POSTHATCHING HISTOLOGICAL DEVELOPMENT OF THE DIGESTIVE SYSTEM AND SWIM BLADDER OF LOGPERCH, *PERCINA CAPRODES* (RAFINESQUE)

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Bachelor of Science

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Stillwater, Oklahoma

1971

Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
MASTER OF SCIENCE
July, 1972

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ACKNOWLEDGMENTS

I wish to express my deepest appreciation to Dr. Milton R. Curd, who served as major adviser, for his patience, valuable suggestions, and untiring guidance during this investigation and the preparation of this manuscript.

Drs. Bryan P. Glass and Jerry G. Hurst served on the committee and aided in the evaluation and editing of the thesis.

Special gratitude is expressed to my wife, Joyce, for the preliminary typing of this manuscript and her understanding and encouragement.

Financial support was provided by a National Science Foundation graduate fellowship.

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CHAPTER I

INTRODUCTION

Little information exists concerning the histology of larval and juvenile teleost fish. Most studies of teleost development have been of prehatching stages and do not consider the changes which occur after hatching. This is unfortunate because much of the larva is poorly differentiated at hatching. Without an understanding of the histology and development of larvae and juveniles, the life history is more difficult to understand. Young teleosts are very susceptible to environmental hazards and have not been adequately utilized in studies of pathology and toxicology.

The logperch, Percina caprodes (Rafinesque) was found to have distinct differences in the digestive system and swim bladder at various ages during the development of the larva and juvenile. Some of the histological and morphological changes were associated with the beginning of feeding, others with the change from larva to juvenile, and some were not associated with any external changes in the fish.

The only teleost species whose digestive system has been described during posthatching development is the carp, *Cyprinus carpio*. Smallwood and Smallwood (1931) found that at hatching (4 mm stage) the larval carp intestine is much like it was when first formed in the embryo. The intestine consists of a single layer of columnar cells surrounding the lumen. After three or four days the yolk is mostly used and folds in the mucosa begin to appear, progressing from the anterior end posteriorly. Smallwood and Derrickson (1933) found that the liver originates in the carp larva on the day of hatching. The gall bladder develops on the terminal end of the right liver duct after most of the yolk is absorbed (7 mm stage). The pancreas develops about the same time as the gall bladder from undifferentiated cells associated with the liver duct. In a 41 mm carp the acinar cells of the pancreas appear adultlike.

Digestion in carp larva was discussed by Smallwood and Smallwood (1931). When the larvae begin feeding the liver and pancreas are not yet functional, and the source of digestive enzymes is secretion masses formed in the syncytial intestinal mucosa. These secretion masses appear much like nuclei, but sometimes extend for several cell widths. These masses apparently form near the basement membrane, move toward the lumen, and fragment into a number of spherical bodies that enter the lumen of the intestine. No evidence to substantiate these findings has been published by other authors.

Teleost swim bladders may be either physoclistous or physostomous and may develop as a diverticulum of the gut or as a solid mass of cells which later develops a connection with the gut. Hoar (1937) found that in the Atlantic salmon, *Salmo salar*, a physostomous bladder originates as a solid mass of mesodermal cells which is later invaded by an epithelial evagination from the gut. Duwe (1955) mentioned that in the rainbow trout, a physostome, the swim bladder develops as a diverticulum of the foregut.

Two physoclistous teleosts whose swim bladder development has been investigated are the green sunfish, *Lepomis cyanellus*, (Duwe, 1955) and the bluegill, *Lepomis macrochirus*, (Duwe, 1952). Both species are physostomous for a brief period as larvae. The bluegill swim bladder develops as a diverticulum from the gut 93 hours after fertilization. Six days after fertilization the swim bladder and rete mirabile are well developed and the pneumatic duct is open. At eight days the rete and pneumatic duct begin to atrophy, and the swim bladder has become physoclistous.

The green sunfish swim bladder originates as an independent solid mass of undifferentiated cells at 50 hours after fertilization which later develop a connection to the gut. Six days after fertilization the pneumatic duct atrophies and the swim bladder becomes physoclistous.

Histology of the adult digestive system in teleosts has been more thoroughly investigated than that of larvae and juveniles but is not well known. The diversity among teleosts makes it difficult to generalize about their histology. The literature on teleost histology is summarized by Barrington (1957), Andrew (1959), and Patt and Patt (1969). The histology of a teleost closely related to logperch or with similar feeding adaptations has not been described.

The logperch is a well known fish distributed "from the Churchill River system in Saskatchewan and the Hudson Bay drainage south through the Great Lakes to Gulf states and the Rio Grande" (Moore, 1968). Logperch inhabit both streams and lakes. They have been collected at depths of 30 feet in Lake Erie (Fish, 1929) and in Clear Lake, Missouri (Patriarche and Cambell, 1958). Clear Lake is mostly shallower than 30 feet and is clear (turbidity usually less than 7 ppm). Logperch are found in several stream types but are usually absent from headwater creeks unless large permanent pools are present, and from streams that are continuously turbid, excessively silty, or that lack riffles over gravel or rubble (Pflieger, 1971), and have been observed breeding along lake shorelines and in riffles (Reighard, 1913; Winn, 1958). Logperch are frequently studied for taxonomic or distributional purposes, but their histology has not been considered.

The food habits of logperch have been investigated, and this is useful in understanding histological adaptations of the digestive system. Young logperch feed primarily on microcrustaceans and progressively change toward a diet of insect larvae when older. The diet of adult logperch was found to be more varied than that of smaller fish. In addition to insect larvae and microcrustaceans; snails, annelids, fish, and plant remains were found in stomach contents in significant quantities, and several other items were found in lesser amounts. Logperch from streams had a less varied diet than fish from lakes (Turner, 1921). Ewers (1933), Ewers and Bosel (1935), and Dobit (1959) confirmed the finding of Turner.

The external features of larval logperch were described by Fish (1932) for larvae of 6.6, 12.15, 14.2, 20.5, and 25.5 mm total length. The larvae were described as having a moderate subinferior mouth, sharp pointed teeth, rudimentary air bladder, and large pectorals. Total length, length to vent, length of head, length of snout, diameter of eye, greatest depth before vent, depth behind vent, and the number of myomeres anterior and posterior to the vent were given for each size fish. Development of fins, body shape, and pigmentation were described for each of the five sizes. Similar information was taken from the fish raised for this study to determine if the laboratory raised individuals were different in external characteristics from the wild specimens collected by Fish.

CHAPTER II

MATERIALS AND METHODS

Logperch were hatched and raised in laboratory aquaria so that fish of known ages could be studied and because collecting wild larvae and juveniles is difficult. Ripe adults were collected in Salt Creek, Osage County, Oklahoma, from riffles and pools below riffles from March to early May, 1968-72. Zygotes were obtained by stripping the adults (Strawn and Hubbs, 1956). Temperature varied from 21 to 23 C and hatching occurred five to seven days after fertilization. A variety of aquaria sizes and water depths were used.

Larvae were fed newly hatched brine shrimp twice daily. Plankton, consisting largely of copepods, was added during some of the attempts to raise the fish. Juveniles were fed frozen adult brine shrimp and living white worms in addition to newly hatched brine shrimp.

