The Air-bladder and Pulmonary and Systemic Circulation of *Amia calva* L., together with a General Description of the Fish.

by

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C O N T E N T S.

Contents (Cont'd).

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I. HISTORICAL INTRODUCTION.

The air-bladder of bony fish, or Osteichthyes, has aroused the interest of scientists for a very long time. According to Goodrich,[1] Rondelet studied the bladder of the Actinopterygii in 1554 and concluded that it helps the fish to swim. In the following century (1667) Needham suggested that it might serve one of several purposes: as a float, as a respiratory reservoir or as an organ to secrete gas to help in digestion. During the seventeenth century Mayow, Ray, Boyle and Borelli studied it by various experimental methods. Discussion on the functions of the bladder continued throughout the eighteenth and nineteenth centuries, and indeed are still carried on to-day.

Experimental investigation of the physiology and contents of the bladder was begun as early as 1680 by Perrault. He, and later Monro (1785), established the fact that gas is secreted by the red gland in closed bladders. Other workers (Priestly, Biot, etc.) found that the proportion of oxygen in the bladders varies. Biot found the gas in the bladders of deep-sea fish to be almost pure oxygen, while that in fresh water fish is mainly nitrogen.

By this time the function of the air-bladder was believed to be that of enabling the fish to rise or sink. The foundation of this belief was shaken when Provençal and Humboldt (1809) showed that a fish can swim well even after the bladder has been removed or punctured. This led quite directly to the establishing of the modern view by Delaroche (1809)

1. Goodrich "Structure and Development of Vertebrates", page 585.

and Moreau (1876), that the bladder does not actively help the fish to rise or sink, but allows it to alter its specific gravity to that of any level in which it finds itself. The fish can adjust the pressure in the bladder by varying the amount of gas present. It can thus bring itself into equilibrium with the water and so encounter least resistance. During the present century work has been done in this field by Hall (1924); Popta (1910-12); Guyènot (1909-12); Baglioni (1908); Tower (1902).

Much study has also been given in the past to the anatomy and circulation of the air-bladder which serves as a lung in the Dipnoi and Polypterus. With the exception of two papers written by Wilder[1] little consideration has been given in the past to a similar organ found in the ganoid fish Amia calva. The present investigation has shown many remarkable features to be present in this fish. The purpose of this paper is to describe these features, and to consider their importance to the question of the relation between air-bladder and lungs.

1. Wilder, B.G., 1875 "Notes on North American Ganoids".
1877 "Respiration of Amia".

II. MATERIAL AND METHOD.

Ten adult specimens of Amia calva were used. Of these, nine were males and one was a female. The males ranged in size from twelve to eighteen inches, and weighed from two to four pounds each. The one female measured twenty-eight and one-half inches and weighed eight pounds. All the fish but one were obtained dead from two fish markets in Montreal. The fish dealers say that they receive these fish in the fall and spring from the lakes in Ontario, especially Lake Ontario. They are shipped from Belleville and other lake ports. Though the fish is known to be in the St. Lawrence and other rivers flowing into it, down at least as far as Sorel, it is seldom caught in this vicinity for market. The one live fish was caught by a fisherman in the St. Lawrence River near Verdun very late at night. It was kept in a tank for a short time, but unfortunately developed a serious external fungus infection before any experiments were done on it.

Two pike (Esox lucius) and one gar-pike (Lepidosteus osseus) were used for purposes of comparison. The pike were obtained at the fish-market. For the three-foot specimen of Lepidosteus I am indebted to Dr. T.W.M. Cameron of Macdonald College.

Fresh fish were used whenever possible for the dissections, since the blood vessels are more readily seen under such conditions. When specimens were used which had been kept in formalin (5%), it was found useful to inject small sections of the main parts of the circulatory system with a solution of blue ink delivered from a pipette. An

attempt at injection with red gelatine proved unsuccessful.

Two fish were injected with a solution of starch coloured with carmine dye. The solution had the consistency of thick cream. The first injection was made through the large gonadial vein in a male fish. This was not very successful, since the vein around the cannula broke a number of times. The fluid only entered the large veins since it was being forced in a backward direction. One very fine injection was made through the caudal artery. It was intended to inject the arteries only, but apparently the fluid passed through the capillaries and entered the veins. Every vessel to the very smallest was filled, with the exception of the renal portal vein. The specimen was of great value, particularly in the study of the circulation in the air-bladder itself.

III. NATURAL HISTORY.

Considering the lack of any inclusive account of the natural history and anatomy of Amia calva in the literature, a general description compiled from various sources is given here.

External Appearance.

Amia calva L. is a primitive ganoid Actinopterygian, belonging to the subdivision Holostei. (Plate 1). It is a very deep olive green when fresh from the water, but, when dry, is practically black. The ventral surface is very much lighter in colour, often yellowish, and is somewhat reticulated in appearance. The back, sides, and head are mottled by slightly darker patches. The body is covered with large cycloid scales which are hard and bony at the base, but soft and flexible at the outer edge. They are not covered with enamel as the scales of the other ganoid fish are. The head is bare of scales and is covered only by a thin layer of skin. Many pores on the surface of the head mark the openings of a complicated system of sensory canals in the bones of the skull. The nostrils are paired, the anterior ones opening at the end of a pair of maxillary barbels. (Plate 2). The eyes are small and near the top of the head. The lateral line is complete and clearly defined.

The fins are all soft-rayed and lack fulcra. The dorsal fin is very long, being three-quarters the length of the whole body, while the anal fin is very short. The caudal fin is rounded and the tail is slightly heterocercal. Dusky stripes cross the dorsal and caudal fins

at right-angles to the fin rays.

The fish is somewhat oblong in shape, compressed laterally toward the posterior end. The snout is blunt and the jaws large and powerful. This feature, combined with the armoured appearance of the head, give an expression of vicious self-satisfaction to the anterior aspect of the fish.

According to a number of sources, (e.g., The Standard Natural History) the male fish is distinguishable from the female by the possession of a dense black ocellus at the base of the caudal fin. This ocellus is often bordered by a yellowish orange band, and the fins are often light green bordered with orange. It is interesting to observe that the female fish which we obtained possessed a well-marked black ocellus, and the fins of all the fish examined lacked the orange borders described by other authors. The latter exception may be explained by the time of year at which they were obtained, i.e., the late fall, for, according to Dean, the fish are more brightly coloured during the breeding season (late spring)[1]. The young are described as being quite light green in colour, having the dorsal and caudal fin tipped with black, and the nose, eye, cheek and opercle crossed by a narrow dusky stripe. (Forbes and Richardson, page 38).

Amia is rarely caught except in nets, for it is a remarkably strong and active fish. When caught on a line baited with a dead minnow it puts up an intense struggle, for it is said to be "one of the hardest

1. Dean, B. "The Early Development of Amia".

fighters that ever took the hook". [1] It is not a particularly large fish, the female exceeding the male in size. The female may attain a length of two feet or more; the one specimen dissected measured twenty-eight and one-half inches. The male rarely exceeds eighteen inches in length.

Distribution and Economic Importance.

The range of Amia is very restricted at the present time. It is found exclusively in Southern and Central North America. It occurs in the Mississippi and St. Lawrence River systems and in the Great Lakes where it is abundant and widely distributed. Little commercial value attaches to the catching of the fish, since its flesh is pasty and not esteemed for food. Almost the whole supply which is marketed in the United States is obtained, according to Forbes and Richardson, from the Illinois River. The small supply called for in Montreal is obtained, according to the dealers, mainly from Lake Ontario, with an occasional small number from the St. Lawrence River. The time to catch it is at night in shallow weedy places where it goes in schools to feed.

This fish is remarkable for the variety of common names by which it is known. It is surprising to find that in Montreal markets it is known exclusively as the "dog-fish", while fishermen on the St. Lawrence call it the "beaver-fish". It is probably most widely known as the "bowfin", which name it gets from its long dorsal fin. There seems to be a different name for it in each district in which it is found. One writer gives a list which includes the following names: the brindle,

1. Jordan, Starr "Fishes".

John A. Grindle, Sawyer, mudfish, mudjack, and the lawyer-fish - the reason given for the last name is that "it will bite at anything, and is no good when it is caught!" (Jordan, Starr, page 35).

The first fossil record of the Order Amioidei is in the Upper Jurassic of France and Bavaria. Fossil remains of Amia itself occur in the Eocene of northern Europe and North America. It apparently became extinct in Europe at the close of the Lower Miocene. (Forbes and Richardson, page 37). To-day it is the only surviving member of a family of Mesozoic ganoids which then included many other genera, e.g. Megalurus from the Upper Jurassic, and Eurycormus and Liodesmus from the Jurassic. Dean claims especial interest for Amia "as most nearly the ancestral form of some, if not all, of the recent teleosts". (B. Dean, 1896).

Food.

Amia calva is a voracious species living almost entirely on an animal diet, which can be correlated with the short length of the intestine. The main item of diet is minnows and other small fish, but it also eats crawfish, molluscs, insects, and larvae. It is interesting to note that a large variety of articles have also been found in the digestive tract. These include a penny, a spoon, and large pieces of raw potato.

Breeding Habits.

The main facts concerning the breeding habits have been taken from Dean's paper on the early development of Amia.[1]

1. Dean "The Early Development of Amia". 1896.

The breeding season is between April the fifteenth and June the first, depending on the warmth of the days. At this season the fish, particularly the males, are brightly coloured, and may be seen migrating in great numbers from the deeper waters where they have passed the winter in a sluggish state, to the shallower breeding grounds. The fish, in groups of one female and several males, remain in the shallow waters sunning themselves for some time. Then they choose a swampy place where there are many reeds and begin at once to swim round and round in a circle until they have bent or broken all the reeds and laid them in a circular nest, roughly resembling a bird's nest. This procedure usually takes place in water of about one foot in depth in a well-sheltered place.

The nest is prepared early, and after a time the eggs and sperm are emitted simultaneously. The fish would appear to rub together to some extent, for scales are often found in the nest. A million eggs may be laid all at once, or at intervals. A single male guards the nest very closely, either by swimming round and round it, or by actually resting in it. This circular movement which keeps the water in motion may serve to aerate the eggs, and also to keep sediment out of the nest.

The eggs hatch in one to four days. The newly-hatched fish are described as having a large yolk sac, and a pre-oral sucker for attachment. Soon after hatching the whole swarm disappears with the male. It is suggested that they may stick to him during the migration. (Dean 1896, page 420). When they return to the nesting ground they are from five-eighths to one and one-half inches long. They remain near the nest for a short time again, and finally are gathered together once more by

the male and taken out to the deeper waters. The males show remarkable audacity while caring for their young. It is said that they will even allow a boat to touch them before leaving the young in time of danger.

IV. ANATOMY.

Skeleton.

The bones of Amia are completely ossified and the vertebrae are amphicoelous as in the Teleostei.

The skull is encased in an armour of bony plates barely covered by skin. This is one of the particularly primitive features of Amia calva. The external surface of these plates is ridged and furrowed by the sensory glands which are in the skull. The jaws are remarkably strong and complex. The U-shaped mandible has the primitive ganoid gular plate between its rami. This gular plate is ridged like the skull bones, but in a radiating pattern. The mandibles are not protractile. Lateral gular plates are present as ten branchiostegal rays, attached by cartilage to the ceratohyal bone. The vicious appearance of the fish is enhanced by the presence of sharp teeth covering much of the interior surface of the mouth. The largest of these conical teeth are on the premaxillae, maxillae, dentaries and palatines; while smaller ones are on the vomers, pterygoids, and paraspenoids.

