that distinction between them is difficult or impossible.

The bony elements of the skeletal system were examined grossly in cleared and stained (using the techniques of Taylor, 1967) specimens ranging from 40 to 100 mm TL and in larger specimens from 20 to 60 cm TL which were cleaned of flesh by boiling. Some parts of the skeleton of smaller fish were also cleaned by boiling. Histological sections were sometimes useful to clarify the relationship between certain structures.

The osteology of *I. nebulosus* has been described by McMurrich (1884b). This reference is useful in the study of the skeleton of *I. punctatus,* but more recent studies and changes in terminology have outdated this reference. Most of the terminology in this chapter follows that found in recent references such as Lagler et al. (1962). The

terminology of the skull and caudal fin is discussed with those portions of the skeleton.

### Skull

The reduction or absence of several bones indicates the specialization of the skull. Bones which are absent include the parietals, opisthotic, subopercular, and symplectic. The maxillae, which support the maxillary barbels, are greatly reduced. Several bones are fused or tightly joined together so that nearly intact specimens are easily prepared.

A drawing of the lateral view of the skull of *I. punctatus* has been published by Gregory (1933) and the similar skull of *I. nebulosus* has been described by McMurrich (1884b) and Kindred (1919). The description by Kindred is detailed and includes developmental information, but does not include the branchial region. The separation of the skull into various regions and other terminology is based on Gregory (1933).

#### NEUROCRANIUM

The bones of the neurocranium surround the brain and the sense organs of the head including
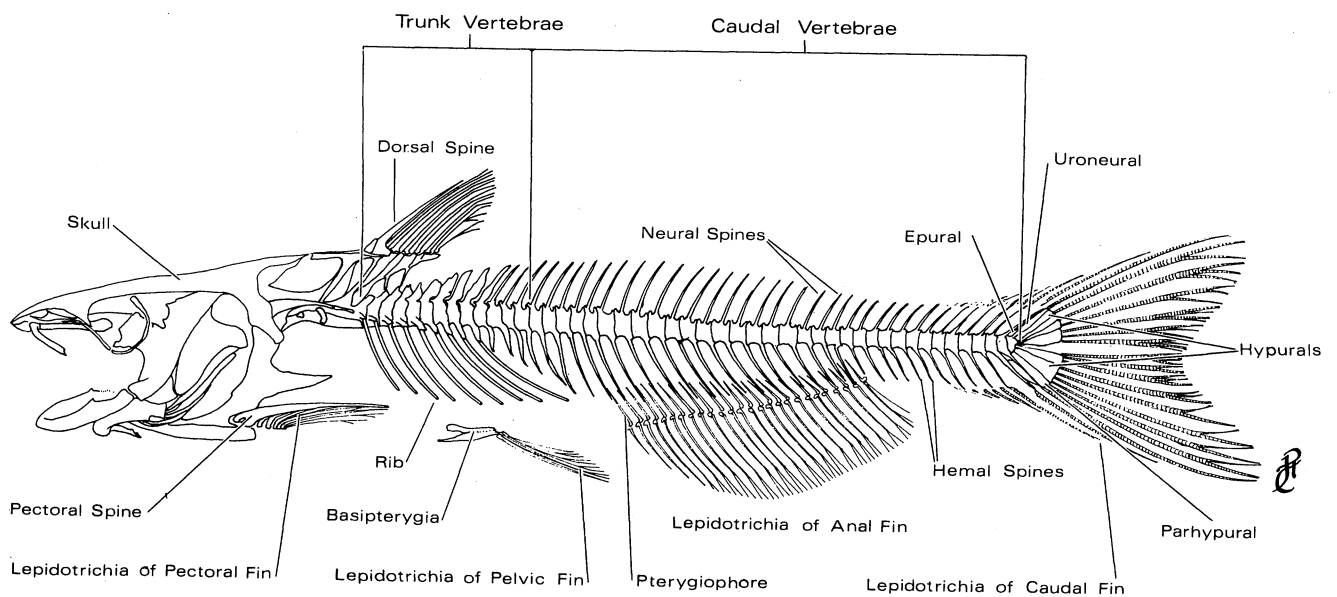


FIG. 157. Lateral view of the channel catfish skeleton.

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much of the cephalic lateral-line canals. The anterior portion of the neurocranium is the olfactory region which is associated with the olfactory organ. The orbital region surrounds the eye, but several of these bones also encase the lateral-line canal. The otic region forms the posterior part of the brain case, the otic capsule, and articulates with the pectoral girdle. The basicranial region forms the base of the neurocranium and points of articulation for the vertebral column and pectoral girdle.

*Olfactory region.* This region forms around the ethmoid cartilage of the larval fish. The mesethmoid (supraethmoid) (Fig. 159) is the most anterior bone of the skull and is unpaired. The shape of the mesethmoid can be used to identify the species of *Ictalurus* and *Pylodictis* (Paloumpis, 1964; Calovich and Branson, 1964). The parethmoids (ectethmoid) (Fig. 159) are lateral to the mesethmoid and form the anterior margin of the orbit. According to Gregory (1933) this bone includes the prefrontal. The vomer (Fig. 160) is unpaired and lies on the ventral side of the neurocranium forming part of the roof of the mouth. The nasals (Fig. 159) are long thin bones which are loosely attached to the skull. These enclose part of the supraorbital lateral-line canal.

*Orbital region.* The frontals (Fig. 159) form the dorsal portion of the orbit and the largest part of the roof of the cranium. Two longitudinal fontanelles lie between the frontals. The orbitosphenoid and alisphenoid (Fig. 158) lie medial to the orbit.