Young fish and adults were fixed in Bouin's, Zenker's, and Kolmer's fluids and 10% neutral buffered formalin at intervals starting at the time of hatching. The fish fixed in Kolmer's were used for a study of eye structure and were of minimal value for the study of digestive system histology. Specimens were fixed daily for the first two weeks after hatching, at two or three day intervals for the next two weeks, and at three to seven day intervals thereafter. The oldest juvenile raised in the laboratory was 103 days old.

Two juveniles were collected from Salt Creek during August, 1970, and were estimated to be 4 months old. They were compared to the larger juveniles raised in the laboratory.

The fixed specimens were studied by dissection and light microscopy. Transverse and sagittal serial sections of young fish and sections of adult tissue were cut from material embedded in Paraplast and stained with hematoxylin and eosin or Masson trichrome stain.

The feeding and swimming behavior of larval and juvenile fish was noted as development occurred in the aquaria.

CHAPTER III

OBSERVATIONS

Most eggs hatched six days after fertilization. The age given for an individual fish assumes that it hatched on the sixth day, although some fish hatched a day earlier or later. This error is negligible considering the variation in growth rate.

In the following descriptions, all measurements are in millimeters and most are defined by Moore (1968). Yolk-sac length is the total length from anterior to posterior end. Oil-drop diameter was measured from anterior to posterior. Yolk-sac larva, larva, and juvenile are defined by Mansueti and Hardy (1967). The following abbreviations are used: total length, TL; standard length, SL; pectoral fin, P_1; pelvic fin, P_2; dorsal fin, D; anal fin, A; caudal fin, C. The measurements and descriptions of fin development and pigmentation are taken from one representative specimen of each age. The extreme of variation in total length of several specimens is given after the total length of the specimen used for the description.

Description of General Morphology

At Hatching

Yolk-sac larva (Figure 1); TL, 4.8 (4.7-5.9, N=9); length to vent, 2.5; greatest depth, 0.87; snout length, 0.18; eye diameter, 0.25; yolk-sac length, 1.2; oil-drop diameter, 0.4; P_1, small buds; P_2, absent. Fin fold is continuous from middorsum to posterior end of yolk sac. Pigment is absent except for well pigmented eyes and a few scattered melanophores near vent.

Two Days

TL, 5.3 (5.1-6.5, N=9); length to vent, 3.2; head length, 0.92; greatest depth, 0.79; snout length, 0.22; eye diameter, 0.30; yolk-sac length, 2.0; oil-drop diameter, 0.41; P_1 length, 0.40; P_2, absent. Fin fold and pigment is unchanged.

Four Days

TL, 6.3 (5.1-6.9, N=7); length to vent, 3.4; head length, 0.95; greatest depth, 0.60; snout length, 0.21; eye diameter, 0.33; yolk-sac length, 0.47; oil-drop diameter, 0.15. Fins are similar to two-day-old fish. Mouth is nearly terminal, and snout is rounded. Scattered melanophores are present in skin over gut and yolk sac and form a line on ventral ridge of tail.

Eight Days

Larva (Figure 2); TL, 6.5 (6.2-6.7, N=4); length to vent, 3.7; head length, 1.3; greatest depth, 0.91; snout length, 0.25; eye diameter, 0.42; P_1 length, 0.70; P_2, absent; yolk sac, absent. Melanophores are as in four-day fish with additional pigment on dorsal side of head.

15 Days

TL, 10.6 (8.3-10.6, N=5); length to vent, 6.0; head length, 2.0; greatest depth, 1.7; snout length, 0.39; eye diameter, 0.63; P_1 length, 1.3; P_2, absent; C, almost heterocercal. Rays are beginning to form in the fins. Snout has grown so that it projects slightly anterior to subterminal mouth. Swim bladder in larva appears as small oval dorsal to gut. Melanophores are more numerous but are limited to the same regions as on eight-day-old fish.

23 Days

TL, 14.3, (12.1-14.8, N=3); SL, 12.7; length to vent, 7.8; head length, 3.0; greatest depth, 2.9; snout length, 0.59; eye diameter, 0.97; P_1 length, 1.3; P_2, small buds; C, homocercal. Spines and rays in medial fins are distinct but not fully developed. Pigmentation is much darker than on younger fish. Caudal spot is distinct.

26 Days

Figure 3; TL, 13.2 (12.2-16.5, N=4); SL, 11.1; length to vent, 7.0; head length, 3.1; greatest depth, 2.0; snout length, 0.75; eye diameter, 0.98; P_1 length, 1.5; P_2, little more than buds; D, X-14; A, II,11. The fin fold is still present anterior to the vent. Scales are not visible.

36 Days

Juvenile (Figure 4); TL, 22.7 (14.7-22.7, N=4); SL, 19.4; length to vent, 12.2; head length, 5.2; greatest depth; 4.2, snout length, 1.3; eye diameter, 1.5; P_2, extends one-third way to vent; D, XIII-16; A, II,12; fin fold, absent. Snout is approaching adult form and mouth is subterminal. There are six or seven vertical bars of pigment on the sides with some bars continuous over dorsum. Scattered melanophores are present over entire body, and top of head is noticeably darker than other regions. Opaqueness prevents observation of internal organs at this stage. Scales are present over entire body.

49 Days

TL, 28.4 (28.4-29.4, N=2); SL, 24.4; length to vent, 15.2; head length, 7.3; greatest depth, 5.0; snout length, 1.7; P_2, extends almost one-half way to vent; D, XIV-16; A, II,11. There are eight to ten vertical bars of pigment on the sides. One band of pigment is on caudal and dorsal fins.

72 Days

TL, 38.2 (29.8-38.2, N=3); SL, 32.6; length to vent, 19.8; head length, 9.2; greatest depth, 7.0; snout length, 2.4; eye diameter, 2.3; P_2, extends more than one-half way to vent; D, XV-14; A, II,12. There are ten or eleven vertical bars of pigment on the sides. Caudal fin has three bands of pigment and the dorsal fin has two.

Histology

Oral Cavity and Pharynx

Adult. The adult oral cavity and pharynx are lined with stratified squamous epithelium with abundant goblet cells. A thin layer of connective tissue lies between the epithelium and the underlying bone or muscle. Papillae are present in the posterior part of the pharynx. Taste buds are scattered throughout the mouth and pharynx but are found only on gill arches and the ends of the papillae in the posterior pharynx. Teeth are very small and are present on the premaxillae, vomer, palatines, dentary, and upper and lower dentigerous plates.

Development. Immediately after hatching the oral cavity has not developed so the pharynx has no anterior opening. Epithelium, connective tissue and muscle have not become differentiated. One poorly defined gill slit is present but the development of the gills is not considered further. During the first day, the oral cavity develops, and some fish were found to have taste buds, goblet cells, and a mouth opening when one day old. Other fish had none of these when two days old. Tissues are differentiated by the second day. Goblet cells and taste buds form by the third day, but taste buds are not as abundant as in older fish. The taste buds bulge because of the thinness of the epithelium. Teeth first form on the upper and lower dentigerous plates at three days. At six days the dentary and premaxillae develop teeth. Palatine teeth are present at 20 days and at 32 days the vomerine teeth develop. A 36-day specimen had developed the papillae in the posterior part of the pharynx which is characteristic of the adult pharynx. A 41-day old specimen appeared very much like an adult except that the epithelium was thinner.

Esophagus

Adult. The esophagus does not have well defined anterior and posterior ends. The pharynx blends into the esophagus posterior to the gills. The esophagus is not as wide as the posterior part of the pharynx and taste buds are absent or very rare in the esophagus. The posterior end of the esophagus gradually changes to stomach as goblet cells of the esophagus disappear, gastric glands appear, and the epithelium changes to simple columnar. No valve is present at the gastroesophageal junction.