Two pairs of small, superficial, serrated appendages are present in the skin covering the branchial skeleton. (Plate 2). The function of these ossified appendages has not yet been ascertained. They are partially hidden by the operculum, and may serve to close the gill chamber more tightly when the animal is taking air into the air-bladder. Wilder has described these appendages in detail in one of his papers on Amia.[1]

1. Wilder, B. G., "Serrated Appendages of the Throat of Amia".

Digestive System.

The digestive tract is short and broad. It has but one curve in it - an S-curve ventral to the air-bladder. The total length would probably not exceed that of the whole fish. There are no pyloric caecae such as are present in the other ganoids and teleosts. The rectum is provided with a reduced spiral valve of three or four turns, similar to the one found in Lepidosteus, Acipenser, Polypterus and the Dipnoi. There is no cloaca, but a separate anus and urinogenital aperture. All of these features bespeak the primitive nature of the fish.

Excretory System.

The excretory system is mesonephric, for the pronephros atrophies early (Dean, "Fishes Living and Fossil", page 271). The mesonephric bodies are grey in colour and lie in parallel position one on either side of the dorsal aorta. They are long and narrow extending from the transverse septum to the level of the anus. It is interesting to observe that there is a large posterior development of the mesonephric bodies behind the anus. This posterior part of the kidney is a triangular retroperitoneal organ which lies just caudal to the posterior end of the body cavity in a post-anal recess. It is well supplied with blood from a rich network of blood vessels which are branches of the right posterior cardinal vein, the renal portal vein (which has no direct connection with the former) and the dorsal aorta. According to Goodrich, a primitive feature in Amia calva is the presence of nephrostomes or mesonephric funnels opening directly into the coelom from the kidney.[1] The ureters open into a pair of small urinary bladders.

1. Goodrich "Structure and Development of Vertebrates", page 662.

Reproductive System.

The sexes are separate. The sperm pass out through the sperm duct and the dilated portion of the segmental duct, and to the exterior by the urinogenital aperture. The eggs fall into the coelom whence they find their way into the Müllerian ducts, and escape in the same way as the sperm.

V. AIR-BLADDER AND CIRCULATION.

It is a well known fact that Amia can live for some hours out of water. The reason for this is that it takes in air not only by the gills, but also through the air-bladder which functions as a lung. Wilder has shown by experiment that when water in which an Amia is kept becomes warm or foul, the fish will rise to the surface often and take in gulps of air.[1] It is interesting to note, however, that if the water is kept cool and pure Amia can live, apparently quite comfortably, without this accessory means of respiration.

The air-bladder in a fresh specimen of Amia (Plate 3) is a large, reddish, spongy organ, somewhat resembling the lung of a frog in appearance. Like the amphibian lung it is soft and cellular, though of course very much larger in every way. It is a median dorsal retroperitoneal organ lying between the gut and the dorsal aorta. It extends from the transverse septum to the level of the anus, and is shortly bilobed in the front, tapering to a point posteriorly. An outer sheath of striated muscle covers the bladder and extends for a short distance over the stomach, thus attaching the bladder to the gut. An inner sheath of tissue lines this outer sheath. The bladder is connected with the dorsal side of the oesophagus by a short but broad pneumatic duct.

Internally the bladder is provided with a double row of muscular trabeculae which extend from the dorsal to the ventral wall. From each of these trabeculae branched and alveolated septa extend to the

1. Wilder, B.G., "Respiration of Amia".

lateral walls, thus dividing the bladder into two rows of six chambers with a central corridor between them. Small thin-walled vascular alveoli in each chamber give a honey-combed appearance to the inner surface of the bladder.

The arterial blood supply is a pair of pulmonary arteries derived from the last efferent branchial (embryonic sixth) (Plate 4). These arteries leave the branchial at the upper end of the gill slit. They pass posteriorly dorsal to the ducts of Cuvier, and emerge near the level of the glottis to run along the ventral surface of the bladder inside the inner sheath.

Blood is collected in two ventral pulmonary veins which lie immediately beside the arteries inside the bladder. The arteries and veins break up into smaller and smaller vessels which remain side by side throughout their course in the air-bladder (Plate 3). These blood vessels, particularly the very small ones, run in the walls of the septa and around the edges of the alveoli, and beside the trabeculae, thus rendering the whole surface a complicated vascular network. There is a considerable amount of anastomosis between the arteries of the two sides of the bladder, and also between the veins.

The two pulmonary veins leave the bladder at the anterior end, passing along either side of the oesophagus till they reach the level of the ducts of Cuvier. There they turn away from the oesophagus to enter the inner side of their respective duct of Cuvier. These veins lie under the coelomic epithelium, as would be expected since the bladder is a retroperitoneal organ. (Plate 5).

Although the two pulmonary veins each enter one duct, there is evidence to suggest that little blood passes into the right duct from the right pulmonary vein. Soon after the pulmonary veins leave the air-bladder they are joined by a bridge dorsal to the oesophagus. (Plate 6, Figs. 1 and 2). This pulmonary connective vessel is as broad as the veins themselves, and provides for a flow of blood between the right and left pulmonary veins. Beyond the bridge in the anterior direction the right pulmonary vein becomes very much narrower than it was posteriorly. As it approaches the duct of Cuvier a large pocket valve, opening posteriorly, is seen in its wall. (Plate 6, Fig. 1). When distended with blood this valve could readily prevent blood from flowing past it into the duct of Cuvier. Blood must therefore pass dorsal to the oesophagus by the pulmonary connective vessel into the left pulmonary vein, and travel thence to the duct of the left side. At the point of entrance of the pulmonary connective into the left pulmonary vein, the opening is divided into two by a fibrous pillar which lies diagonally across the opening (Plate 6, Fig. 2). This is an interesting structure whose function has not yet been discovered.

Thus the flow of pulmonary blood is largely directed to the left, so modifying the circulation as to permit a partial separation of pulmonary and systemic blood analogous to that found in the Dipnoi, as will be seen later.

The modification of the circulation does not stop here, however. Adaptations for separation are also seen in the other large veins entering the sinus venosus and ducts of Cuvier.

The right posterior cardinal vein arises from the right longitudinal mesonephros, and also from the large posterior mesonephros in the post-anal recess. (Plate 7). The right is a much larger vein than the left posterior cardinal which actually communicates most of its blood to the former by a system of seven connecting vessels which lie ventral to the aorta. Only a very short portion (approximately one-third) of the left posterior cardinal carries blood to the left duct of Cuvier. Only a very small branch of the left posterior cardinal receives blood from the posterior mesonephros. It is not uncommon for the two posterior cardinals to communicate or even anastomose during development[1], but in this case the communication serves a distinctly useful purpose.

It is obvious that most of the blood from both the left and right mesonephroi is returned to the right duct of Cuvier, and that very little returns to the left duct. Thus most of the blood flowing into the right duct of Cuvier is systemic or venous blood, while most of that flowing into the left duct is pulmonary and therefore somewhat oxygenated.

The other veins entering the ducts of Cuvier are the anterior cardinals and the gonadial veins and are the same on both sides. (Plate 5). The anterior cardinal enters each duct at the distal border, and is a combination of three veins which unite just prior to entering the duct. The entry of the anterior cardinal into each duct is directly opposite the entry of the posterior cardinal and gonadial vein. The latter vein runs outside the coelomic epithelium until it reaches the

1. G. Kerr "Text-Book of Embryology", Vol. II, page 410.

level of the duct of Cuvier where it passes through the coelomic epithelium to enter the duct in almost exactly the same place as the posterior cardinal. In fact, in the left duct, where the latter vein is small, the blood from both enters a common vestibule, passing thence into the duct as one stream.

The separation of pulmonary from systemic blood in the ducts of Cuvier would be of no avail if it were permitted to mix again in the sinus venosus. Here a further adaptation assures the continued separation of the two streams.

Just dorsal to the entry of the two hepatic veins in the floor of the sinus venosus is a large white fibrous plug which projects into the lumen of the sinus. (Plates 8 and 9). It lies directly opposite to the enlarged dorsal member of the three sino-atrial valves. The latter valve forms an endocardial cushion which touches the hepatic plug. (Plates 9 and 10). The sinus venosus is thus roughly divided into two parts. The blood from the ducts of Cuvier descends into the sinus venosus. That from the left duct, which is mainly pulmonary, flows into the left side of the sinus venosus; while that from the right, which is mainly systemic, flows into the right side.

The hepatic plug, rising like a wall behind the openings of the hepatic veins, serves also to divert the hepatic blood to the right. That it is diverted to the right, and not to the left, is strongly suggested by the fact that the opening of the left lateral vein into the sinus venosus is very close to the left side of the plug, tending to place a further barrier to the hepatic stream in that direction. (Plates 5, 8, 9 and 11).

The left lateral vein drains a much smaller area of the body wall than does the right; in fact the right vein receives a large branch from the left side in the anterior abdominal region. (Plate 11). The left lateral vein passes anteriorly to the level of the left duct of Cuvier where it receives the subclavian vein from the pectoral fin and pectoral musculature, a pericardial vein from the median region of the tissue covering the heart ventrally and another from the muscle dorsal and lateral to the heart. (Plate 5). This composite vein runs along the floor of the sinus venosus to enter, as previously noted, very close to the left border of the hepatic plug. The opening of this vein into the sinus is very much enlarged and resembles a large cup-shaped valve. The enlargement and valve-like appearance of the opening of the vein further support the view that it serves as a barrier for the hepatic blood. It was noted very early in this investigation that the blood from the left lateral vein, in a fresh fish, can be seen flowing into the right side of the sinus venosus in front of the plug.

The right lateral vein is much larger than the left. It receives the left subclavian vein and one from the muscle lateral and dorsal to the heart. It crosses the floor of the sinus, and opens into it not far from the hepatic veins. The opening of the right lateral vein into the sinus is not enlarged as is that of the left one, and it is not applied to the border of the plug. The blood from it is free to enter the right side of the sinus venosus directly.

Thus it would appear that there is a separation of the blood in the sinus venosus into two parts, the left being that from the left

duct of Cuvier which is mainly pulmonary or oxygenated blood; the right, from the right duct, the hepatic veins, and the two lateral veins, is largely systemic or venous blood.

In the atrium this separation is maintained by an incomplete lace-like septum which hangs from the dorsal wall, but is free ventrally. It is formed from the fibrous supporting cords of the largest of the three sino-atrial valves, which was previously referred to as the endocardial cushion. The net-work of cords runs from the anterior side of the valve to the atrio-ventricular opening. The other valves of the heart are of course also provided with fibrous supporting threads which extend between them and the atrial wall. Their development does not compare, however, with that of the larger valve and actual septum. This septum divides the atrium roughly into a right and a left half.

There is no immediate evidence of the separation of blood being continued in the ventricle. No actual partition is present which would divide the ventricle into right and left halves. The inner wall is, however, provided with many ramifying muscular strands and strong fibrous pillars between which are deep indentations into the muscular wall. (Plates 10 and 12). A similar adaptation in the frog serves the purpose of separating the blood, and very likely has the same function here.

