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UNIVERSITY OF LOUISVILLE

THE ANATOMY, SYSTEMATIC POSITION, NATURAL  
//  
HISTORY AND ECONOMIC IMPORTANCE OF THE  
SPOONBILL GANOID, POLYODON SPATHULA

A DISSERTATION SUBMITTED TO THE FACULTY  
OF THE GRADUATE SCHOOL OF THE UNIVERSITY  
OF LOUISVILLE IN PARTIAL FULFILMENT OF  
THE REQUIREMENTS FOR THE DEGREE OF MASTER  
OF SCIENCE

DEPARTMENT OF BIOLOGY

BY

OSCAR H. STEINBERG  
///

1935

**DEDICATION**

MY HIGHEST APPRECIATION AND DEEPEST GRATITUDE ARE DUE DR. HARVEY B. LOVELL OF THE DEPARTMENT OF BIOLOGY OF THE UNIVERSITY OF LOUISVILLE FOR HIS DIRECTION AND CONSTRUCTIVE CRITICISM OF THIS STUDY

## PREFACE

This thesis aims to describe the anatomy of Polyodon spathula, a ganoid, showing its position between the cartilaginous group of fishes, the Elasmobranchs and lower forms, and the higher group, the Teleosts or bony fishes. Changes between Elasmobranchs and Ganoids are most marked in the development of the large pyloric caecum, type of swim bladder, and the skeletal system. The skeletal system is both cartilaginous and bony in structure.

To a lesser degree, this thesis aims to give an account of the economic importance, breeding habits and range of the spoonbill fish, as well as a general classification of the Actinopterygii from which Polyodon have advanced.

Acknowledgments are due to the University of Louisville, the University of Illinois, and the University of Tennessee for reference material obtained; also to Dr. H. B. Lovell for his constructive criticism of this study, Dr. P. A. Davies for giving me access to use facilities necessary for study, Dr. J. F. Bradley for corrections in English of part of the thesis, and Mr. F. Melton for the photography.

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## INTRODUCTION

The fishes of the family Polyodon, in addition to their growing economic importance in America, are of exceptional interest to biologists on account of their primitive shark-like form and character, and their consequent importance in tracing the descent of the bony fishes.<sup>1</sup>

It is remarkable that the anatomy of such an important food fish as the spoonbill, Polyodon spathula, has been so little studied. It is, therefore, the main purpose of this study to present a detailed account of such anatomical structures as could be traced by gross dissection.

Assistance in identifying these structures was obtained from the previous work of Forbes and Richardson (1909), who briefly described the skeletal system. Alexander (1915) gives a brief resume of the viscera. Goodrich (1930), shows figures on the skull and pectoral girdle of Polyodon folium. Quite recently, Adams (1933) shows figures on the digestive system of Polyodon spathula.

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<sup>1</sup>S. A. Forbes and R. E. Richardson, 1909, p. 15.

The studies mentioned above, however, are so fragmentary that further identification of structures had to be worked out by comparing the spoonbill with forms whose anatomy is more thoroughly described. Pratt (1905) and Hegner (1931) on the Teleosts; Cahn (1926), Hyman (1928), Daniels (1928, 1932) on the Elasmobranchs proved to be of valuable assistance. Kingsley (1925), Lankester (1909), and Walter (1929) proved to be most useful comparative anatomies.

Although actual field studies were not possible, a critical discussion of the economic importance, breeding habits, and range has been made through careful study of the writings of numerous authors on the subject. Foremost among these authors were Hussakof (1911), Coker (1930), Gowanloch (1933).

The larval stages of the spoonbill are almost unknown, except for the discovery of post-larval stages by Thompson (1933).

The author recommends that the further investigation of the breeding habits and larval development be undertaken as a most fruitful field of research. Studies on the embryo might well add important evolutionary data.