Anteriorly the esophagus of the adults is flattened dorsoventrally and posteriorly it becomes circular. The epithelium is stratified squamous but the surface cells are sometimes only slightly flattened and the tissue could be considered stratified cuboidal. Goblet cells are extremely abundant and compose a large part of the epithelium.

Longitudinal folds are composed of mucosa and submucosa. The longitudinal, striated muscularis mucosae is very thick in the anterior part of the esophagus and the submucosa between it and the muscularis externa is very thin. This gives the appearance of a longitudinal muscle layer internal to the circular layer of the muscularis (Figure 5). The muscularis mucosae becomes thinner in the posterior part of the esophagus and disappears before the gastroesophageal junction. The muscularis mucosae is not found posterior to the esophagus. The muscularis is composed of a circular layer of striated muscle. No longitudinal muscle is found in any part of the muscularis. The anterior part of the esophagus is surrounded by adventitia and the posterior part has a very thin serosa.

Development. At hatching the esophagus is not well differentiated. The lumen is absent or very small. The muscularis and submucosa are difficult to distinguish. There are no goblet cells or longitudinal folds. After one day a lumen is present in most parts of the esophagus and some goblet cells are present. Longitudinal folds are beginning to form and the epithelium appears stratified. The muscularis and submucosa are not well differentiated. On the third day it can be determined that the muscularis of the anterior end of the esophagus is striated but the muscularis and submucosa are very thin compared to the mucosa. Longitudinal folds are well developed by the third day. The posterior end of the esophagus is marked by a very short region with no lumen. Specimens of four days have abundant goblet cells in the anterior part of the esophagus, and few goblet cells posteriorly. The submucosa and muscularis are not well differentiated until the eleventh day. By the eleventh day some muscularis mucosae can be found in the anteriormost part of the esophagus. The connective tissue is much thinner than in an adult.

After the eleventh day the density of goblet cells and the amount of muscularis gradually increases. A 41-day-old specimen appears much like an adult although the mucosa is somewhat thinner than in an adult.

Stomach

Adult. The stomach is J-shaped so that food passes from the stomach into the intestine by moving anteriorly. There are two well defined regions of the stomach with a sharp boundary between them. The fundic region is largest and extends from the esophagus to the flexion of the stomach. The pyloric region continues to the pyloric valve which has a well developed sphincter.

The fundic stomach (Figure 6) has simple columnar epithelium and large folds when empty. The folds include mucosa and submucosa, and the submucosal folds are simple. The mucosa contains numerous gastric glands and a tunica propria fills spaces between glands. The epithelium forms gastric pits into which the simple tubular gastric glands empty. There are no goblet cells. The submucosa tends to be much thinner than the muscularis. The muscularis consists of two layers of smooth muscle.

The pyloric region of the stomach has no glands of any type. The submucosa and muscularis are much thicker than in the fundic region. Large folds composed of mucosa and submucosa are present. In contrast to the fundic region, the submucosal folds are compound. The epithelium is simple columnar and no gastric pits are present (Figure 7).

<u>Development</u>. The earliest indication of a stomach is at 15 days when goblet cells begin appearing in the intestine. The presumptive stomach remains free of goblet cells. A specimen of 26 days was the youngest with a pyloric valve. It is not until 32 days that a few gastric glands can be found. The pyloric sphincter is present but not well developed. At this age the division into fundic and pyloric regions is not clear, but some folding in the mucosa and submucosa is present. A 36-day specimen shows well developed gastric glands, a second layer in the

muscularis, and a well developed pyloric valve. A 41-day specimen had a stomach resembling an adult.

Intestine

Adult. The intestine extends from the pyloric valve to the rectum. Immediately past the pyloric valve, five to seven pyloric ceca branch off of the intestine. The pyloric ceca extend posteriorly from their origin to surround the pyloric stomach region. The histology of the pyloric ceca is very similar to that of the intestine. A slightly smaller diameter and a thinner muscularis are the only differences. The pyloric ceca were from 2 to 4 mm in length in an adult 90 mm SL.

The intestine passes from the stomach anteriorly, bends ventrally, and proceeds directly to the anus. Toward the posterior end of the intestine there is an ileorectal valve (Figure 8) consisting of a large fold of mucosa, submucosa, and the circular layer of the muscularis. The muscularis does not form a sphincter. The intestine posterior to this valve is designated as the rectum, but the histological structure of the two is identical.

The epithelium of the intestine is simple columnar. Very tall, slender branching folds composed of epithelium and a core of connective tissue zig-zag in varying directions (Figure 9). Goblet cells are the only glands present in the intestine. The muscularis has an inner circular and outer longitudinal layer of smooth muscle. The muscularis constitutes more than one-half the total thickness of the intestinal wall exclusive of folds. The anterior part of the intestine is often distended by large amounts of food whereas the remainder of the intestine contains so little food that the folds are not compressed.

Development. At hatching the tissues of the intestine are poorly differentiated (Figures 10 and 11). The lumen has not formed in the anterior part of the intestine and no folds are present in the posterior region. The ileorectal valve is not present. By the first or second day the lumen is very nearly complete. The anteriormost part of the intestine is the last area to gain a lumen. By the second day some folds are present posteriorly. These folds run circularly and usually extend less than half-way around the intestine. By two days the epithelium is clearly simple columnar but the tissues of the remainder of the wall are not differentiated. At the age of three days the ileorectal valve is recognizable but poorly developed. Circular folds in the mucosa are found throughout the intestine. Specimens which were four days old had well developed ileorectal valves, differentiated submucosa, and a muscularis of circular muscle only. Little change occurs in the intestine from the fourth day until the fifteenth day when a few goblet cells appear and the first trace of longitudinal muscle in the muscularis is found. The muscularis and submucosa are still very thin at 15 days (Figure 12). A very small pyloric cecum was observed on a

20-day specimen. By the age of 32 days, both the circular and longitudinal muscle layers are well developed. Two pyloric ceca are present, and the folds in the intestine are short and rounded.

One specimen of 36 days had developed the curve in the stomach and intestine which is characteristic of adults, but another specimen of 36 days still had a relatively straight gut. All specimens of 41 days and older had the adult-shaped gut. At the age of 41 days the histology of the intestine is almost like the adult, with a well developed pyloric valve and four pyloric ceca. However, at this age the folds are short and rounded instead of tall and slender. A 74-day specimen had six pyloric ceca but an 81-day specimen had four. At 103 days (the oldest fish raised in the laboratory) the folds were still thicker in relation to height than in adults (Figure 13).

Anus

Adult. The epithelium changes abruptly from simple columnar to stratified squamous at the anus. Just anterior to the anus the diameter of the rectum is reduced and the folds of the rectum become longitudinal. The circular layer of the muscularis is slightly thickened forming an anal sphincter.

Development. The anus is open at hatching. No sphincter is present and a reduction in size of the intestine occurs at the anus. The rectum immediately anterior to the anus develops shorter folds than the remainder of the intestine and the folds terminate anterior to the anus.

At one month the circular layer of the muscularis has increased in thickness. The development of this sphincter continues until two months when the anus appears like that of an adult.

Liver

Adult. The liver is surrounded by a very thin serosa. Lobules are poorly defined and there are few central veins. The cytoplasm stains very lightly and cell boundaries are distinct.