There is no twisting of the bulbus or conus arteriosus or their valves. The wall of the conus is provided with two tiers of three small, muscular, cup-shaped valves which open anteriorly. The presence of these valves appreciably lessens the diameter of the passage between the

ventricle and the bulbus. Anterior to these valves lie two very large deep pocket valves, one dorsal and one ventral, in the walls of the bulbus. They arise at the anterior border of the smaller valves and extend for nearly the full length of the bulbus. Each valve is a rectangular body, tapering to a blunt point at the anterior end. The base and sides are continuous with the wall of the bulbus, while the pointed anterior end is continuous with a fine meshwork of cords on each side, which in turn is attached to the wall of the bulbus. The presence of the meshwork increases the width of the valve at the top and permits a wider gape to the mouth. Two hard fibrous ridges lie between the two valves. (Plate 12).

Leaving the bulbus arteriosus blood passes into the ventral aorta. There are four afferent branchial arteries to the branchial arches. Their relation as they leave the aorta is rather unusual. (Plate 13). The third and fourth arise nearest the conus as a single vessel which is somewhat dorsal in position. This vessel later divides into the third and fourth branchials. The second leaves at almost the same level as the combined third and fourth, but slightly ventral to it. At some distance anteriorly, the aorta divides completely into two branches giving the right and left first afferent branchials.

The first efferent branchial gives off a hyoidean artery ventrally and anteriorly. Dorsally, i.e. at the upper end of the first branchial arch, it gives off a common carotid artery and a hypopercular artery before joining the corresponding vessel of the other side to form the dorsal aorta. The second efferent branchials join the aorta directly. Ventrally the second efferents join to form the median hypobranchial artery below the

ventral aorta. This artery has an anterior mandibular branch, and also a coronary branch to the heart.

The third and fourth (embryonic fifth and sixth) efferent branchials do not join the dorsal aorta. The third efferents join a median branch of the dorsal aorta to form the coeliac artery. The fourth efferents turn in a posterior direction from the upper end of their branchial arches to form the pulmonary arteries. A short bridge joins the third and fourth efferents at the upper end of the arch. It would appear that blood flows from the third to the fourth efferent across this bridge, but this has not been ascertained. The subclavian arteries arise from the dorsal aorta, just anterior to the origin of the aortic branch of the coeliac.

It is interesting to note that the whole somatic arterial circulation including the vessels to the brain, heart, and striped musculature of the body comes from the first two efferent branchial arteries. The third and fourth efferents, on the other hand, send blood to the viscera and air-bladder. (Plate 13). (A certain amount of the visceral blood is supplied also by the dorsal aorta).

The explanation for this manner of division of function of the efferent branchials is at first a little obscure. Consideration of the condition found in certain Amphibia and reptiles may serve to throw light on the question. In the Alligator where the heart is completely four-chambered, the pulmonary arteries and the left systemic arch arise together from the right ventricle (Plate 14). Blood in the left systemic arch then as well as in the pulmonary arteries is deoxygenated, except for the small amount which enters by the Foramen of Panizza.

Blood from the left ventricle is pumped out through the right systemic which gives off the carotid and subclavian arteries. This blood is oxygenated except for a small quantity which passes through the Foramen of Panizza from the right systemic. Instead of joining the left systemic, the right continues separately as the aorta while the left forms the coeliac artery. Where they should join, a tiny bridge vessel only is present.

The oxygen requirements of various tissues differ very considerably. Those requiring most oxygen are nerve tissue, - especially the brain, - and cardiac and striated muscle, while smooth muscle and viscera require little. "Asphyxia affects nerve tissue first, striped muscle next, and other tissues afterwards."[1] This is well illustrated by the above reference to the condition found in the Alligator. Oxygenated blood goes to the head (by the carotids), and to the striped muscle (by the aorta), while deoxygenated blood goes to the lungs and viscera. The viscera do require a very large volume of blood, but that blood need contain very little oxygen.

With these facts in mind it is readily seen that the oxygen content of the blood in the third and fourth branchial arteries of Amia need not contain a high percentage of oxygen. On the other hand, the oxygen content of the blood in the first and second branchials must be relatively high since they supply blood for the brain as well as striped and cardiac muscle. (The difference in extent of gill surface between the third and fourth, and first and second branchial arches, though considerable, is not sufficient to account for the probable differences in O_2 content).

1. Wynne-Edwards and Graham, MS.

Some process of continued separation must therefore take place as the blood is sent out of the heart.

No division is present in the ventral aorta to bring about this separation. The existence of a pressure gradient has been previously suggested as the most likely means of separation.[1] "In man the arterial pressure in the aorta is five times the pressure in the pulmonary arteries. In the frog the so-called carotid gland is evidently designed to raise the pressure in the base of that artery above the arterial pressure of the aorta, so that the oxygenated blood from the left auricle, which remains last in the ventricle as it contracts, is only ejected at the peak of ventricular pressure. By that time the pulmonaries and systemics are already full, and thus the last and richest blood is forced into the carotids."[1]

In view of the fact that the aortic pressure is always higher than the pulmonary in the Amphibia and Amniotes, it is likely that a similar relation exists in Amia. That the gill filaments, and hence presumably the capillaries, in arches one and two are more numerous than in three and four further substantiates this probability, since the larger number of capillaries would cause a higher pressure in the afferent aortic arches (one and two). The deoxygenated systemic blood from the right almost certainly leaves the ventricle in front of the oxygenated blood from the left. The first blood to be sent out would enter the vessel offering least resistance, namely, the combined third and fourth afferent. The oxygenated blood, sent out last, at the height of the pressure of contraction would be forced into the aortic

1. Wynne-Edwards and Graham, MS.

arches.

There is every probability that some such pressure gradient does function in Amia. This process then completes the system of adaptations which are present in this fish for the purpose of maintaining the separation of oxygenated from deoxygenated blood, so as to use each to the best advantage in the animal's economy.

Before discussing the significance of the features of the air-bladder and circulatory system of Amia calva, it is necessary to consider the air-bladder in its simplest form, that is, as it is found in the Teleostei, and again in its most complex form as the "lung" of the Dipnoi and Polypterus.

VI. AIR-BLADDER AND CIRCULATION IN THE TELEOSTEI.

Structure.

The air-bladder of the true bony fish is a simple, usually single, hollow, retroperitoneal organ, situated dorsal to the alimentary canal and ventral to the dorsal aorta. It is an elongated, membranous sac which, unlike that of Amia, is usually taut when fresh, and is often pigmented and black or silvery in appearance. It is present in practically all bony fish, with the exception of the adult Pleuronectidae, and certain other bottom-living forms. Goodrich states that the free-swimming larvae of these fish possess the air-bladder.[1]

The air-bladder arises as a mid-dorsal evagination from the walls of the oesophagus, just behind the region of the gill clefts. The developing bladder grows backwards, burrowing its way into the splanchnocoele, and often carrying its connection with the oesophagus some distance from its original position. "In many fishes the dorsal wall of the air-bladder bulges out in a headward direction forming a diverticulum which may reach a great size, so that in the adult the organ has the appearance of being composed of two segments marked off from one another by a constriction, the pneumatic duct communicating with the hinder one of the two."[2] This condition is well seen in the carp (Cyprinus sp.).

The bladder may remain connected to the oesophagus by a long or a short pneumatic duct, or the duct may atrophy, or become a solid

1. Goodrich "Structure and Development of Vertebrates," page 587.
2. Kerr, G. "Text-Book of Embryology," Vol. II, page 166.

rod. The Teleosts are divided into two groups according as they do or do not possess an open pneumatic duct to the air-bladder. The Physostomi are characterized by the presence of an open duct, while in the Physoclisti the duct is either absent or a solid rod in the adult, though always present in the embryo. In the former group are included the carp, salmon andeel; in the latter, the cod, bass and perch. According to Hall, however, "the basis for the distinction between the two groups is far from invariable and many exceptions occur in both."[1]

Function.

"The variety of functions performed by the air-bladder is perhaps greater than that of any other organ possessed by fish."[1] This variety of functions includes 1) hydrostatic effects, 2) respiration, 3) sound production, 4) accessory audition.

It was noted in the introduction that the most important function of the air-bladder in most modern Teleosts is considered to be that of an hydrostatic organ. It permits the fish to adjust its specific gravity to that of different levels of water. This adjustment is possible only within limits. If a fish be brought up rapidly from great depths, the air-bladder expands so much that it prevents the fish from moving. The gases cannot escape through the pneumatic duct or be absorbed into the blood with sufficient rapidity to prevent the extreme expansion. Conversely, if a fish goes to great depths very rapidly it often cannot increase the size of its air-bladder quickly enough, and so continues to sink to the bottom. If the bladder be pricked the fish can still swim,

1. F.G. Hall, "Functions of the Swimbladder of Fish", 1924.

but it is confined to a definite stratum of water where the pressure fits its specific gravity.

Blood Supply.

The method of gas exchange which allows for the expansion or contraction of the hydrostatic air-bladder in the higher teleosts is concerned with the circulatory system of the bladder. Among the more primitive teleosts and the ganoids air is taken in and expelled by way of the mouth, gullet and pneumatic duct.

For the most part gas is increased in the bladder by secretion from the blood and is reabsorbed by the blood. Definite oxygen-secreting and oxygen-absorbing areas tend to develop. These are usually anterior and posterior respectively, and occupy definite chambers. According to Goodrich the secreting areas or "red bodies" in the simpler forms possessing the pneumatic duct usually consist of a thin layer of internal oxygen-secreting epithelium which is in more or less close contact with a "rete mirabile" or capillary net of arteries and veins which do not communicate until they reach the gland.[1]

In the physoclistous forms, the "rete mirabile" is covered with a thick glandular epithelium which is thrown into folds or sunk into crypts, and is called the "red gland". The rest of the anterior chamber of the bladder is lined by thick impermeable tissue covered internally with simple epithelium. The posterior absorbing area seems

1. Goodrich "Structure and Development of Vertebrates".

to be derived from the pneumatic duct itself. It is lined by thin epithelium, through which oxygen can pass to the blood vessels overlying it. In more specialized forms the absorptive area becomes confined to an oval which can be closed off by a circular fold provided with sphincter and dilator muscles.[1]

The blood supply to the air-bladder of the Teleosts is relatively simple. The red-glands receive blood from the coeliac artery and return it to the hepatic portal vein. The absorptive areas receive blood from the dorsal aorta and return it to the right posterior cardinal vein.

1. Goodrich "Structure and Development of Vertebrates".

VII. AIR-BLADDER AND CIRCULATION IN THE DIPNOI AND POLYPTERUS.

Dipnoi.

The air-bladder of the lung-fish is dorsal in position, as it is in the Teleosts. It is single in Ceratodus, but bilobed in Protopterus and Lepidosiren. The pneumatic duct is broad and open, and passes ventrally round the right side of the oesophagus to enter it ventrally. The left pulmonary artery also passes over the left side of the oesophagus, runs ventral to it and emerges at the right side where it enters the air-bladder sending a branch to each lobe. This artery supplies blood to the ventral surface of both lobes. The right pulmonary artery passes directly to the dorsal surface of the air-bladder where it also sends a branch to each lobe. That the bladder was originally ventral is clearly shown by the path followed by the left artery and also by the twist in the oesophagus where the pneumatic duct has pulled it to the right. These features were clearly visible in a dissection of a specimen of Protopterus.

Function.