The remaining bones of the orbitual region constitute the suborbital (infraorbital) series (Fig. 158) and enclose the infraorbital lateral-line canal. The most anterior member of this series is the lacrymal which lies dorsal to the olfactory organ. The second suborbital (jugal) lies anterior to the parethmoid. The remaining four suborbitals lie ventral and posterior to the eye with the most dorsal of these being very small and occasionally absent. The entire suborbital series is loosely attached to the skull. The suborbital series of *I. nebulosus* as described by Kindred (1919) is slightly different than above and is composed of a total of seven bones including the lacrymal instead of six as in *I. punctatus*.

*Otic region.* The sphenotic and pterotic (Fig. 159) form part of the dorsum of the skull and part of the side of the neurocranium. The pterotic is one of two points of attachment of the posttemporal of the pectoral girdle. The remainder of

the dorsum of the skull is composed of the unpaired supraoccipital (Fig. 159) which extends posteriorly to attach to the dorsal fin. The prootic (Fig. 160) forms a large portion of the side of the neurocranium. The epiotic and exoccipital (Fig. 160) lie on the lateroposterior corner of the neurocranium and the exoccipital forms the lateral margins of the foramen magnum.

The posttemporal (Fig. 158, 159, and 160) and supratemporal (scale bone) (Fig. 158 and 159) are involved in support of the pectoral girdle and are firmly attached to the skull. The posttemporal is attached to the skull dorsally at the pterotic and epiotic and ventrally at the basioccipital. The supratemporal covers the dorsal portion of the posttemporal and is tightly joined to the posterior margin of the pterotic and lateral margin of the supraoccipital. The sutures between the supratemporal and surrounding bones are easily seen on well cleaned specimens, and these bones can be separated after prolonged boiling. The supratemporal is not shown on the drawing of *I. punctatus* in Gregory (1933) and is not mentioned by McMurrich (1884b) or Kindred (1919).

The subtemporal (Fig. 158 and 159) is a small, loosely attached bone lying between the dorsal end of the preopercular and the pterotic. The subtemporal surrounds part of the preoperculo-mandibular lateral-line canal. This bone is not mentioned by Gregory (1933) but is described by Kindred (1919).

*Basicranial region.* The parasphenoid (Fig. 160) is a very long bone extending from the mesethmoid to the basioccipital. A portion of its ventral surface is covered anteriorly by the vomer. The basioccipital (Fig. 160) forms the ventral portion of the foramen magnum, and a posterioventral disc serves as the attachment for the vertebral column.

### BRANCHIOCRANIUM (VISCERAL SKELETON)

This portion of the skeleton includes the branchial arches which support the gills and the mandibular and hyoid arches which have evolved from the anterior two visceral arches (Goodrich, 1930). The oromandibular region includes the bones which are formed from the palatoquadrate cartilage, bones of the secondary upper jaw, and bones of the mandible. The hyoid region includes bones developing from the cartilage of the hyoid arch plus several other bones located in this region of the skull. The branchial region includes bones forming the gill arches and supporting the pharyngeal teeth.

Supraoccipital
Pterotic
Supratemporal
Tripus
Locking ray
Dorsal spine

Orbitosphenoid
Pterygoid
Frontal
Hyomandibular
Sphenotic
Subtemporal

Mesethmoid
Nasal
Parethmoid
Suborbitals

Modified pterygiophores

Lacrymal
Maxilla
Palatine

Pterygiophores
Ribs

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Branchiostegal rays
Quadrate
Epihyal
Articular
Dentary

Complex vertebra
Posttemporal
Cleithrum
Opercular
Preopercular
Interopercular

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**FIG. 158. Lateral view of the skull, anterior vertebrae, pectoral girdle, and dorsal fin.**