Coker (1930) points out our fundamental lack of knowledge of the most elemental facts concerning the life histories of common fishes. "To say nothing of the

spoonbill or hackleback sturgeon, who knows when, where, and under what conditions occurs the breeding of freshwater drum, blue sucker, river herring, or Ohio shad? The last mentioned fish, potentially an excellent food and fairly abundant, as observation indicates has not even been recorded hitherto from the Mississippi River (1930). Who has observed the breeding (in nature) of any of the larger catfishes of the Mississippi basin? Where is the "niggerlip" catfish during the ten months of the year, when it is rarely taken by commercial fishermen? Who has studied the modifications of form and color corresponding to habits or ages of any of the catfishes or buffalo fishes? These are excellent opportunities for useful studies of fishes that can be readily found in various streams of the Mississippi basin."

. . .  
CHAPTER ONE

ECONOMIC IMPORTANCE,  
BREEDING HABITS, AND RANGE OF THE  
SPOONBILL (POLYDOR  
SPATHULA)

. . .  
.

The economic importance of the paddlefish or spoonbill is worthy of consideration. As a food its flesh is used both fresh and smoked. In the females the roe is used as caviar. As a species it is of peculiar interest, being markedly different in form and structure from any other fish now living except a single species occurring in certain rivers of China. Shark-like in form, but not in behavior or in quality of meat, it ranks as one of the most estimable aquatic resources. At times it has seemed upon the verge of extermination from overfishing or other unfavorable conditions; yet apparently it shows remarkable powers of endurance or recuperation. Coker (1930) estimates the roe of an individual fish to weigh from ten to fifteen pounds, and it may have a value of more than two dollars a pound. A large spoonbill usually means a valuable catch.

For the past few years, the flesh of the fish was not generally sold under its own name but appeared in the markets under the name of "sturgeon". Now, however, it is known as spoonbill meat. In the vicinity of Lake Pepin, in fact, the fishermen commonly applied the name "shovelnose sturgeon" to the living fish.

### Edibility

Jordan (1925) says that the meat of the spoonbill is coarse and is not much esteemed. Recent statistics show us that the meat of the spoonbill is in demand (Sette, 1925).

From personal experience, and in discussion with several fish dealers, I found the following to be true in regard to spoonbill meat: The spoonbill possesses a tough axial membrane (notocordal tissue) extending from the head to the tail. If this axial cord is removed before cooking, the meat of the spoonbill is excellent; otherwise the gristly structure makes the fish unsatisfactory food. Hence, we see how different points of view arise in regard to the edibility of spoonbill meat.

### Range

The range of the spoonbill is in rivers and lakes of the Mississippi basin and in some other tributaries of the Gulf of Mexico. The spoonbills that the author worked upon were taken from the Mississippi River in March, 1934. While this fish is rare in shallow tributaries and has been supposed to prefer waters exceeding

ten feet in depth, yet it occurs throughout the whole course of the Mississippi River and is widely distributed in the basin. According to the United States Bureau of Fisheries, one of the largest specimens of record was taken in Lake Chautauqua, New York. Coker (1930) says the more important fisheries for spoonbills have been in lakes of Louisiana, Mississippi, and Arkansas and in the Ohio, Illinois and Mississippi Rivers as far north as Lake Pepin between Minnesota and Wisconsin. Spoonbills usually are taken along with catfishes, buffalo-fishes, and carp in large seines, which may be hauled from barges by the use of reels or pulled ashore by the use of stationary winches. They are also taken in nets at night. In the Mississippi River in recent years the sizes generally taken range from four to twelve pounds. Large examples of twenty-five to thirty-five pounds in weight have been reported but are rare. Fish of twelve to twenty-five pounds weight are said to be more common in the last few years (before 1926) at points on Lake Keokuk.

### Breeding Habits

In spite of the most careful searches by various investigators working in many localities, virtually nothing has been learned concerning the breeding habits of the spoonbill fish. It is reported to breed in Louisiana (Alexander, 1915) and it has been found in a nearly ripe condition at Louisville, Kentucky. (Everman, 1902). There is also testimony that it spawns in central Illinois (Richardson, 1913).

Coker (1930) states that fishermen and dealers at and near Keokuk report that they frequently take examples containing eggs and that the roe is marketed for preparation as caviar. Wagner (1908) examined about 1,500 specimens from Lake Pepin, between Minnesota and Wisconsin, from June 11 to September 1, but none were found that were nearly ripe or recently spawned.