The function of the air-bladder in the Dipnoi is respiration. The respiratory bladder here exists in its most perfect form among fish. Protopterus lives in the rivers of Central Africa where yearly drought necessitates a period of aestivation. During this time the fish can obtain only atmospheric air. It buries itself in a mud and slime cocoon and breathes by means of its air-bladder or "lung". The

Australian lung-fish Ceratodus cannot live out of water, but its air-breathing "lung" enables it to supplement its gill respiration by rising to the surface to take in gulps of air when the water is foul with sand or rotting vegetable matter. Very little is known of the habits of the Amazon lung-fish Lepidosiren.[1]

Structure.

The structure of the lung of the Dipnoi resembles that of Amia internally. Though the lung of the Dipnoi is somewhat smaller, it is much more compact in form. The number of trabeculae and septa is much greater, and thus the lung is divided into many more chambers. The lobes of the bladder of Protopterus are considerably more lung-like in appearance than the single bladder of Amia. They are long and narrow, lying close to the dorsal aorta and extending from the level of the lowest gill cleft to the anus.

Blood Supply.

The arterial blood supply comes from a pair of pulmonary arteries arising from the last branchial arches (embryonic 6th).

The two pulmonary veins unite to form a single large vein, which enters the left side of the heart. The blood which is thus returned to the heart has been somewhat oxygenated by contact with the air in the lung. Adaptations in the dipnoan heart serve the purpose of separating the blood into two streams, the oxygenated being sent to the arteries of the head and striated musculature. These adaptations take the form of

1. Thomson, "Outlines of Zoology".

valves in the conus and bulbus arteriosus, and plugs or septa in the auricle and ventricle.

Polypterus.

All the features of the air-bladder and its blood supply are essentially the same here as in the Dipnoi. The bladder is bilobed forming two "lungs" as in Protopterus, but the right one is larger than the left. The "lungs" open into the oesophagus ventrally by way of a short, common pneumatic duct. They ascend on either side of the gut and lie lateral to it. Only the apex of the right "lung" which is some distance posterior to that of the left is dorsal in position, having shifted towards the mesial plane for the sake of balance. The pulmonary vein does not enter the heart directly, but empties into the hepatic vein. Since no evidence of division is present in the auricle, ventricle or conus, it would appear that separation of blood is less efficient here than in the Dipnoi.

VIII. DISCUSSION.

Origin of the Air-bladder.

The question of the origin of the hydrostatic air-bladder has long been a controversial one. The problem arises as to whether the hydrostatic function was the primitive one or has been secondarily acquired. The view now most commonly held is that the original function was a respiratory one. This is upheld by the fact that all primitive fish existing at the present time, with the exception of the sturgeon (Acipenser) and the paddle-fish (Polyodon) do use the lung for respiratory purposes.

Several theories have been advanced by way of attempting to derive the hydrostatic and respiratory bladder from a common ancestor. The lungs of some of the amphibia arise as a pair of ventral pharyngeal pouches resembling a seventh pair of gill rudiments. Spengel (1904) believed that the lungs originally arose from the union of such branchial pouches below the gut, while the air-bladder arose from a similar union dorsally above the gut.[1]

According to a theory advanced by Norman, the air-bladder arose as a respiratory organ when, at some Paleozoic time, the supply of oxygen in the water was insufficient for successful gill breathing. He visualizes a time when, with improved conditions, some fish no longer required the bladder for accessory respiration, and it began to serve a

1. Goodrich "Structure and Development of Vertebrates".

hydrostatic function. Other fish preserved it as a lung, and using it more and more, became the ancestors of the air-breathing amphibia.[1]

It is probable, however, that only two species of fish acquired the expansion of the gullet which he describes, and that one of these gave rise to the Dipnoi, while the other gave rise to the teleostomes. Since it is generally accepted that the amphibian lung and that of the higher vertebrates either arose from the dipnoan "lung" or that of a common ancestor, this theory would rule out the possibility of homology between the hydrostatic air-bladder and lungs of higher forms.

Homology of Air-bladder and Lungs.

The theory most generally accepted to-day is, however, that air-bladder and lungs are homologous. According to Kerr (1919) and Ballantyne (1927) the right lobe of the dipnoan lung has migrated up the right side of the oesophagus to form the single dorsal hydrostatic air-bladder, while the left lobe has disappeared. At first sight it does seem probable that some such relation does exist between air-bladder and lungs, and one might conclude with Ballantyne (1927), Kerr (1919) and Morris (1885), that it is impossible not to accept the view that air-bladder and lungs are homologous.

The importance of the anatomical features found in Amia here becomes evident. The hydrostatic bladder of the true bony fish is a simple sac which is dorsal in position and opens dorsally into the oesophagus, while that of the Dipnoi is a true lung which, though dorsal

1. Norman "History of Fishes".

in position, opens ventrally into the oesophagus. Amia appears to be the link between these two, for its air-bladder is dorsal in position and opens into the oesophagus dorsally, but it is a true lung whose anatomy and blood supply closely parallel that of the Dipnoi. Both Amia and the Dipnoi use the bladder as a respiratory organ. In both it is well chambered and trabeculated, with a complicated system of blood vessels and capillaries in the walls. Blood is supplied in both cases by a pair of pulmonary arteries from the last branchial arch. Numerous adaptations in the heart and large vessels provide for separation of blood in both cases.

It would seem that a complete series could be readily built up illustrating the homology between air-bladder and lungs.

Polypterus may represent the most primitive of the lung-breathing fish since the ventral position of its "lungs" and the presence of pulmonary arteries place it as most nearly ancestral to the Amphibia. In the Dipnoi the pulmonary arteries are still present and the lungs, though still opening ventrally into the oesophagus, are dorsal in position. Various adaptations to separation of blood are here met with. In Amia the pulmonary arteries are again present, and also adaptations to separation of blood, but the "lung" has assumed a dorsal position, and opens dorsally into the oesophagus. In Lepidosteus the pulmonary arteries are replaced by branches from the aorta, but the lung is again dorsal, and adaptations to separation of blood are still present. Finally, in the true bony fish the air-bladder is dorsal in

position, is no longer a "lung", and is supplied with blood by the coeliac artery and branches of the dorsal aorta.

It may be, on the other hand, that Amia represents a primitive generalized stock from which arose three distinct branches - the Amphibia, the Dipnoi, and the Teleostomes.

IX. COMPARATIVE ANATOMY OF THE PULMONARY CIRCULATION.

At first sight it seems evident that *Amia* has many features which closely relate it to other forms. Its lungs, pulmonary arteries, pulmonary blood return to the left side of the heart, and its inter-auricular septum all find parallels in the Dipnoi and Urodele Amphibia. Superficially these similarities do exist, but, on closer examination, they prove to be parallel adaptations.

Lepidosteus is probably the closest living relative to *Amia*. It resembles the latter in the possession of a dorsal lung which is similar in structure but more closely trabeculated. There the similarity ends. *Lepidosteus* possesses no pulmonary arteries. The lung is supplied with blood from a series of median branches of the dorsal aorta. Potter and Self (1934) have described the development of the posterior cardinal veins in relation to the air-bladder in *Lepidosteus*. They state that the right posterior cardinal vein is smaller than the left and that the pulmonary vein which receives blood from the posterior end of the air-bladder joins with a branch from the anterior end to enter the right posterior cardinal, and thus make up the largest part of that vein.[1] Pulmonary blood is thus returned to the right side of the heart, rather than the left. No actual pulmonary vein is present, but one of the posterior cardinals serves the purpose instead. Provision for separation of blood takes the form of complete division of the sinus venosus into two separate

1. G.E. Potter, and J. Teague Self (1934), Journal of Morphology, Vol. 56.

chambers each opening separately into the atrium. (Plate 15). A fibrous septum incompletely divides the atrium into right and left halves. This septum is attached ventrally to the wall of the atrium, rather than dorsally as in Amia.

Thus the adaptations of the respiratory system and heart, though ultimately serving the same purpose in Amia and Lepidosteus are evidently independent in origin.

A number of features of the vascular system of Protopterus closely resemble those of the Amphibia. These can only be the result of convergence since the primitive dipnoan Ceratodus does not possess them. Ceratodus does not possess the interauricular septum, and the spiral valve in the conus is very poorly developed. These structures must therefore have been separately acquired in the Amphibia and higher Dipnoi. The atrio-ventricular plug of the Dipnoi is characteristic only of that group. Lepidosiren and Protopterus even show an advance on the amphibian condition in the possession of the interventricular septum.

Amia is so well equipped with adaptations to aerial respiration and separation of pulmonary from systemic blood that it is well called the North American lung-fish. Nevertheless, although the adaptations follow the same general lines as those in the Dipnoi, they differ very much in actual detail. The hepatic plug is very characteristic of Amia as is also the pulmonary connective vessel above the oesophagus. The septum in the atrium differs in origin from such a structure in any other fish. The presence of the large endocardial cushion at the

sinoatrial opening, and its function in the division of the sinus venosus is unique in Amia. The bilateral symmetry of pulmonary arteries, and the great enlargement of the right posterior cardinal in comparison to the left, are all strikingly new features. Adaptations serving exactly the same ends are found in the Dipnoi, but it is obvious that they have been independently acquired in these fish.

Polypterus and Calamoichthys resemble the Dipnoi, in general, in the structure of the vascular system. Pulmonary blood is, however, returned to the hepatic vein rather than directly to the heart. The pulmonary arteries arise from the lower end of the last efferent branchial, rather than near the epibranchial confluence with the aorta as in the Dipnoi. No septa divide the atrium or ventricle and no spiral valve is present in the conus. Separation of blood is probably much less efficient here than in other air-breathing forms.

Adaptations of the heart and vascular system for the purpose of separating venous from pulmonary blood have thus followed five parallel, but independent, lines as exemplified by the Amphibia, Dipnoi, Polypterus, Amia and Lepidosteus. They may have arisen from some common ancestor in which the circulation was unadapted except for the possession of pulmonary arteries, since these are the only feature which they have in common. Even these differ considerably, in their position of origin from the last branchial arch. In Amia they arise from the upper end of the fourth efferent branchial, and may receive some blood from the third also. In Polypterus they arise from the lower end of the arch; in the Dipnoi from a median position near the confluence with the dorsal

aorta, receiving blood probably from the second and third branchials as well as from the fourth.

It is interesting to observe that extremely important differences exist between the group including the Amphibia, Dipnoi and Polypterus, and that including Amia, Lepidosteus and the Teleosts. These differences are so fundamental as to suggest that they have been distinct from very early times.

In the Amphibia, Dipnoi and Polypterus the opening of the glottis into the oesophagus is always ventral, and the lungs are bilobed or double. The pulmonary veins are ventral and enter into the hepatic vein, or, in the more specialized forms, into the atrium. The innervation is autonomic and, wherever it has been possible to check it, the muscles have proven to be smooth.

In Amia, Lepidosteus and the Teleosts, on the contrary, the bladder is dorsal and opens dorsally into the oesophagus. The pulmonary veins, though ventral, empty into the posterior cardinals or ducts of Cuvier, both of which are dorsal vessels. The muscles of the bladder, both of the external sheath and of the internal trabeculae are to a large extent striated. Innervation is to some extent autonomic, but largely spinal. Respiration, though assisted by gulping, is induced by voluntary contraction of the bladder, a condition unknown in the ventral bladder where respiration always involves the use of extrinsic muscles.