Maxilla

Nasal

Lacrymal

1st suborbital

Dentary

Mesethmoid

Parethmoid

2nd Suborbital

3rd

4th

5th

6th

Frontal

Quadrate

Pterygoid

Hyomandibular

Preopercular

Opercular

Sphenotic

Subtemporal

Pterotic

Supratemporal

Posttemporal

Supraoccipital

Complex vertebra

Pectoral spine

Articular

5th Vertebra

Modified pterygiophores

Locking ray

Dorsal spine

Ribs

Peter H. Carrington
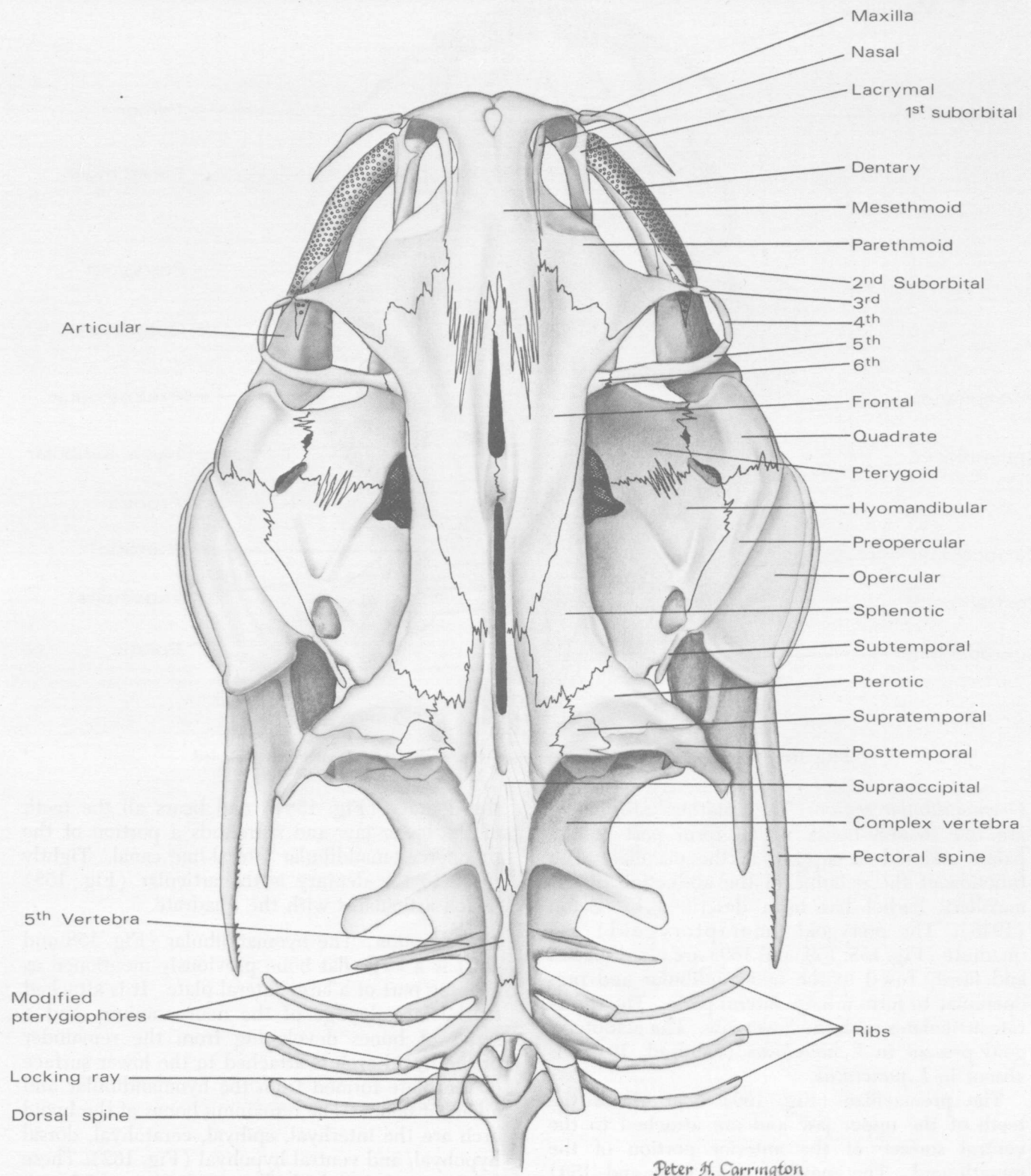
**FIG. 159. Dorsal view of the skull, anterior vertebrae, pectoral girdle, and dorsal fin.**

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Premaxilla ___             Mesethmoid

Maxilla ___

Palatine ___           Vomer

          Parethmoid

          Pterygoid

          Quadrate

Parasphenoid ___           Preopercular

Sphenotic ___           Hyomandibular

          Prootic

Basioccipital ___           Pterotic

Posttemporal ___           Exoccipital

Supraoccipital ___           Epiotic

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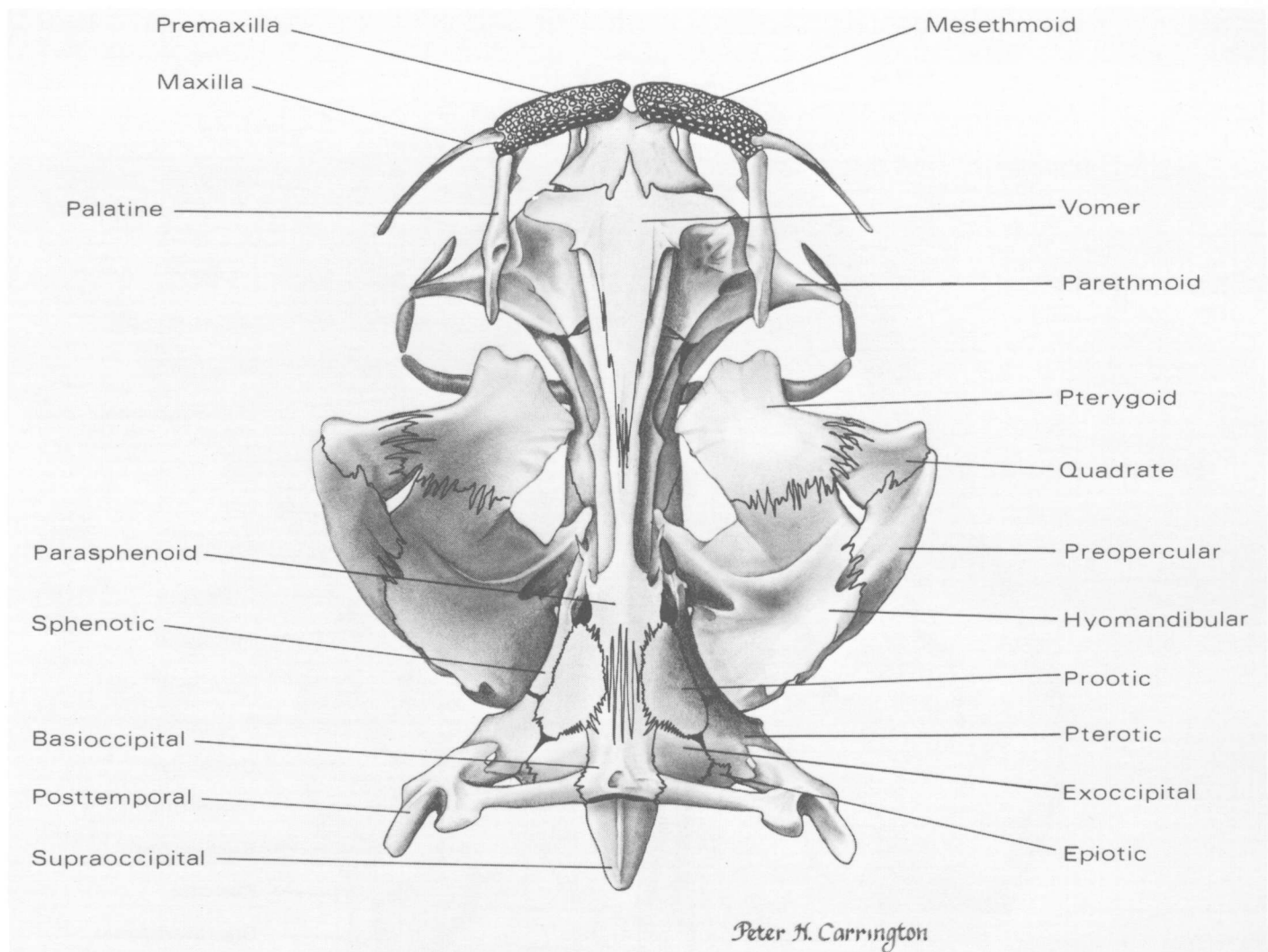
FIG. 160. Ventral view of the neurocranium with several additional bones included.