Development. At hatching, liver cells are basophilic, lobules are not present, and cells do not seem to be arranged in plates as in adults. Small clear vacuoles are present in the cytoplasm of all cells (Figure 14). The liver is confined to the left side of the gut. By the third day the liver has grown into the adult position and plates of parenchyma cells have formed. Specimens which were four days old were found to have cytoplasm which was more eosinophilic than in adults. By the fifth day the liver appeared like that of the adult.

Gall Bladder and Bile Ducts

Adult. The gall bladder has simple columnar epithelium over a layer of connective tissue. Irregular, simple folds occur in the epithelium and connective tissue. A thin muscularis is present, covered by a thin serosa. The bile duct has the same structure as the gall bladder. The duct has longitudinal folds and enters the right side of the anterior bend of the intestine. The hepatic ducts join the cystic duct from the gall bladder close to the intestine. The gall bladder is located posterior to the liver on the right side and is not enclosed in it.

Development. The gall bladder is not present until the second day after hatching. Before this it appears that the hepatic ducts enter the intestine directly. A specimen three days old has a swelling of the duct representing a gall bladder with simple cuboidal epithelium and very thin walls (Figure 15). The gall bladder extends to the right of the duct. The duct, lined with simple cuboidal epithelium, enters the intestine on the midventral side. This condition persists until 20 days when the gall bladder branches off of the hepatic duct and forms a cystic duct. The gall bladder lies ventral to the gut and the cystic duct proceeds posterodorsally to the intestine. The walls of the gall bladder are still very thin but the epithelium has become low columnar. At the age of 32 days the gall bladder of some specimens has moved dorsally so that the ventral side of the gall bladder is at the level of the ventral side of the intestine. Older fish have adultlike gall bladders and ducts. The amount of folding in the wall of the gall bladder and the height of the epithelium changes according to the fullness of the bladder.

Pancreas

Adult. The pancreas is disseminated (terminology from Patt and Patt, 1969) and no macroscopically visible organ can be found. Pancreatic tissue is found in the mesenteries of the stomach, anterior intestine, and pyloric ceca. The pancreas is most concentrated around the bile duct but also concentrates along blood vessels and between pyloric ceca. Pancreatic acini were not found around the blood vessels in any part of the liver. Except in the region of the bile duct, adipose tissue is often intermingled with the pancreatic acini (Figure 16). Pancreatic ducts could not be found. Islets of Langerhans were always imbedded in exocrine pancreas in the area around the bile duct. Pancreatic acini are much more basophilic than liver and are easily distinguished from it (Figure 17).

Development. At hatching the pancreas is a compact mass of cells on the right side of the gut in the region of the pylorus. The acini are not differentiated. The cells appear less vacuolated than in the adult and similar to the liver at this age (Figure 18). One islet of Langerhans is present and it is larger than the exocrine pancreas. By the second day pancreatic histogenesis has progressed so that the cells appear more like those of an adult and are easily distinguished from liver tissue. A specimen of four days had some of the exocrine pancreas extending posteriorly along the gut, but mostly it is still compact and primarily on the right side of the pyloric valve. Little change is seen in the pancreas until the age of 41 days when it is more diffuse and has three islets. The pancreas is still more compact than in adults. Older juveniles have a more disseminated pancreas and by 55 days it resembles that of an adult.

Swim Bladder

Adult. The swim bladder is physoclistous and has a well developed gas gland. The lengths of the swim bladders in two 90 mm SL specimens were both 9.0 mm. The swim bladder was found to be deflated with one exception. The wall of the swim bladder consists of a thick outer layer of loose connective tissue, a layer of dense connective tissue and the inner epithelium. Most of the swim bladder is lined with stratified cuboidal epithelium which is supplied with blood by retia mirabilia (Figure 19). The epithelium which lines almost all of the swim bladder appears the same as the epithelium of the gas gland on sections made of the yellow perch. The dorsal, posterior region is lined with a single layer of squamous cells but does not have the vascular tissue characteristic of the oval of the yellow perch. The inner surface of the swim bladder has several simple folds.

Development. The swim bladder can first be recognized in eight-day fish. At this age the swim bladder is poorly differentiated and is connected to the foregut. The swim bladder is lined with simple cuboidal epithelium and no rete mirabile is present (Figure 20). It is probable that presumptive swim bladder tissue is present at an earlier age but it was not identifiable in the specimens available.

The first changes in the histology of the swim bladder consist of the differentiation of the connective tissue around the swim bladder and the development of a rete mirabile. The swim bladder is physostomous during this development and has a rete on the anterior part. The epithelium progressively becomes stratified cuboidal.

There is considerable variation in the rate of development of the swim bladder. It is visible in live larval fish, and it was noticed that the swim bladder is visible in some specimens several days before it could be seen in slower-growing fish of the same age. In sections of an 11-day specimen the swim bladder had enlarged and differentiated, but a 13-day specimen had an undifferentiated swim bladder similar to that of a younger fish.

As the swim bladder continues to grow the walls become folded and the stratified cuboidal epithelium increases in thickness. A 49-day-old swim bladder appears similar to that of an adult except that the pneumatic duct is still open from the anterior end of the swim bladder to the posterior side of the stomach flexion (Figure 21). Several well developed retia mirabilia are present. The entire swim bladder is lined with stratified cuboidal epithelium. This same condition was found in a specimen 81 days old. Between the age of 81 days and 103 days the pneumatic duct degenerates, and the swim bladder becomes physoclistous.

Variation in the Histology of Fish of the Same Age

There is variation in the size of the fish at hatching and a larger variation in the rate of growth of individuals. In order to gain insight into the amount of variation in the histological development of fish of the same age, four fish from each of three ages were compared. The fish were chosen randomly and no attempt was made to determine the maximum variation.

One day. The four fish had total lengths of 4.6, 4.7, 4.7, and 4.9. Very little difference in the histology of these fish could be determined except for a small variation in the amount of gut without a lumen.

Four days. The total lengths of the fish were 5.1, 5.8, 5.9, and 6.2. The 6.2 mm fish had an extremely small lumen in the intestine in the area of the liver, while the other fish had a well developed lumen throughout the intestine. The pancreas of the 5.1 mm fish had just begun extending posteriorly from its original position compared to the slightly more developed posterior extentions on the pancreas of the other specimens. The histological differences were not as pronounced as the differences in total lengths.

32 days. These four fish were from the same hatch, but a pronounced difference in size had developed. The total lengths were 11.0, 14.0, 14.2, and 15.7. In the largest fish the stomach and intestine had begun to bend and a few gastric glands were present. The 14.0 and 14.2 mm fish had no gastric glands and a straight gut. The 11.0 mm fish had no pyloric valve, no pyloric ceca, and a mid-ventral gall bladder. The histology of this fish was more similar to a 12.0 mm, 20-day fish examined than to the other 32-day fish.

Swimming and Feeding Behavior

Immediately after hatching the larvae spend most of the time lying on their sides on the bottom. There is some tendency to swim into tight places as they often become trapped beneath petri dishes left in the water. By the time the larvae are two days old most are strong swimmers and lie on the bottom only occasionally. Some of the larvae begin feeding when they are three days old and all of the survivors are feeding two days later. Five-day-old larvae are good swimmers, seldom rest on the bottom, and dart rapidly if pursued with a net.