"Lungs and air-bladder are not the only pulmonary organs found

in fishes. The branchial or pharyngeal cavities are sometimes extended upwards to form air-chambers, as in Anabas and Ophiocephalus; or backwards, as in Clavia and Saccobranchus. In the latter the twin chambers extend through the abdominal cavity as far as the base of the tail. It is often the case that these accessory organs are associated like the air-bladder and lungs, with the last branchial arteries. In a number of other fish, including some South American Siluridae, oesophageal and intestinal respiration occur, and in one of the loaches (Misgurnus fossilis) the used air is finally voided at the anus. (Cambridge Natural History "Fishes" page 292)." [1]

Conclusions.

It is evident from the study of the comparative anatomy of the pulmonary circulation in the air-breathing fish that many structures which appear on first sight to be homologous have actually arisen quite independently. "If air-bladder and lungs are homologous, and did arise as accessory respiratory organs, then their initial efficiency has been to a greater or less extent increased in each group by subsequent and independent adaptation of the heart and vascular system!" [1] It is more than likely, however, since independent adaptations for air-breathing, similar only in function, have arisen on several different occasions in fresh-water fish, that parallel adaptation best defines the relation between air-bladder and lungs.

1. Wynne-Edwards and Graham, MS.

X. SUMMARY.

1. Although much study has been given to the air-bladder of the true bony fish and the Dipnoi by various workers, practically no work has been done previously on the bladder and circulation of *Amia calva.*

2. *Amia calva* is a primitive ganoid fish, living exclusively in central North America. Its natural history, as well as its anatomy, exhibits many interesting features.

(a). *Amia* possesses an air-bladder which, like that of the Teleosts, is dorsal in position. Under certain conditions this air-bladder is used as a lung, and it is provided with typical pulmonary arteries identical with those in the Dipnoi and *Polypterus* as well as the land vertebrates.

(b). The right pulmonary vein is almost occluded and blood is detoured to the left pulmonary vein and thence to the left duct of Cuvier and left side of the sinus venosus.

(c). The left posterior cardinal communicates most of its blood to the right posterior cardinal by seven short cross veins which pass ventral to the dorsal aorta. Thus most of the systemic blood is returned to the right side of the sinus venosus.

(d). This separation is maintained in the sinus venosus by the presence of the hepatic plug which meets an endocardial cushion,

thus forming a rough partition.

(e). A thin lace-like septum is present in the atrium.

(f). There are four branchial arteries. The first two efferents form the dorsal aorta, the third helps to form the coeliac, while the fourth becomes the pulmonary artery. A pressure gradient probably differentiates blood going to these four branchial vessels.

3. The air-bladder of the Teleosts is a simple organ which may serve one of a number of different purposes; the most important is that of a hydrostatic organ. It is always dorsal in position, and opens dorsally into the oesophagus. It is supplied with blood from the dorsal aorta and coeliac artery, and returns it to the hepatic portal vein and posterior cardinals.

4. The air-bladder of the Dipnoi and Polypterus resembles a lung in structure and function. It is chambered and alveolated inside, and provided with a thick net-work of capillaries. It is dorsal in the Dipnoi and ventral in Polypterus, but in each case it opens ventrally into the oesophagus. Blood is supplied to it by a pair of pulmonary arteries from the fourth efferent branchial vessel, and leaves it by way of a pair of pulmonary veins which unite and enter either the hepatic vein or the atrium.

5. The air-bladder of Amia seems, on first sight, to show the homol-

ogy of air-bladder and lungs. Closer consideration of the comparative anatomy of the bladder and its circulation in many different fish, however, points to parallel adaptation, rather than homology, as the relation between air-bladder and lungs.

XI. CLASSIFICATION.

(From Goodrich "Structure and Development of Vertebrates.")

Class Pisces

Subgrade Osteichthyes

Subclass Dipnoi

Lepidosiren, Ceratodus, Protopterus

Subclass Teleostomi

Division Actinopterygii

Subdivision A

Order Chondrostei

Suborder Acipenseroidei

Order Polypterini

Polypterus, Calamoichthys

Subdivision B Holostei

Group a

Order Amioidei

Amia calva *

Order Lepidosteoidei

Lepidosteus

Group b Teleostei

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XIII. LIST OF PLATES.

Plate 1.

Amia calva

Plate 2.

Figure 1. Dorsal view of the head of Amia showing nasal cavity and anterior nostril at end of barbel.

Figure 2. Ventral view of the head showing gular plate, branchiostegals, and serrated appendages of the throat.

Plate 3.

Circulation in the air-bladder of Amia.

Plate 4.

Diagram of the large arteries of Amia particularly the coeliac and pulmonaries, and also the pulmonary veins.

Plate 5.

Ventral dissection of anterior region of Amia to show the heart, ducts of Cuvier, and large veins.

Plate 6.

Figure 1. Right duct of Cuvier; right pulmonary vein, showing valve and connective vessel and fibrous pillar in *Amia*.

Figure 2. Left duct of Cuvier; left pulmonary vein and entry of connective vessel with fibrous pillar.

Plate 7.

Mesonephroi and posterior cardinal veins in *Amia*.

Plate 8.

Sinus venosus cut open to show entry of hepatic veins, and hepatic plug in *Amia*.

Plate 9.

Atrium and ventricle cut open ventrally to show the course of the two streams of blood in the heart of *Amia*. Also shows the relation between the hepatic plug and the endocardial cushion.

Plate 10.

Diagram of the inside of sinus venosus, atrium, ventricle and bulbus, showing the relation between the endocardial cushion and the

Plate 10 (cont'd).

hepatic plug, and also the septum in the atrium of Amia.

Plate 11.

Dissection showing of the right and left lateral veins of Amia.

Plate 12.

Auricle, ventricle and bulbus cut dorsally to show the inner wall of the ventricle, the partition in the auricle and the pocket valves in the bulbus and conus of Amia.

Plate 13.

Diagram of heart and afferent and efferent branchial arteries in Amia.

Plate 14.

Diagram of ventricles and great vessels from the ventral aspect in Alligator.

Plate 15.

Dorsal view of the heart and sinus venosus of Lepidosteus cut open to show the division of the sinus and the septum in the auricle.

XIV. INDEX TO PLATES.

Plate 3.

int., intestine; L. pul. V., Left pulmonary Vein; L. pul. A., Left pulmonary Artery; R. pul. V., Right pulmonary Vein; R. pul. A., Right pulmonary Artery.

Plate 4.

a b, air-bladder; c. car. a., common carotid artery; d. ao., dorsal aorta; ef'., first efferent; gl., glottis; g.v., gonadial vein; l.a.c., left anterior cardial vein; l.p.c., left posterior cardinal vein; l.p.v., left pulmonary vein; scl. a., subclavian artery.

Plate 5.

C.a., Conus arteriosus; Hep. vv., Hepatic veins; Hep. plug, Hepatic plug; L.D. Cv., Left Duct of Cuvier; L. Gon. V., Left Gonadial Vein; L. Lat. V., Left Lateral Vein; L.P.C.V., Left Posterior Cardinal Vein; L. Pul. V., Left Pulmonary Vein; open.L.L.V., opening of Left Lateral Vein; open. R. Lat. V., opening of Right Lateral Vein; Pul. Conn. Vessel, Pulmonary Connective Vessel; Peric. VV., Pericardial Veins; R.A.C.V., Right Anterior Cardinal Vein; R.L. V., Right Lateral Vein; Scl. V., Subclavian Vein; S. Ven., Sinus Venosus.

Plates 6 and 7.

D. Ao., Dorsal Aorta; Pul. Conn. Vessel, Pulmonary Connective Vessel; R. Ant. Card. V., Right Anterior Cardinal Vein; R. Gonad.V., Right Gonadial Vein; R. Post. Card. V., Right Posterior Cardinal Vein; R. Pul. V., Right Pulmonary Vein.

Plates 8 and 9.

Hep. VV., Hepatic Veins; Hep. plug, Hepatic plug; L. Duct. Cuv., Left Ductus Cuvier; open. of L. Lat. V., opening of Left Lateral Vein: open. of L. Post Card. V., opening of Left Posterior Cardinal Vein.

Plate 10.

See Plates 8 and 9.

Plate 11.

Br. of R. Lat. V., Branch of Right Lateral Vein; Hep. plug, Hepatic plug; Hep. V.V., Hepatic Veins; Left Lat. V., Left Lateral Vein; open. of L. Lat. V., opening of Left Lateral Vein; Peric. VV., Pericardial Veins; R. Lat. V., Right Lateral Vein; Scl. V., Subclavian Vein.

Plate 13.

A., Auricle; af., afferent; B.a., Bulbus arteriosus;

c.c.a., common carotid artery; coel. a., coeliac artery; cor. a., coronary artery; D. Ao., Dorsal Aorta; e.c., external carotid; ef., efferent; i.c., internal carotid; hy. a., hyoidean artery; hypop. a., hypopercular artery; hybr. a., hypobranchial artery; l.a.c.s., left anterior cardinal sinus; l.p.card. s., left posterior cardinal sinus; l. pul. a., left pulmonary artery; l. pul. s., left pulmonary sinus;, Mand. branch, Mandibular branch; scl. aa., subclavian arteries; S.V., Sinus Venosus; V. ao., Ventral aorta; V., Ventricle.

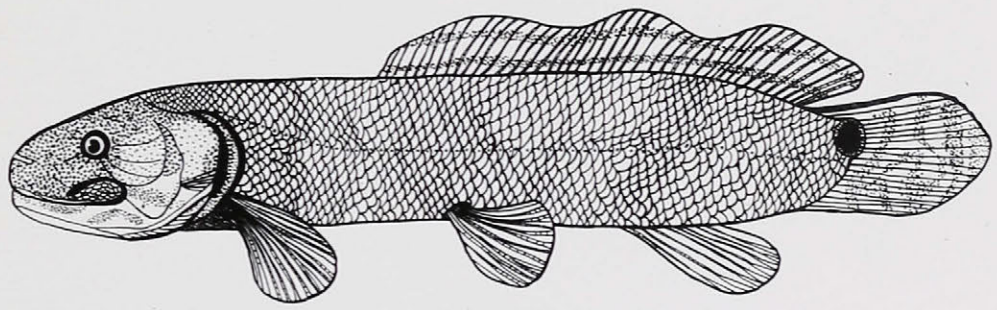
Plate 14.

Abd. Aorta, Abdominal Aorta; L. Dors. Carotid a., Left dorsal Carotid artery; R. Pul. a., Right Pulmonary artery; Subcl. a., Subclavian artery.

Plate 15.

Hep. V., Hepatic Vein; Left Ant.,Card.V., Left Anterior Cardinal Vein; Sin. Ven., Sinus Venosus.

Plates 1 and 2



Amia calva — the Bowfin ♂

Plate 1

Amia calva L.