Stockard (1907), from observations made in Louisiana and Arkansas, concluded that the breeding season in that part of the country was about the middle or latter part of April. Allen (1911) obtained specimens four to six inches long on July 1 near Cairo, Illinois, and larger ones six to twelve inches in length in late August or early September. He inferred that



the breeding season was in March.

All evidence indicates that the spoonbill fish breeds either late in winter or early in spring; and as young specimens have been obtained at Cairo, Illinois, and Lake Pepin, Minnesota, and in Montrose, Iowa, there is at least some evidence to indicate that its breeding activities are confined neither to the northern nor southern extremes of its territory.

There appears to be a lack of any definite record of an extended migration of paddlefish in an upstream or downstream direction. It has not been known whether the paddlefish or spoonbill of Louisiana and Minnesota were bred and reared in their respective localities or whether migrations occurred between the extreme limits of the range of the species. A "spring run" of spoonbill fish is sometimes spoken of, but this expression is used so generally that no particular attention can be attached to its bearing upon a migration of the sort in question.

Stockard (1907) furnishes observation of a conspicuous lateral migration from rivers to lakes and from lakes to rivers.

"During the spring, when the water of the Mississippi River rises for several feet and backs into the bayous, thus establishing connections with large lakes, *Polyodon* begins immediately to come into the lakes from

the river and continues to come in large numbers so long as a sufficient connection is maintained. To do this it must often make long journeys through rather shallow water, in which many obstructions, such as bushes and trees, are frequently met. Thus it finally reaches the lakes in a rather emaciated condition and with its body scarred and scratched. It is equally true that the fish in the river lakes (the lakes more directly connected with the river) migrate out into the river when the water begins to back in during the spring, so that fishermen often abandon their fishing in these places at such a season, since most of the desirable Polyodon have made their escape."

Wagner (1908) says, "Seemingly the spoonbill is of a rather roving disposition, cruising up and down the lakes in large schools." He observed that it might be taken abundantly in the seine one day, whereas the next day there might be none.

Because very little definite information is known concerning the breeding habits of the spoonbill, mention of the breeding of the long-nosed gar, a close relative of the spoonbill, should

be made. According to Fish (1932), the long-nosed gar spawns in late spring and very early summer in warm shoal water, often running up smaller streams in company with the sturgeons. The eggs are probably attached to weeds, and the young remain among the weed beds close inshore during their first summer.

Stockard (1907) says that *Polyodon* does not spawn in large clear water lakes as does the related gar-pike.

#### Feeding Habits

The peculiar feeding habit of the spoonbill makes necessary an active life with extensive local migrations in search of food. The spoonbill, unlike other fish of like size, does not take other animals of large size as food, but subsists upon minute plant and animal life, which it obtains by straining enormous quantities of water by means of its gill rakers. It must be in constant movement when feeding and its daily local distribution must be affected by conditions affecting the abundance of food supply.

Observations on the spoonbill's behavior have thrown some little light upon its strange feeding habits. When normally swimming forward by the slow movements of its caudal fin, the paddle-

fish alternately swings its head and paddle from left to right, covering a wide band with the tip of its snout. Feeding seems to depend upon the straining of immense quantities of water which pass rapidly into the huge mouth and out through the comb-like structures on the large gill slits. Kofoid<sup>2</sup> writes of his observations. "In swimming, the mouth is held wide open without the rhythmical respiratory movements common in most fishes, though it is occasionally closed energetically. The plankton (minute plants and animals that float in water) is thus strained from the water by long gill-rakers, and *Polyodon* is a living plankton net. It quickly perceives plankton or ground fish added to the water of the tank, and, when feeding, circles rapidly over the same path at times dragging the lower fins on the bottom".