*Oromandibular region.* The palatines (Fig. 160) are rod shaped bones which form part of the palate and aid in support of the maxillae. The function of the palatine in the abduction of the maxillary barbel has been described by Eaton (1948). The pterygoid (metapterygoid) and quadrate (Fig. 158, 159, and 160) are plate shaped and firmly fused to the hyomandibular and preopercular to form a large lateral plate. The quadrate articulates with the lower jaw. The ectopterygoid present in *I. nebulosus* (Kindred, 1919) is absent in *I. punctatus.*

The premaxillae (Fig. 160) bear all of the teeth of the upper jaw and are attached to the ventral surface of the anterior portion of the mesethmoid. The maxillae (Fig. 158 and 159) are reduced and are merely rods supporting the base of the maxillary barbels.

The lower jaw consists of two bones which form around Meckel's cartilage. The anterior bone is the dentary (Fig. 158)) and bears all the teeth of the lower jaw and surrounds a portion of the preoperculomandibular lateral-line canal. Tightly fused to the dentary is the articular (Fig. 158) which articulates with the quadrate.

*Hyoid region.* The hyomandibular (Fig. 158 and 160) is a large flat bone previously mentioned as forming part of a large lateral plate. It is attached to the lateral edge of the neurocranium, and a series of bones developing from the remainder of the hyoid arch is attached to the lower surface of the plate formed from the hyomandibular and adjacent bones. The remaining bones of the hyoid arch are the interhyal, epihyal, ceratohyal, dorsal hypohyal, and ventral hypohyal (Fig. 162). These form an arch to which the anterior branchial arch is attached.

Eight branchiostegal rays (Fig. 161) are attached to the epihyal and ceratohyal. The most

dorsal ray is flattened and is closely attached to the lower side of the opercular and interopercular. The three medial rays are considerably shorter than the other rays.

The urohyal (Fig. 161) is an unpaired bone attached to the posterior edge of the hypohyals and extending posteriorly beneath the anterior branchial arches. The urohyals of 713 fish species are described by Kusaka (1974) including those of several Siluriformes.

The opercular series (Fig. 158) has only three bones, the opercular, interopercular, and pre-opercular. The opercular is flat and triangular, and it articulates with the hyomandibular. The interopercular is much smaller and is located between the hyomandibular, epihyal, and opercular. The preopercular has been previously mentioned as part of a lateral plate containing the hypomandibular and adjacent bones. The preopercular surrounds part of the preoperculomandibular lateral-line canal.

*Branchial region.* Portions of five branchial arches are present but only the anterior four bear gills. The various bones present in these arches are the basibranchials, hypobranchials, cerato-branchials, epibranchials, and pharyngobranchials (Fig. 162), but not all arches contain all of these. The bones present in each arch are indicated in Table 4. The basibranchials are unpaired and are associated with the arch with which their anterior end articulates. The pharyngobranchials are also a member of the arch with which their anterior ends articulate. Considerable cartilage is present around the bones forming the floor of the pharynx.

The pharyngeal teeth (Fig. 162) are located in the posterior pharynx and are associated with the posterior branchial arches. The lower teeth are present on the lower pharyngeal (hypopharyn-geal) which is completely fused to the fifth ceratobranchial. The upper teeth are located on a disc-shaped upper pharyngeal (epipharyngeal) which is attached to the pharyngobranchial and epibranchial of the third arch and the epibranchial of the fourth arch.

The gill filaments (Chapter 11) are located on

the ceratobranchials and epibranchials of the four anterior arches. Bony gill rakers are also present on the ceratobranchials and epibranchials.