After the yolk sac disappears the swimming attitude of the fish changes. Since hatching there has been a tendency to swim with the tail lower than the head, and after the consumption of the yolk sac the tail is maintained much lower than the head so that the body is between 30° and 60° from horizontal. In light the fish swim continuously, and chase live food organisms, but in darkness the larvae do not feed and rest on the bottom.

When the fish are about three weeks old, a few of the larger fish begin spending some time resting on the bottom like adult darters. There is much variation between individuals as to the age when this adultlike behavior begins. At the age of four weeks more time is spent on the bottom, but most of the fish still feed while swimming in midwater. At this same age, the larger fish begin swimming with the body horizontal.

Most five-week-old fish are large enough to eat small worms and frozen adult brine shrimp. An increasing number associate with the bottom and eat while resting on the bottom. By the time the fish are six weeks old they all remain on the bottom except when disturbed or in pursuit of a food organism.

CHAPTER IV

DISCUSSION

The first feeding occurs on the third day after hatching, although the yolk sac has not been totally consumed. The digestive system becomes functional before feeding commences. The lumen of the alimentary canal becomes complete, and taste buds and goblet cells form in the oral cavity and pharynx during the first day. The esophagus develops longitudinal folds which allows prey to be swallowed, and circular folds increasing the absorptive area of the intestine develop. The pectoral fins develop so that swimming ability is increased. The liver cells appear different from adults cells when feeding begins, but the enlargement of the bile duct forming a gall bladder indicates that the liver may be functional. The development of teeth at the time feeding begins indicates that teeth are important in capturing prey. The pancreatic cells appear adultlike when feeding begins and are the only visible source of digestive enzymes. Intestinal secretion bodies of enzymes as found in carp larvae (Smallwood and Smallwood, 1931) were not present in the logperch.

The yolk is totally consumed by five days after hatching. The liver appears adultlike and is probably fully functional. Goblet cells have begun forming in the esophagus.

The swim bladder forms at about eight days, but additional specimens fixed less than one day apart are needed to study early development more precisely. The formation of the swim bladder occurs slightly later than in the bluegill and green sunfish (Duwe, 1952; Duwe, 1955). The developing swim bladder is physostomous, and the pneumatic duct enters the incipient stomach.

The swimming attitude of the larva is 30° to 60° from horizontal, and while feeding they swim continuously. In darkness when they are not feeding they rest on the bottom. The swim bladder does not provide the bouyancy needed for maintaining a position in midwater without swimming actively although the swim bladder of the larva is inflated. The function of the larval physostomous swim bladder needs further investigation.

When the fish are about a month old the larger ones have become juveniles. The juveniles have teeth on the premaxillae, vomer, palatines, dentary, and upper and lower dentigerous plates. The same arrangement of teeth is found in the adult. The change to a juvenile includes an increase in density of goblet cells in the esophagus, development of gastric glands, bending in the stomach and intestine, and movement of the gall bladder to a more dorsal position.

By the time the fish were one month old the larger fish were approximately 50% longer than the smaller fish.

The larger fish were often more mature than the smaller fish but there was little correlation between length and histological development. The differences in rate of development makes it impossible to determine the exact age when specific developmental events occur. This is illustrated by the differences among the four 32-day fish.

As the juvenile matures, the epithelium of the oral cavity and pharynx becomes thicker, the muscularis and submucosa become thicker throughout the alimentary canal, and the pancreas becomes more diffuse. The juveniles tend to stay on the bottom and midwater swimming occurs infrequently. The digestive system appears adultlike at 49 days, except that the intestinal folds are proportionately shorter.

The number of pyloric ceca increases with age although the final number appears variable. The first pyloric cecum is present at 20 days, the second at 32 days, and four are present at 41 days. Older juveniles have four to six compared to five to seven for adults. Some older fish obviously have fewer that some younger fish.

The large stomach, straight intestine, numerous small teeth, and subterminal mouth are adaptations of juveniles and adults for feeding on bottom-dwelling insects and similar prey organisms. The pancreas and gastric glands are the only recognizable sources of digestive enzymes. The anterior end of the intestine seems to be a major site of digestion as large amounts of food were usually found there. The few short pyloric ceca and the short intestine have numerous tall folds which increase the absorptive area.

The pneumatic duct atrophies between 81 and 103 days. The functional reason for the persistence of this duct is unknown. The swim bladder of the juvenile is lined entirely with stratified cuboidal epithelium which has the same appearance as the gas gland of the yellow perch. Several retia miribilia are present, but an oval for absorption of gases from the swim bladder is not present. It is possible that the gas gland of the logperch functions both in excretion of gas into the swim bladder and in absorption. The functional implication of a large, well developed gas gland in a small swim bladder which is usually deflated is not known.

The ratios presented in Table I could be useful in taxonomic studies or for comparison of wild fish to the laboratory-raised fish used in this study. The total length-length to vent ratio might be the most significant because it is relatively constant. The decrease with increasing age in the total length-snout length ratio was expected because the snout becomes noticeably longer as the fish matures. The decrease in the total length-head length ratio is also caused by the increase in snout length. The total length-greatest depth ratio is highly variable due to differences in fullness of the gut. The fluctuation in total length-eye diameter ratio may be due

TABLE I

RATIOS BETWEEN VARIOUS MEASUREMENTS OF LABORATORY RAISED LOGPERCH

Age	Total Length / Greatest Depth	Total Length / Length to Vent	Total Length / Head Length	Total Length / Snout Length	Total Length / Eye Diameter
Hatching	5.5	1.9	-	26.7	19.2
Two Days	6.7	1.7	5.8	24.1	17.8
Four Days	10.5	1.9	6.6	30.0	19.1
Eight Days	7.1	1.8	5.0	26.0	15.5
15 Days	6.2	1.8	5.1	27.2	16.8
23 Days	4.9	1.8	4.8	24.2	14.7
26 Days	6.6	1.9	4.3	17.6	13.5
36 Days	5.4	1.9	4.4	17.5	15.1
49 Days	5.7	1.9	3.9	16.7	16.7
72 Days	5.5	1.9	4.2	15.9	16.6

to a difference in the way the eye is measured as the fish becomes opaque.

Descriptions of external characteristics given for wild logperch larvae and juveniles by Fish (1932) fit the laboratory raised fish used in this study. The fish in this study were slightly deeper in relation to length, but this was probably because many of the fish in this study were fixed and measured with very full stomachs, and had large amounts of adipose tissue.

Histological examination of a juvenile from Salt Creek revealed no differences from the juveniles raised in the laboratory, indicating that the development of artificially spawned fish was normal although the rate of development may have been faster due to more abundant food and less activity.

CHAPTER V

SUMMARY

Histological examination of laboratory raised logperch revealed numerous changes during posthatching development of the digestive system and swim bladder. The newly hatched larva has an incomplete alimentary canal and poorly differentiated liver and pancreas. After three days the digestive system is functional and feeding begins. The intestine has circular folds, the esophagus has longitudinal folds and goblet cells, some teeth are present, and the pancreatic cells appear like those of the adult.

Differentiation and development of the mucosa, submucosa, and muscularis continues throughout larval development. The larva develops a physostomous swim bladder at eight days and the gas gland develops as the larva grows. The pneumatic duct opens into the stomach. The larvae swim in midwater.