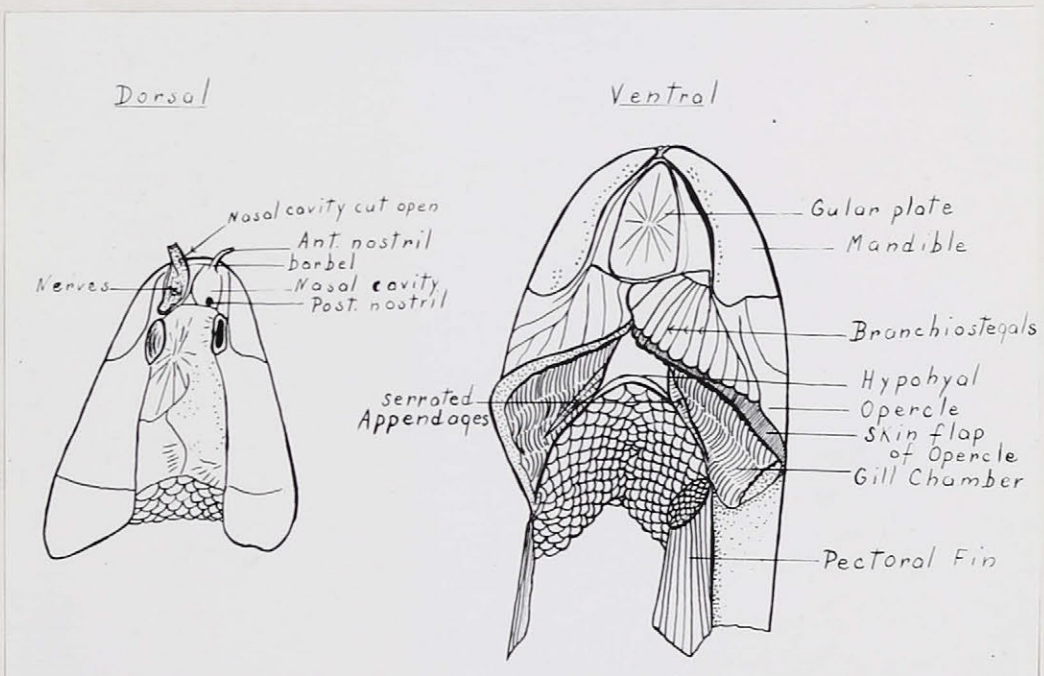


Plate 2

Dorsal and Ventral Views of Head

Plate 3

Circulation in Air Bladder

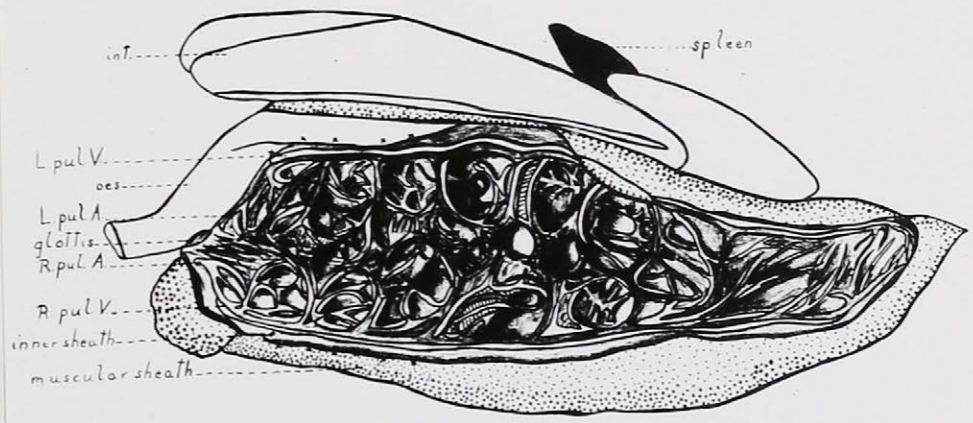


Plate 3

Amia calva

Circulation in Air Bladder

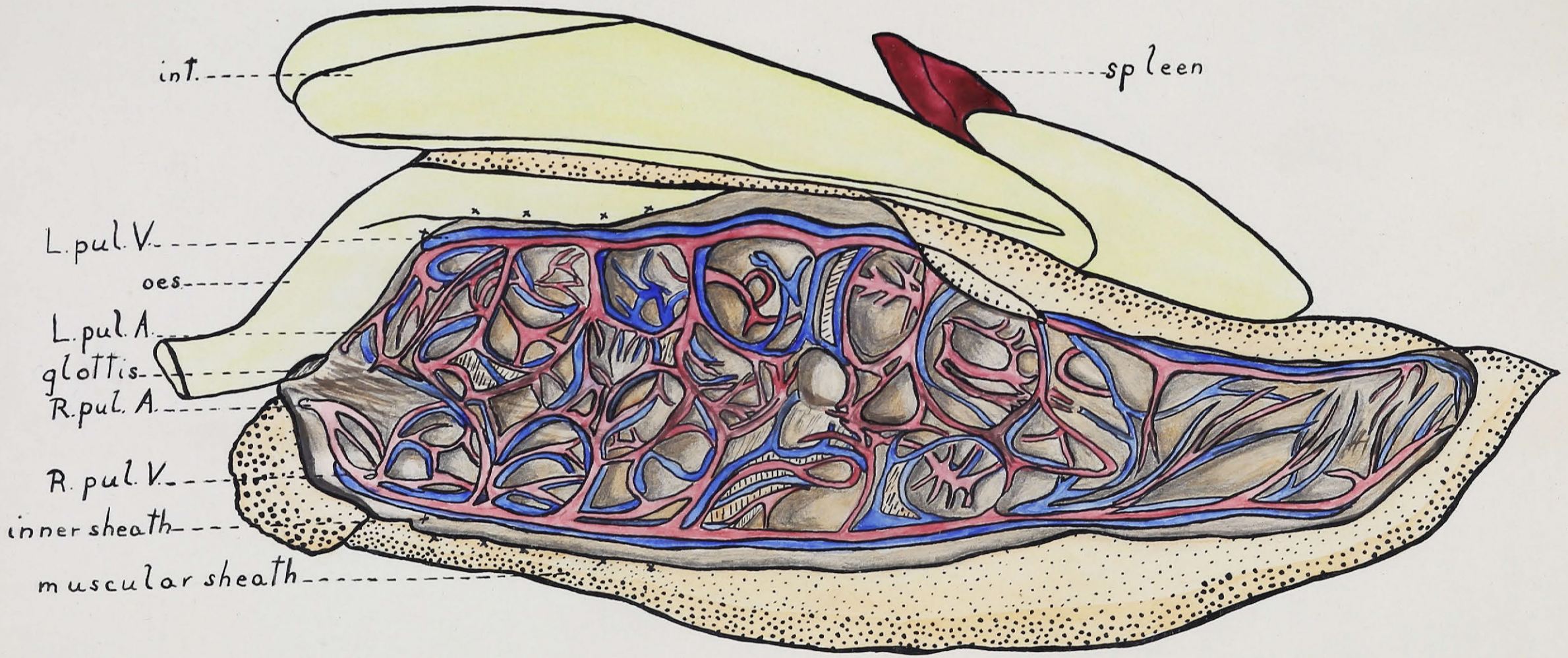


Plate 3

Amia calva

12:6:39

Plate 4

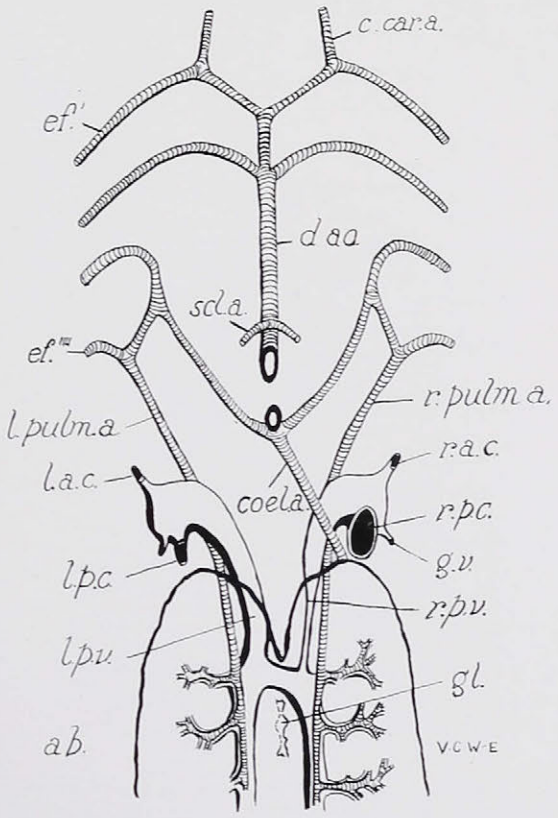
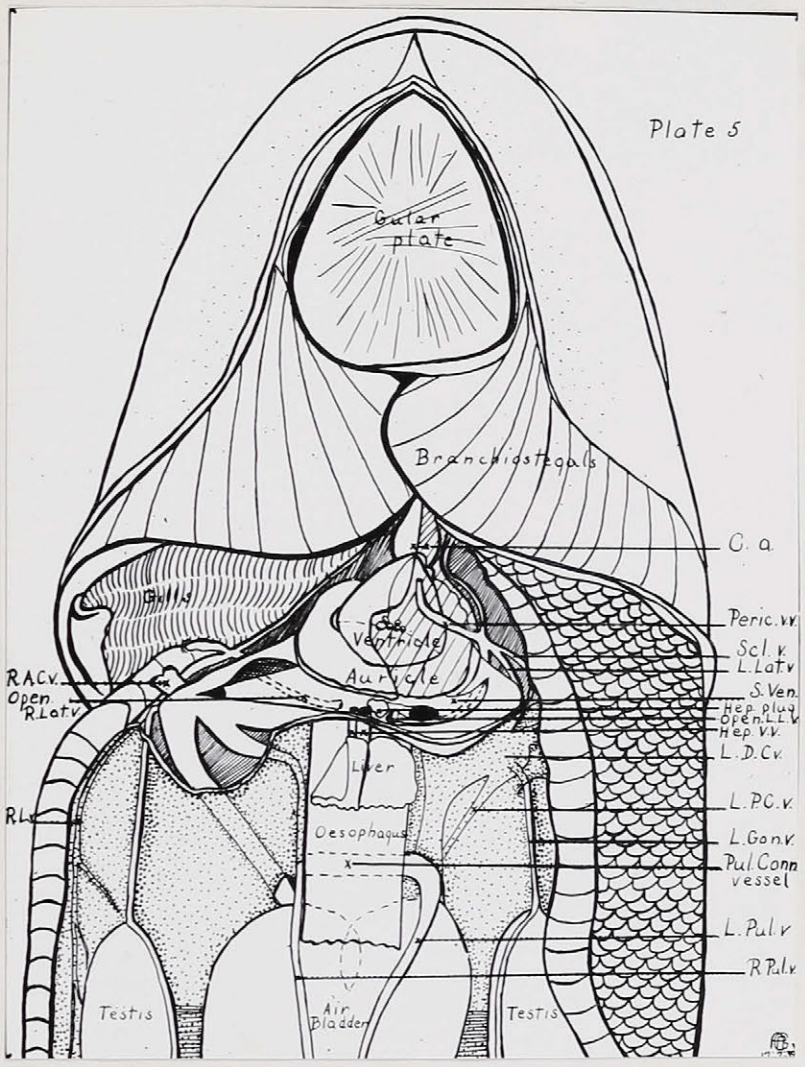