## Vertebral Column and Ribs

Most of the vertebrae are similar to those found in most teleosts. However, the five anterior vertebrae are highly modified to form the Weberian apparatus which is the characteristic common to all ostariophysian fishes. The unmodified vertebrae vary structurally in different parts of the vertebral column. Although the vertebrae can be classified as caudal or trunk, each vertebra is different. Particularly distinctive vertebrae are found near the Weberian apparatus, in the transitional zone between the caudal and trunk region, and near the caudal fin.

### CAUDAL VERTEBRAE

Each of these vertebrae has an amphicoelous centrum surrounding the notochord. Pre- and post-zygopophyses on the centrum increase the area of contact between adjacent vertebrae. A neural arch which continues dorsally as the neural spine (Fig. 157) is firmly attached to the dorsal surface of the centrum. The spinal cord lies within the neural arches. Hemal arches extend from the ventral surface enclosing the caudal artery and continues ventrally as the hemal spine (Fig. 157).

### TRUNK VERTEBRAE AND RIBS

These vertebrae have centra similar to caudal vertebrae but do not have hemal spines. Neural arches and spines are present, but the neural spines ventral to the dorsal fins are bifid for articulation with the pterygiophores supporting the fin. Hemal arches are absent except for the transitional posterior trunk vertebrae.

Transverse processes (parapophyses) extend laterally from most trunk vertebrae. Nine to 11 of the vertebrae bear pleural ribs (Fig. 157). Epipleural ribs and intermuscular bones are absent. The upper surface of the proximal portion of the rib articulates with the lower surface of the transverse process. The sixth vertebra is the most anterior one with ribs since the five anterior verte-

TABLE 4. BONES PRESENT IN THE BRANCHIAL ARCHES OF CHANNEL CATFISH

| Branchial arch | Bones of the branchial arches | | | | |
| --- | --- | --- | --- | --- | --- |
| | Basibranchial | Hypobranchial | Ceratobranchial | Epibranchial | Pharyngobranchial |
| first | present | present | present | present | |
| second | present | present | present | present | present |
| third | | | present | present | present |
| fourth | | | present | present | |
| fifth | | | present | | |

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Premaxilla

Maxilla

Dentary

Hypohyal

Ceratohyal

Urohyal

Articular

Epihyal

Branchiostegal rays

Cleithrum

Coracoid

Basioccipital

Radials

Posttemporal

Tripus

Complex vertebra

Pectoral spine

5th Vertebra

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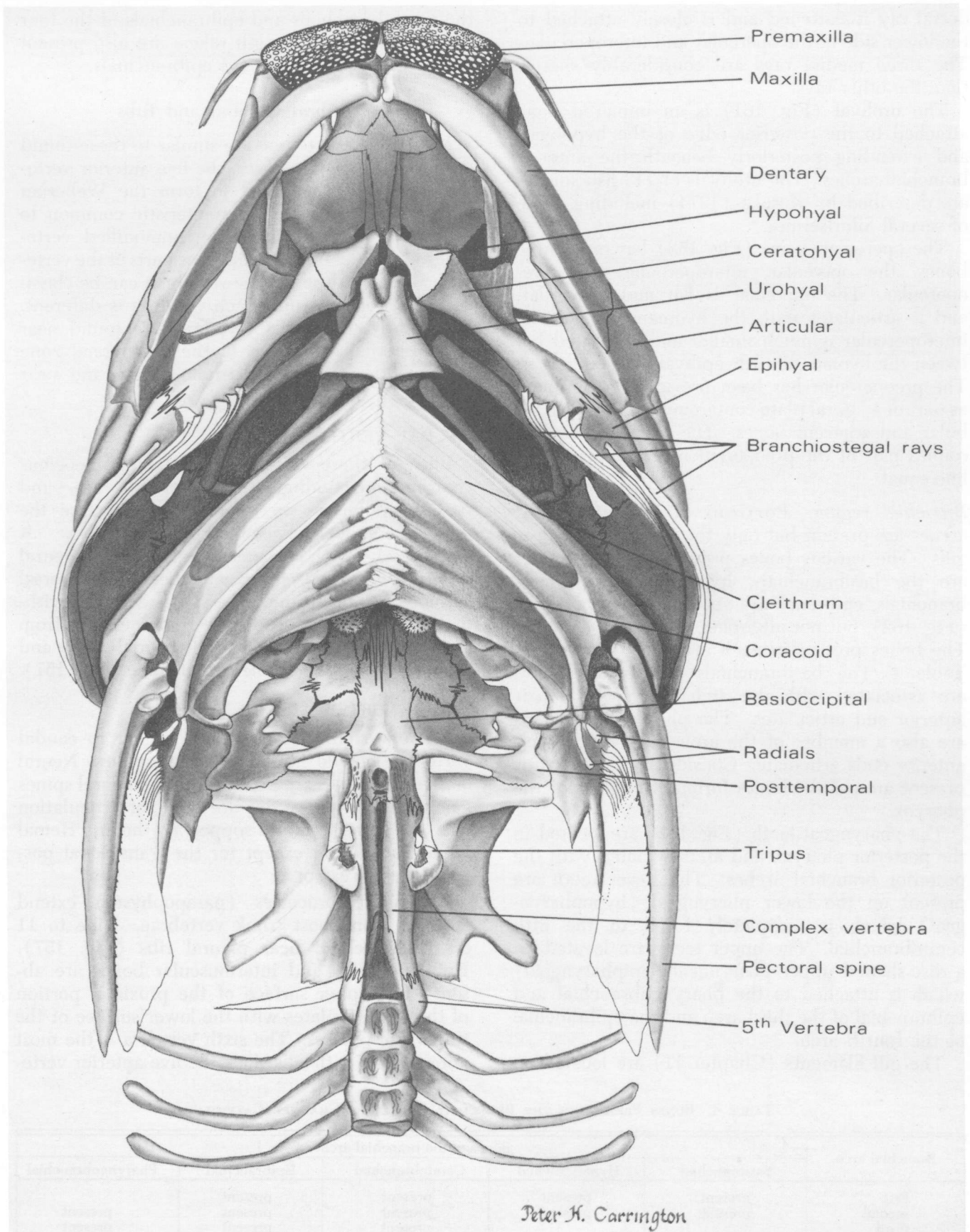
FIG. 161. Ventral view of the skull, anterior vertebrae, and pectoral girdle.