The change from larva to juvenile corresponds to the development of adultlike gall bladder, tooth distribution, gastric glands, flexion of stomach and intestine, and goblet cell density in the esophagus. Juveniles stay on the bottom instead of swimming in midwater.

As the juvenile matures the thickness of the muscularis and submucosa and the number of pyloric ceca increase. The pancreas becomes more diffuse with increasing age. The pneumatic duct atrophies between 81 and 103 days, but the gas gland remains well developed. The intestinal folds are taller in relation to thickness in the adult than in the oldest juvenile examined.

The adult has a stomach with a distinct fundic region with well developed gastric glands and a pyloric region with no glands. The straight intestine and the five to seven pyloric ceca have a similar histological structure including tall, thin folds. The pyloric valve has a thick sphincter and the ileorectal valve has very little muscle. The pancreas is disseminated along the bile duct, blood vessels, and between the pyloric ceca. Several questions concerning the swim bladder remain unanswered.

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APPENDIX

Figure 1. Yolk-sac Larva at Hatching, 4.9 mm TL

Figure 2. Larva Eight Days After Hatching, 6.5 mm TL

Figure 3. Larva 26 Days After Hatching, 13.2 mm TL

Figure 4. Juvenile 36 Days After Hatching, 22.7 mm TL

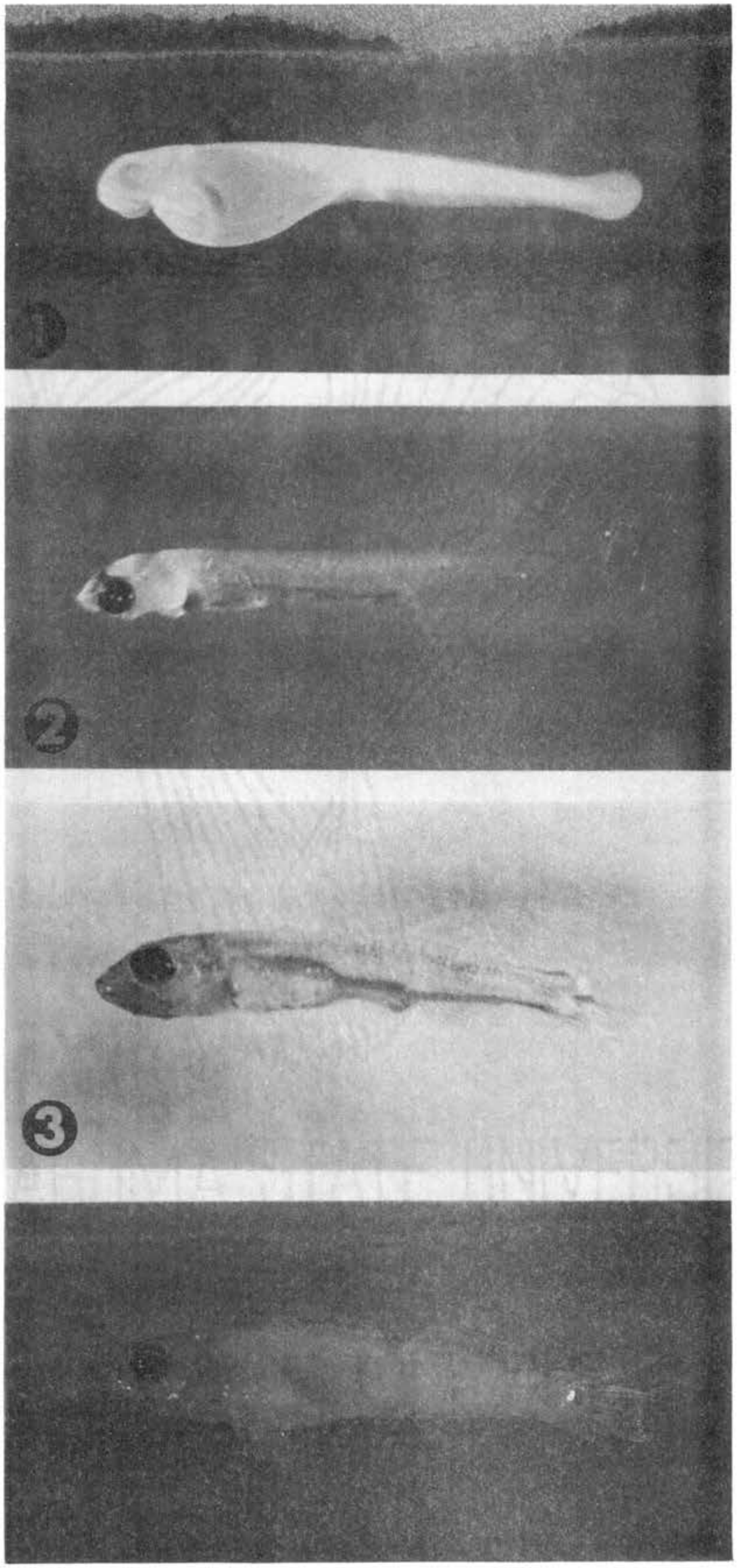

Figure 5. Anterior Esophagus of Adult. Transverse Section Showing Numerous Goblet Cells and Thick Muscularis Mucosae, MM

Figure 6. Fold of the Adult Fundic Stomach. Note the Gastric Pits, Tubular Glands, and Simple Submucosal Folds

Figure 7. Pyloric Stomach of Adult. Note the Compound Submucosal Folds and Absence of Glands

Figure 8. Ileorectal Valve of Adult. Longitudinal Section. Intestine, I; Rectum, R