Plate 4

Afferent Branchial Arteries

Plate 5



Ventral Dissection of Anterior Region of Amia

Plates 6 and 7

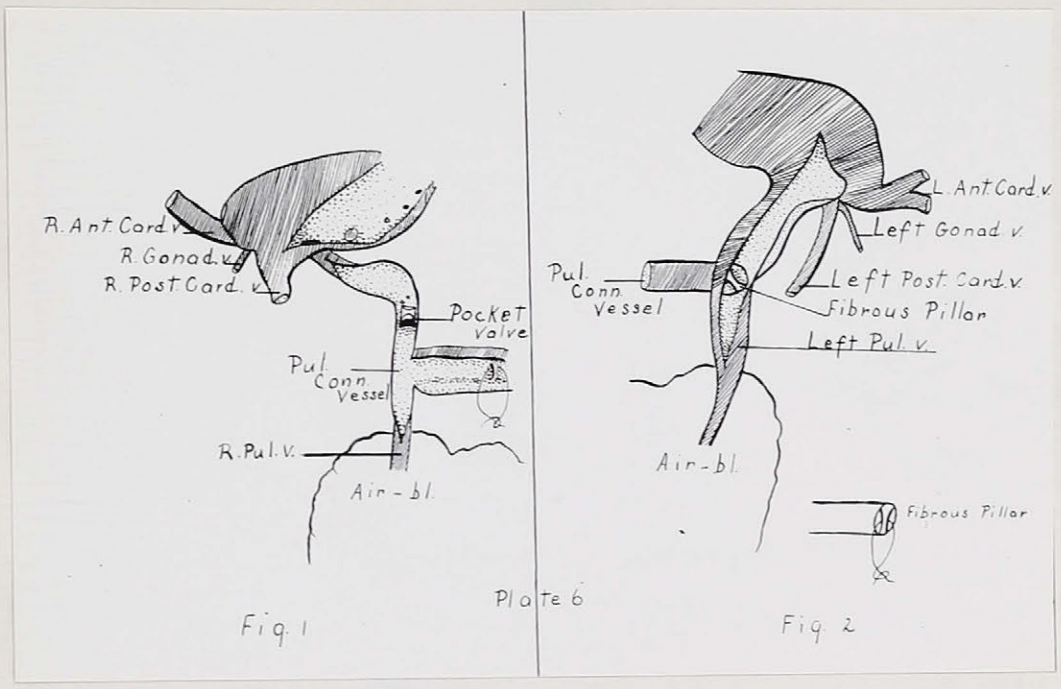


Fig. 1 Plate 6 Fig. 2

Right and Left Ducts of Cuvier and Pulmonary Veins

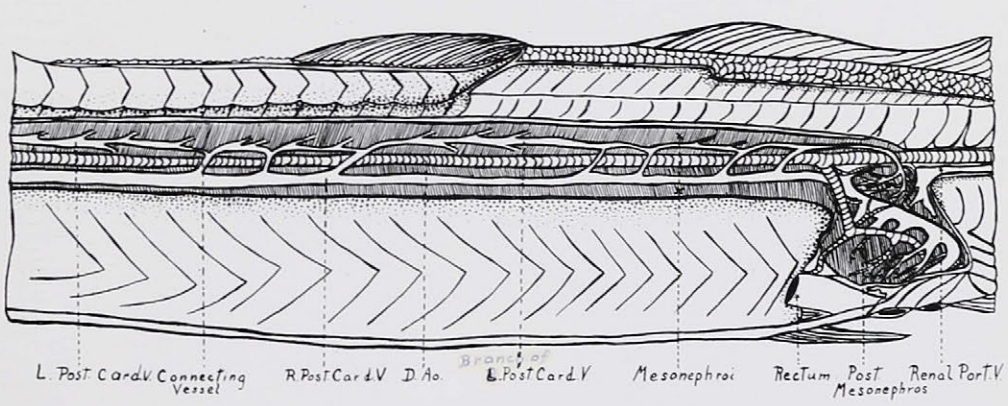


Plate 7

Amia calva

Plates 8 and 9

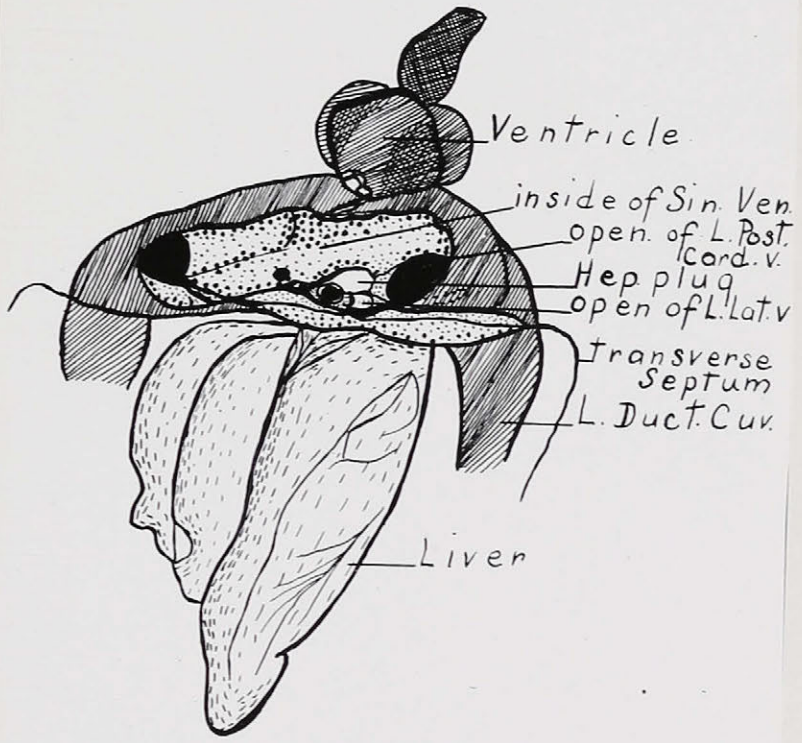


Plate 8

Sinus Venosus cut open

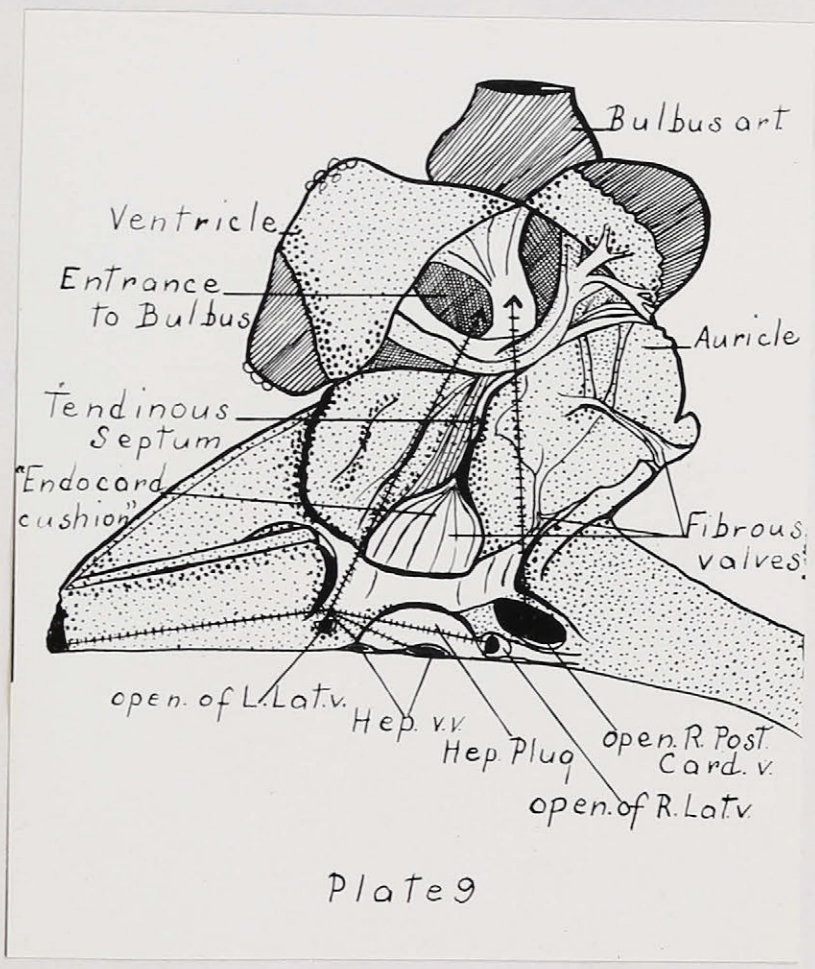


Plate 9

Sinus Venosus, Auricle, and Ventricle cut open ventrally

Plate 10

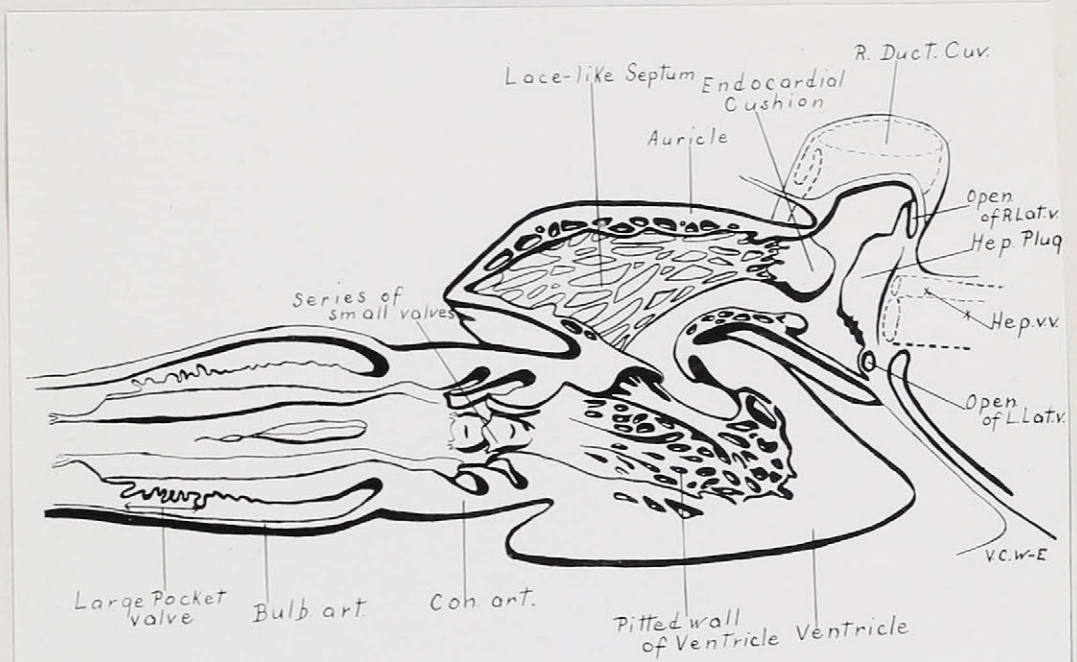


Plate 10

Inner view of Sinus Venosus, Auricle, Ventricle and Bulbus

Plate 11

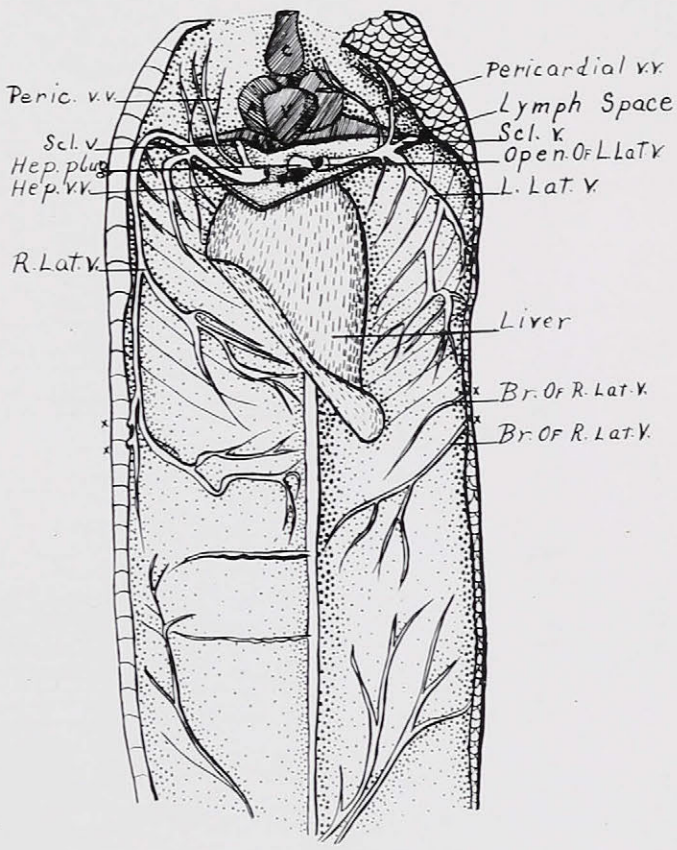


Plate II

Lateral Veins

Plate 12

Auricle Ventricle and Bulbus
(cut dorsally)