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**A**

Ventral hypohyal

Dorsal hypohyal

Ceratobranchials

Ceratohyal

Epihyal

Interhyal

Interopercular

Gill
rakers

Epibranchials

Pharyngobranchials

Upper pharyngeal

Dentary

Basibranchials

Hypobranchials

Articular

Joint

Pterygoid

Quadrate

Hyomandibular

Preopercular

Opercular

Lower pharyngeal

**B**

Branchial region

**C**

Pharyngobranchials

Epibranchials

Upper pharyngeal

**D**

Pharyngobranchials

Epibranchials

FIG. 162. (A) Dorsal view of the branchial arches, hyoid arch, and lower jaw. Most gill rakers were omitted from the second, third, and fourth arches; (B) Dorsolateral view of the skull with mouth open to expose the branchial arches; (C) Posterior view of the right upper pharyngeal bone; (D) Ventral view of the right upper pharyngeal bone.

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brae are modified in conjunction with the Weberian apparatus.

The absence of ribs from the anterior vertebrae results in an area of the body cavity which is not enclosed by ribs. The lateral cutaneous area is formed in the dorsal portion of this region where muscle is also absent. The anterior chamber of the swim bladder is in direct contact with the skin in this location.

## WEBERIAN APPARATUS

The development and anatomy of the Weberian apparatus of the channel catfish was described by Al-Rawi (1967). This modification of the anterior vertebrae connects the swim bladder to the ear to increase the sensitivity to sound. Additional discussion of the Weberian apparatus is in Chap. 9. The anterior vertebrae are fused to form the pars sustentaculum which supports the pars auditum consisting of small ossicles which develop from the vertebrae.

*Pars sustentaculum.* The second, third, and fourth vertebrae are fused into a complex vertebrae (Fig. 161) in which no clear demarcation between vertebrae can be found. The first vertebrae and fifth vertebrae are firmly united to the complex vertebra. A deep groove present on the ventral surface of the complex, first, and fifth vertebrae contains the dorsal aorta. A broad plate extends laterally from the complex vertebrae covering the dorsal surface of the swim bladder. A dorsoposteriorly projecting process from the complex vertebrae (Fig. 158) aids in the support of the dorsal fin and a dorsoanteriorly projecting process is attached to the skull.

*Pars auditum.* A chain of ossicles is present on each side of the pars sustentaculum. Each set of ossicles is composed of a tripus, intercalarium, scaphium, and claustrum (Fig. 129). The tripus, largest of the ossicles, connects firmly to the swim bladder near the middle of the complex vertebra and extends anteriorly to the first vertebra (Fig. 161). The interossicular ligaments connect the tripus to the intercalarium and the intercalarium to the scaphium. The scaphium contacts the sinus impar of the ear enabling sound received by the swim bladder to be conducted to the ear. The claustrum is also in direct contact with the sinus impar but is not directly involved in the conduction of sound.

## Fins

All of the fins are supported by skeletal elements except for the adipose fin. The histological structure of fins is discussed in Chap. 7.

### ANAL FIN

This fin (Fig. 157) is similar to the medial fins of most teleosts. The fin contains 24 to 30 lepidotrichia (soft rays) which articulate at the base of the fin with pterygiophores projecting between the hemal spines to which they are loosely connected. The two anterior lepidotrichia articulate with one pterygiophore, and the two posterior lepidotrichia articulate with one pterygiophore so that there are two more lepidotrichia than pterygiophores. Each lepidotrichia is composed of bilateral elements which separate basally to articulate with the lateral surfaces of the pterygiophore.

### DORSAL FIN

The anterior lepidotrichia and pterygiophores are highly modified to form a defensive spine and locking mechanism (Fig. 158 and 159). This fin is also firmly attached to the skull through a connection to the supraoccipital and the complex vertebrae. Six unmodified rays are posterior to the spine. The pterygiophores of these rays have anteriorly and posteriorly projecting bony plates which interconnect the pterygiophores. Except for the posterior pterygiophore which supports the posterior two rays, these supporting elements reach to the short bifid neural spines to which they are attached.

The spine is supported by a nuchal shield formed by the posterior projection of the supraoccipital and the first three pterygiophores (Gregory, 1933). The two pterygiophores which extend ventrally from the spine are greatly enlarged and firmly united to the posterior neural spine of the complex vertebra. The defensive spine seems to be the highly modified second lepidotrichia with the first lepidotrichia reduced to a small locking device lying on the anterior surface of the base of the spine (Bertin, 1958b). McMurrich (1884b) presented developmental evidence that the spine represented the third ray, the locking device the second, and the anterior portion of the horizontal plate represented the first ray.