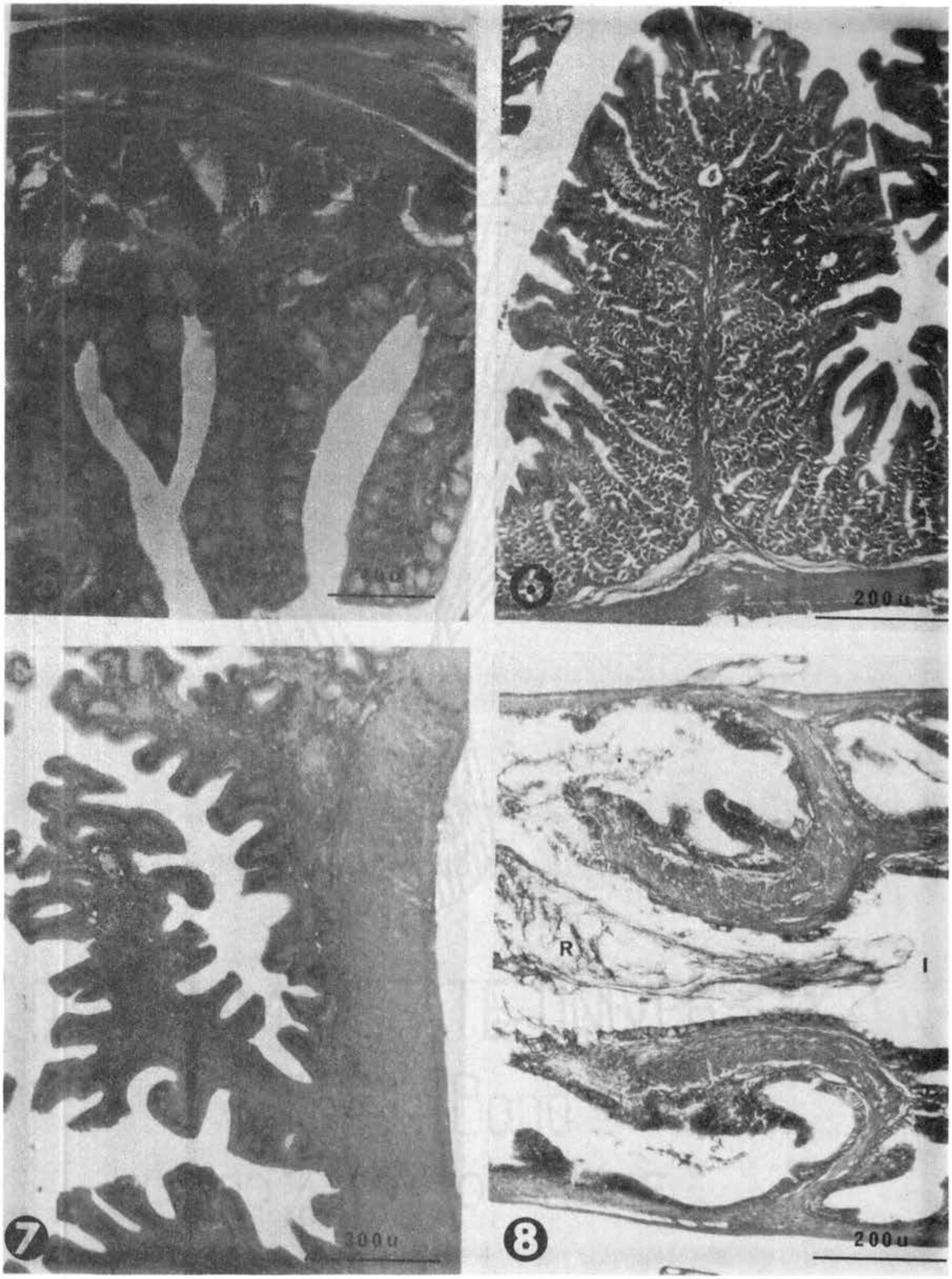
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Figure 9. Intestine of Adult. Transverse Section Showing High, Thin Compound Folds

Figure 10. Intestine of Yolk-sac Larva at Hatching. Transverse Section in Region of Yolk Sac. Layers of Intestinal Wall Poorly Differentiated

Figure 11. Intestine at Hatching. Transverse Section in Region of Liver. Note Absence of Lumen

Figure 12. Intestine of 15-day Larva. Transverse Section. Note Thinness of Submucosa and Muscularis and Nature of Folds

Figure 13. Intestine of 103-day Juvenile. Transverse Section Showing Nature of Folds. Compare with Figures 9 and 12

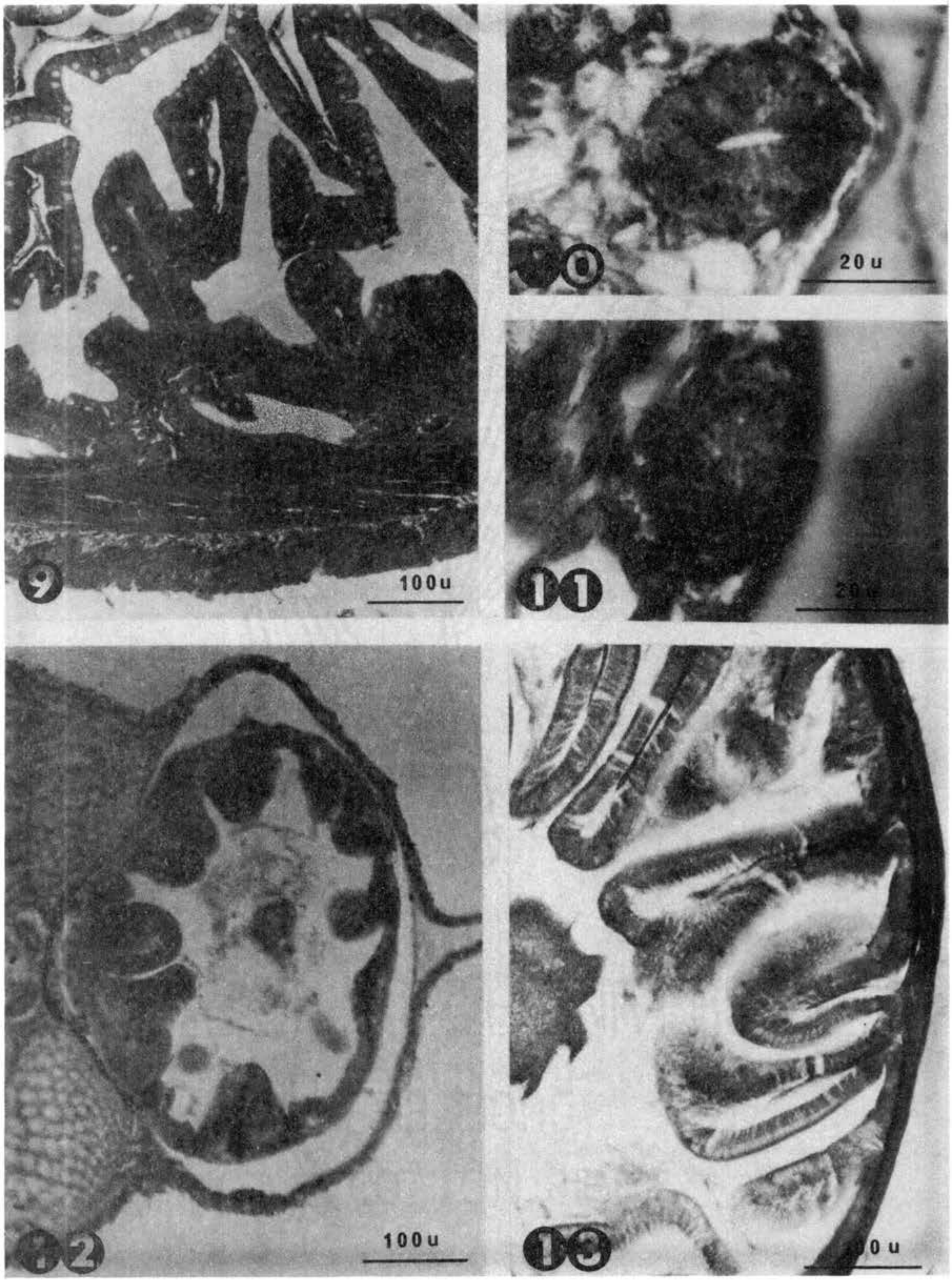
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Figure 14. Liver at Hatching. Sagittal Section. Compare to Liver in Figure 17

Figure 15. Sagittal Section Showing Liver Ducts of Three-day Larva. Hepatic Duct, H, Joins Gall Bladder, G, Which Opens Into Intestine Through Bile Duct, B. Dark Tissue Around Bile Duct is Pancreas

Figure 16. Disseminated Pancreas of Adult. Note the Association of the Pancreas With a Vein and Interspersed Adipose Tissue