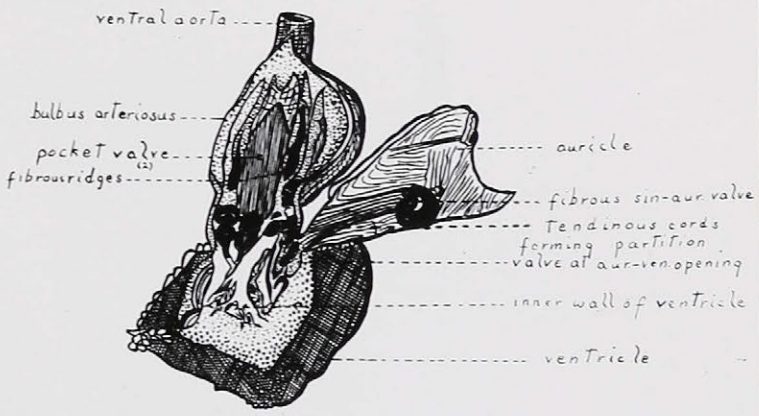


Plate 12

Amia calva.

Plate 13

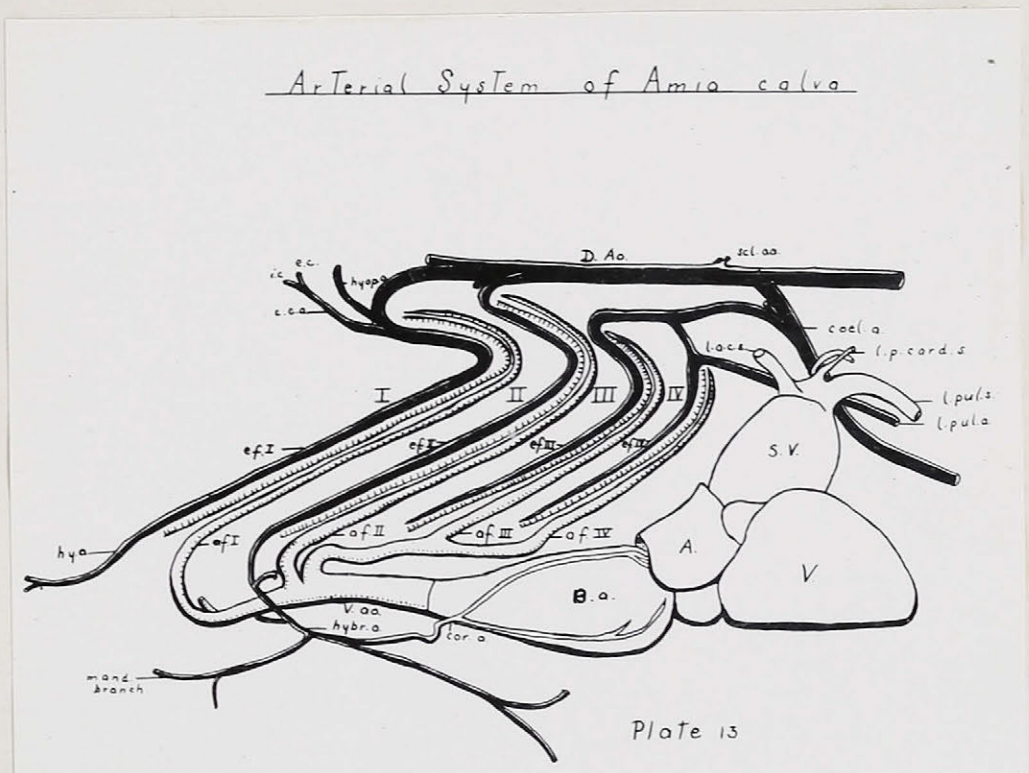
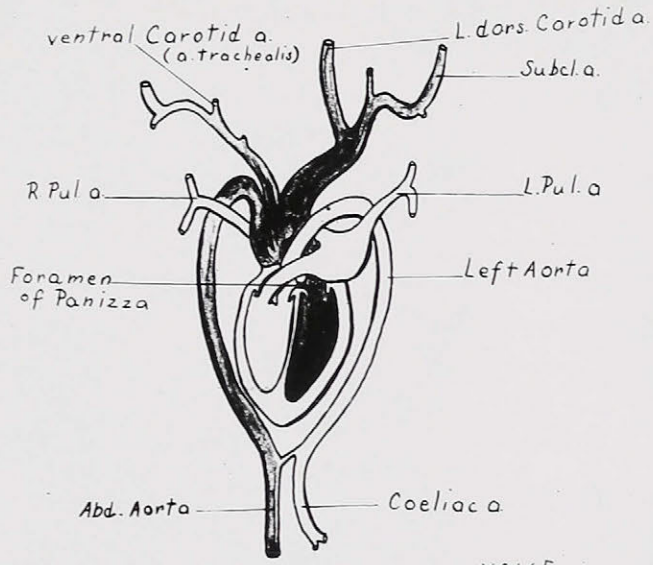


Plate 13

Plate 14

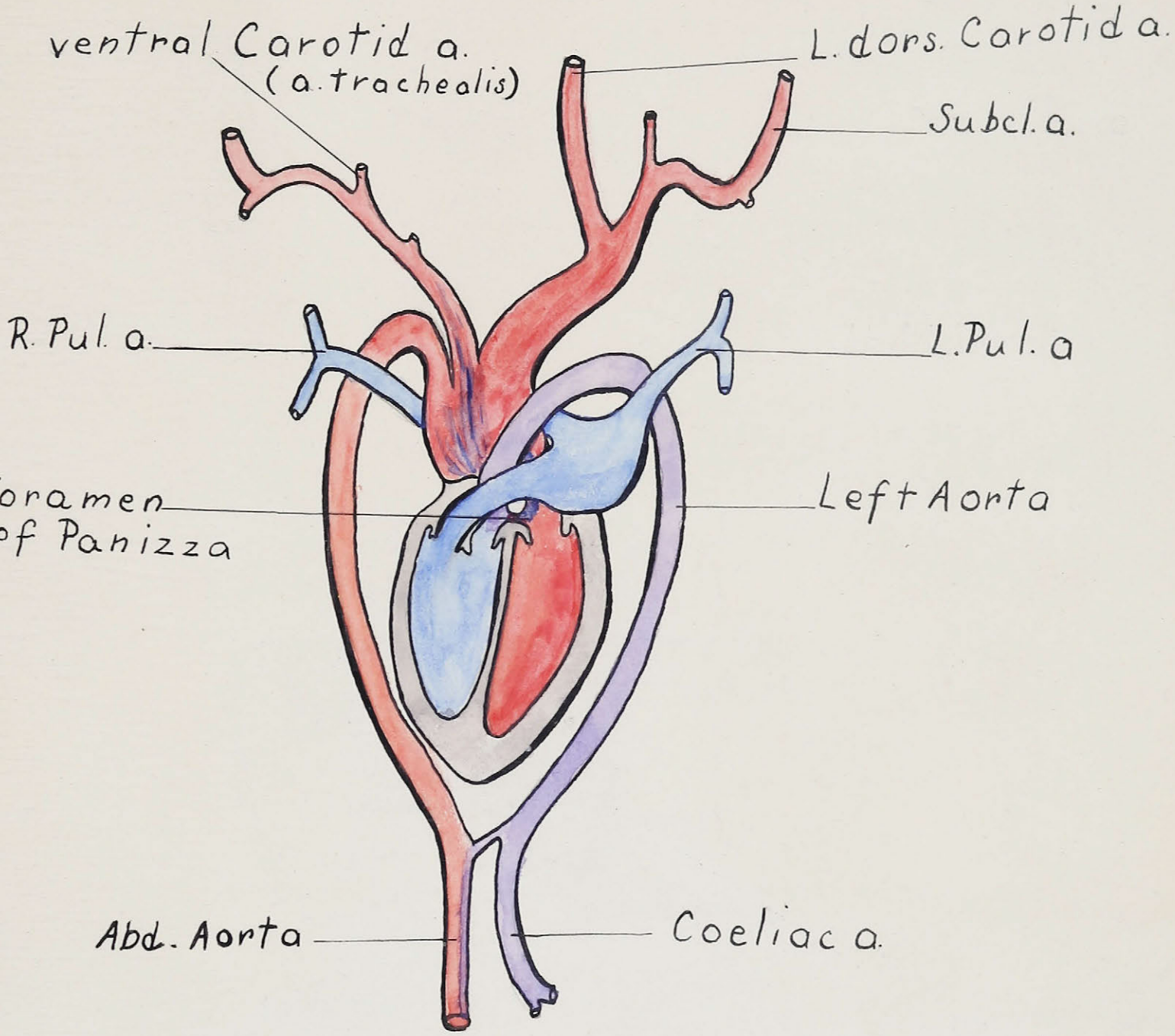


V.C.W-E.
23:1:36

Alligator mississippiensis

Plate 14

Principal Arteries in Alligator

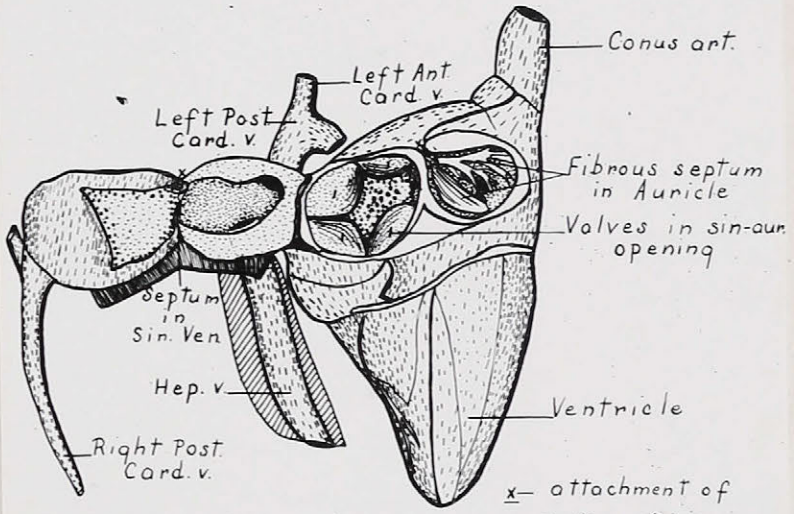


V.C.W-E.
23:1:36

Alligator mississippiensis

Plate 14

Plate 15



Dorsal view
Sinus cut open and turned to Left

Lepidosteus Plate 15

Heart of Lepidosteus