The spine of the dorsal fin can be locked into an erect position by the U-shaped locking ray at its base (Fig. 159). Locking occurs when the locking ossicle slides anteriorly and ventrally over the dorsal extremity of the underlying pterygiophore so that it is held in the erect position by the surrounding bone. The locking ossicle is firmly connected to the anterior surface of the spine by

a strong ligament so that the locking of the small ossicle also locks the spine in an erect position.

## CAUDAL FIN

The terminology used to describe the elements of the caudal fin is that used by Lundberg and Baskin (1969).

The lepidotrichia articulate with bony plates and spines which develop from the posterior caudal vertebrae (Fig. 157). The last caudal vertebrae is highly modified and develops from the first preural and first ural centra (Lundberg and Baskin, 1969). The hemal spine of the compound vetrebra is modified to form a parhypural which is ventral to six hypurals. Dorsal to the hypurals is a uroneural. One epural is present and lies above the neural arch of the compound vertebra. The parhypural, the two ventral hypurals and the uroneural are fused to the compound vertebra. In addition to the supports associated with the compound vertebra, several vertebrae anterior to it have lengthened neural and hemal spines which support the dorsal and ventral portions of the fin.

## PECTORAL FIN

The pectoral girdle supporting this fin is massive and firmly attached to the skull by the post-temporal bone (Fig. 158). The cleithrum and coracoid are firmly joined together, and the suture between these bones can be seen only on very well cleaned specimens. The cleithera and coracoids of each side join midventrally and cover the heart region. The coracoids have an elaborate dovetailed suture where they join but the cleithra do not (Fig. 161). The supracleithrum, scapula, and postcleithrum are absent.

The fin is composed of nine unmodified lepidotrichia and a bony spine similar to the spine in the dorsal fin. Two radials are present between the pectoral girdle and the unmodified rays. The spine articulates in a deep socket of the girdle and can be locked in an extended position by a slight rotation.

## PELVIC FIN

The pelvic girdle is composed of two basipterygia which are not attached to any other element of the skeletal system (Fig. 157). The basipterygia tend to fuse at the midline in adults. Eight lepidotrichia articulate with each basipterygium. A horse-shoe shaped cartilage projects posteriorly from the pelvic girdle so that a cartilaginous process lies on each side of the anus.

## BONE

Histogenesis of bone occurs in two ways, and this difference is often apparent in sections of small fingerlings. Direct bone formation results in dermal (membrane) bone formed in association with the dermis. Indirect bone formation is the perichondral ossification of hyaline cartilage. The skeletal element is preformed in cartilage, and this core of cartilage surrounded by bone is distinctive (Fig. 163). Production of bone by osteoblasts and destruction by osteoclasts resulting in remodeling of bone structure in some teleosts seems similar to that of mammals (Lopez, 1970).

Bone is laminated (Fig. 164 and 165) with some bones having a spongy appearance due to numerous spaces. The spaces within the bone contains blood vessels and areola connective tissue. Hemopoietic tissue is not present within any bones.

## NOTOCHORD

This unique tissue is located in the center of the centra of the vertebrae (Fig. 166) and is much more prominent in juveniles than in adults. The notochord is compressed by each vetrebrae and expands near the junction of adjacent vertebrae. The structure of notochord is unlike that of bone or cartilage because the matrix is intracellular. Only the cell membrane and nuclei of the notochordal cells are visible in histological sections (Fig. 165). The notochord is surrounded by sheaths (Patt and Patt, 1969) which are surrounded by the vertebral centra.

## HYALINE CARTILAGE

This tissue forms a large portion of the skeleton



FIG. 163. Perichondral bone formation is characterized by the formation of bone (B) around a cartilaginous template (C). In fingerlings, bones which are formed by this indirect process have a central core of hyaline cartilage. The bone in this figure is a rib from a 65 mm TL fingerling. Bouin's; H & E; × 120.
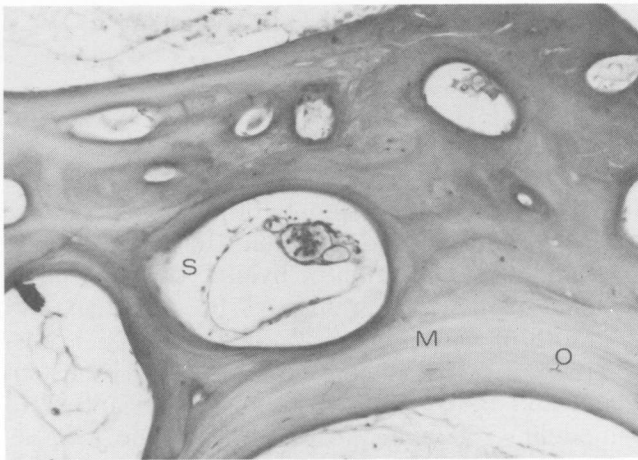
FIG. 164. Bone from the skull of a juvenile has osteocytes (O) in lacunae and calcified matrix (M) arranged in lamellae. Lacunae are probably connected by canals located between bony lamellae. Most bones have numerous spaces (S) containing loose connective tissue and blood vessels, but bone marrow is not present. Bouin's; H & E; × 160.



FIG. 166. Sagittal section of notochord (N), vertebrae (V), dorsal aorta (A) and spinal cord (S) from a juvenile. Notochord is composed of large turgesent cells in which a vacuole has displaced the contents of the cell. The vertebrae compress the notochord giving it an hour-glass shape. Bouin's; H & E; × 32.