Figure 17. Pancreas (Darker Tissue) and Liver of Adult

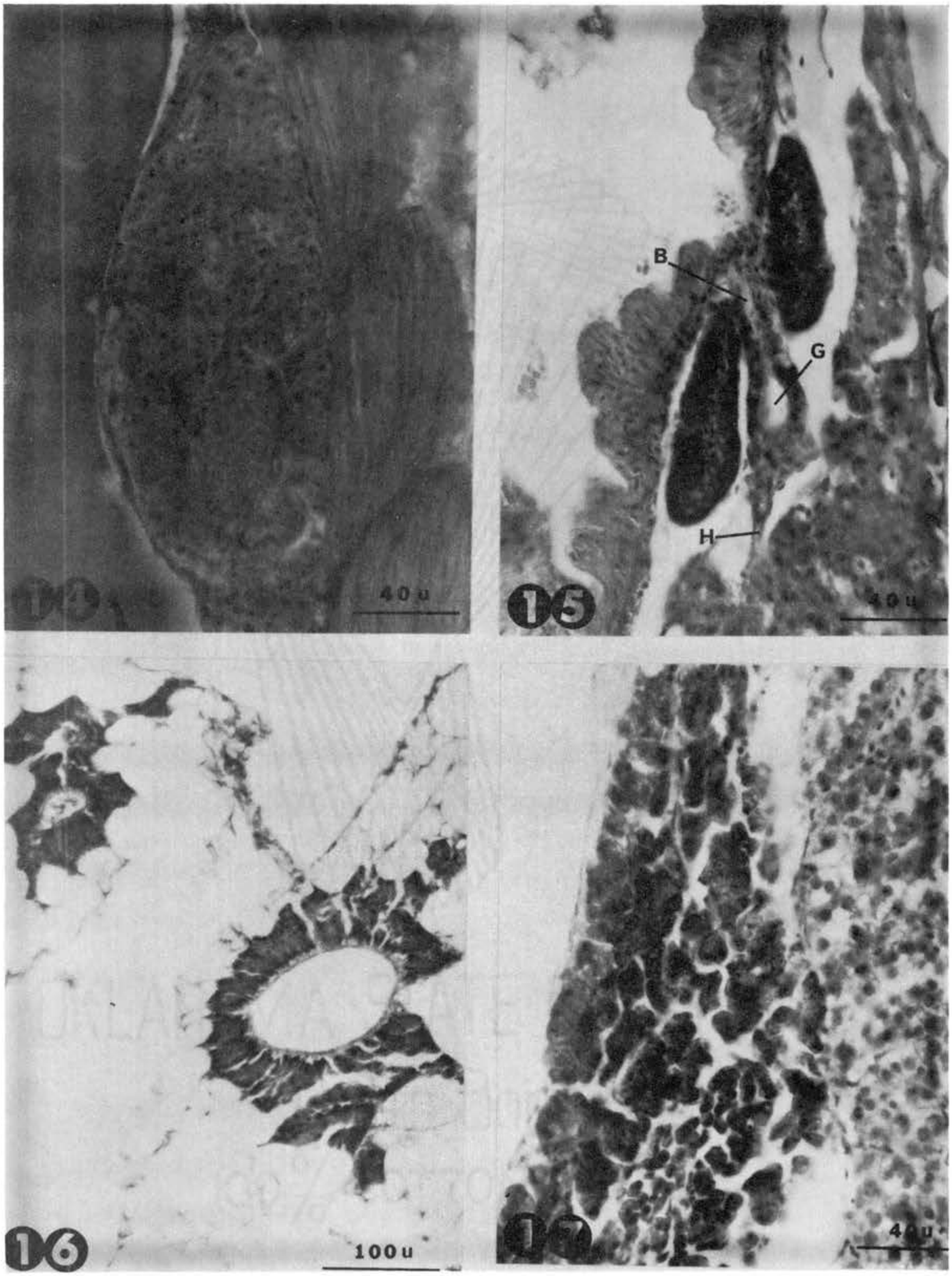
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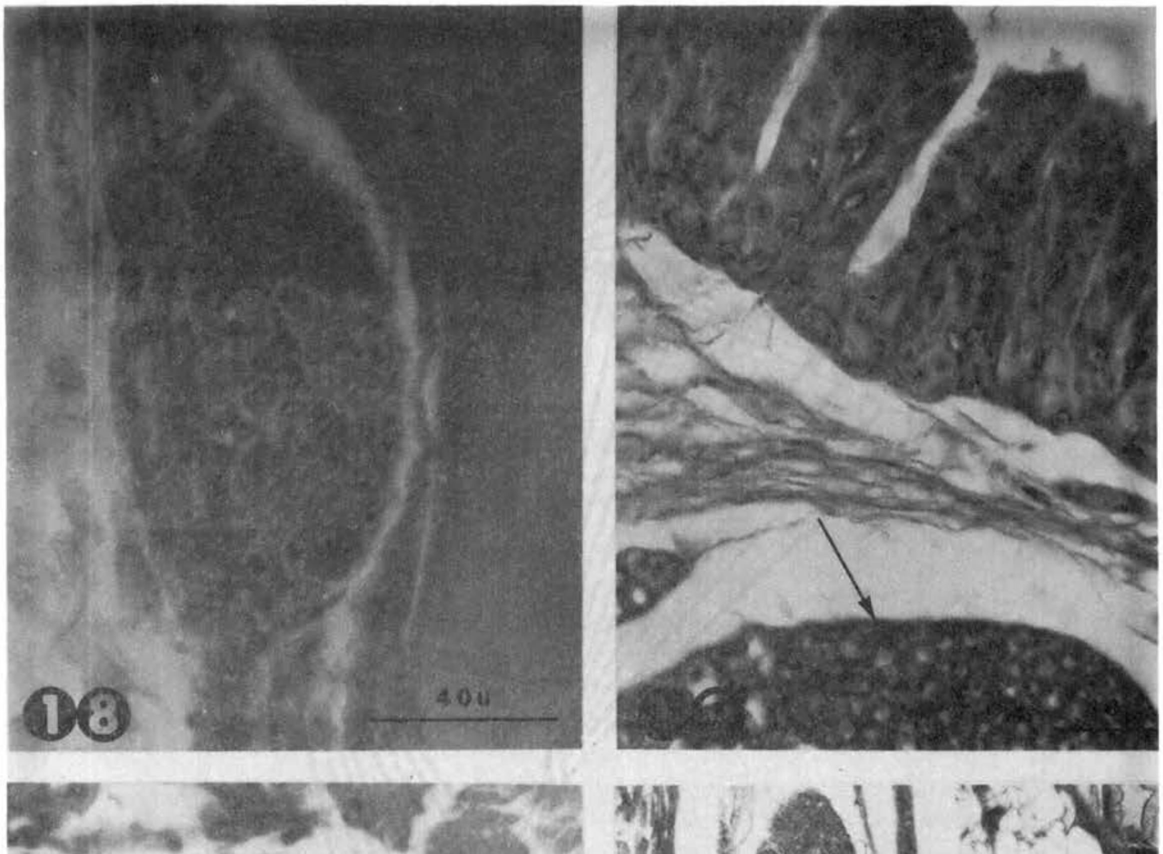
Figure 18. Pancreas at Hatching. Sagittal Section. Note Compactness and Compare with Figures 16 and 17

Figure 19. Gas Gland of Adult Swim Bladder. Transverse Section Showing Epithelium and Rete Mirabile (Arrow)

Figure 20. Transverse Section of Nine-day Larva Showing the Swim Bladder Dorsal to the Gut

Figure 21. Swim Bladder of 74-day Juvenile. Left Side of Photograph is Dorsal. Sagittal Section Showing Swim Bladder, SB, Connected by Pneumatic Duct (Arrow) to Stomach, S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VITA

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Master of Science

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