FIG. 165. Bone composing the centrum of a vertebra (B) is similar to that in other regions of the body. It surrounds the notochord (N). Bouin's; H & E; × 320.
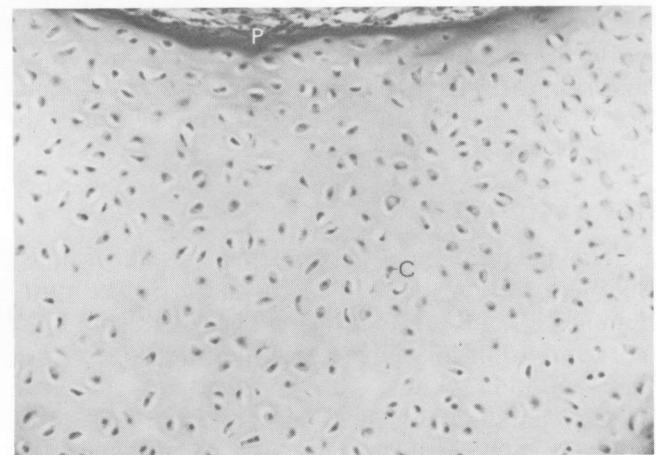


FIG. 167. Hyaline cartilage from the skull of a fingerling has chondrocytes (C) which are located in lacunae surrounded by a variable amount of interstitial matrix. Perichondrium (P) surrounds this cartilage which is replaced by bone in the adult. Bouin's; Masson's; × 160.

in small fingerlings, and several parts of the adult skeleton remain cartilaginous. The chondrocytes are separated by variable amounts of clear matrix (Fig. 167). This tissue is very similar to the hyaline cartilage of other vertebrates.

## PSEUDOCARTILAGE

Pseudocartilage is found only in the barbels (Fig. 168 and 126) and in strips attached to the intermandibularis posterior muscles (Fig. 96). These strips of pseudocartilage are attached to the mental and mandibulary barbels. The term pseudocartilage is that used by Bertin (1958c) to describe this tissue.

## GILL-FILAMENT CARTILAGE

This tissue type is found only in the filaments of the gills and is probably the same as the cartilage with capsular stroma which Bertin (1958c) men-



FIG. 168. Pseudocartilage of the barbel is composed of large oval cells lying close together with a homogenous interstitial matrix. Nuclei are oval, small, and usually located near the periphery of the cell. Bouin's; H & E; × 240.

tions being found in gill filaments. There is less matrix between cells than in hyaline cartilage, and the matrix tends to be acidophilic (Fig 169, 151, and 153).

## CHONDROID

Tissue resembling this type of cartilage is found covering the opercular bone, hypurals of the caudal fin and perhaps other locations. This tissue is composed of closely spaced, rounded cells and scattered fibers which stain green with Masson's trichrome stain (Fig. 171 and 172). This tissue is a primitive type of cartilage (Patt and Patt, 1969).



FIG. 171. Chondroid of the operculum. Higher magnification of area in Fig. 170. Bouin's; Masson's; × 240.
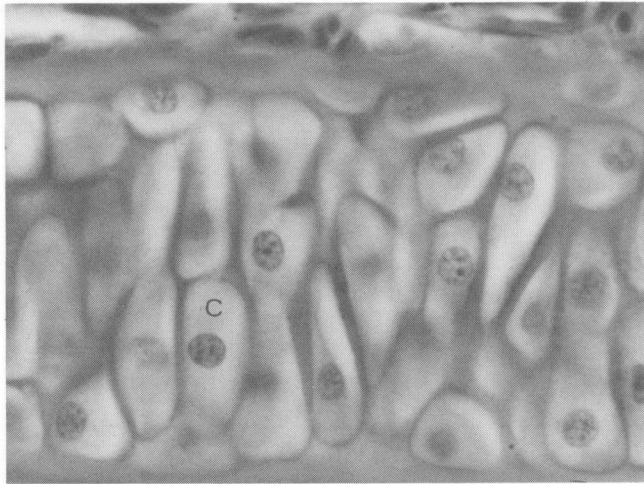


FIG. 169. Cartilage of a gill filament has chondrocytes (C) which are uniformly spaced and tend to have a rectangular shape. The matrix is more acidophilic than that of hyaline cartilage. Ossification of this cartilage may occur on the margins near the base of the lamellae. Bouin's; H & E; × 800.
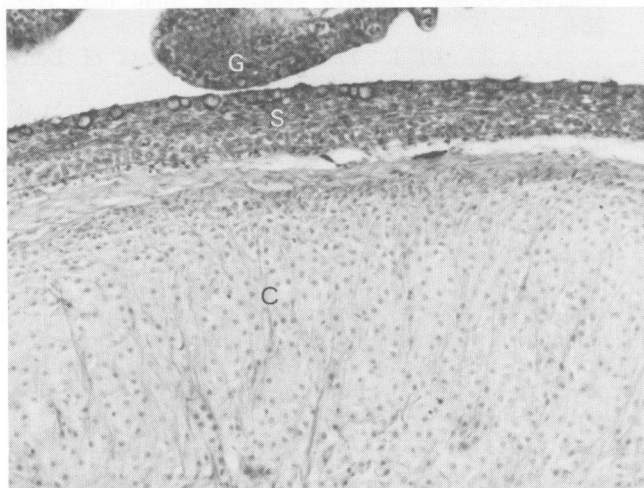


FIG. 170. Chondroid (C) lies between the opercular bone and the skin covering the inner surface of the operculum. Chondroid is composed of closely spaced cells with dispersed collagenous fibers. The skin (S) covering the inner surface of the operculum is similar to that covering the body except that alarm substance cells are absent. G, portion of gill filament. Bouin's; H & E; × 120.

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