As is known, the most remarkable thing about the feeding habits of the spoonbill is the fact that though living on a muddy bottom, it manages to avoid eating mud, and as Forbes and Richardson (1909) have said, "The relatively minute size of many of the objects on which it feeds, the absence of mud from the intestine, and its seeming preference for animal

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<sup>2</sup>Kofoid, as quoted by C. R. Stockard (1907)

food indicate that it is not only able to gather large quantities of very minute objects from among the weeds and muddy bottom, without filling itself with mud, but that it can separate the Entomostraca (water fleas) from the Algae (minute water plants) among which they swim.

During the course of dissection we observed dried mud beneath the comb-like gill-rakers. This would be a point of proof that the spoonbill's comb-like rakers serve as perfect strainers to prevent mud from entering the intestine.

Thus by adjustment in structure and habit this great fresh water fish has come to support itself entirely and most successfully upon myriads of tiny living organisms that swim in the water where it lives.

Coker (1930) says R. A. Muttkowski determined the stomach contents of five spoonbills taken by Stringham in Louisiana, at various dates from April to August, and found the material to consist chiefly of insect larvae (May fly nymphs, caddisfly larvae) and insect remains, with small quantities of plant and other debris. Pieces of wood and some parasitic nematodes were also included. The stomach contents of a spoonbill submitted to the

Bureau of Fisheries from Louisiana and examined by Coker (1930) contained almost exclusively the pelagic and translucent *Corethra* larvae. Such observations indicate that the spoonbill may feed either at the bottom or in the water above, a matter about which there has been a difference of opinion.

### Size

Paddlefish attain great size, the maximum available record being 173 pounds. Measurements of one museum specimen will indicate the proportions of the species. Six feet, two inches in length, this individual measured four feet in its greatest circumference and weighed 150 pounds. According to Gowanloch (1933), usual specimens scale at thirty to fifty pounds. His view differs with Coker (1930) who says these reported cases are rare.

It is natural that a fish so remarkable in form should at an early date attract attention to the New World.

J. H. Gowanloch (1933) says: "Pere Marquette in 1673 to 1677 provided what is probably the first mention of this species when in the Jesuit Relations he says of it: near its nose (paddle) is a large bone shaped like a woman's busk, three fingers wide

and a cubit long, at the end of which is a disc as wide as ones hand.

"Walbaum who originally described the paddlefish in 1792 thought it was a shark".

### Reaction

From personal experience, it seems that the spoonbill feeds mostly at the bottom of the water. As much as twenty feet of reel cord had to be used before any bites of the spoonbill could be felt. It is interesting to note that the reaction taken by the spoonbill is peculiar. It will make one attempt to escape and then remain motionless for several minutes. It does not put up a battle as does the carp or trout. The reaction of the spoonbill appears to be similar to that of the flounder or porgy.

Hussakof (1911) describes the action of the spoonbill at close range, during a catch of different species of ganoids. "As the seine is gradually wound up and the fish become confined to narrower and narrower space they dart wildly about seeking means of escape. One may then study the spoonbill at very close range. Its sense of sight is poorly developed as one might infer from its small beady black eyes.

if its "nose" is caught in the seine it makes only feeble efforts to free itself and usually fails to do so. The contrast between the clumsiness of the spoonbill and the alertness of an active fish is strikingly brought out if a gar pike is taken in the same haul; for the gar makes tremendous efforts to escape and unless rendered unconscious by a blow with a mallet, will flash through the seine as if it were guaze. Leaning over the side of the boat, near the corkline of the seine, one may seize a five foot paddlefish by the nose (paddle) or the tail and haul it into the boat; the only resistance is that of weight. The fish has absolutely no sport value".

According to oral reports of several fish dealers of Louisville, Kentucky, the spoonbill does put up a battle at times. Its chief weapon of defense is the caudal portion of its body, which it can swing around freely (because it has a cartilaginous spinal column) and strike its opponent. They report its striking is painful enough to allow the escape of the fish. Of course, the size of the spoonbill would determine its reaction during a catch.

The above statements seem to contradict Kussakof's description of the catch of the spoonbill.



We may conclude that although the spoonbill has no sport value, it at least makes one attempt to react violently in order to escape, and thus shows more resistance than merely its weight.

According to Hussakof (1911), the spoonbill has very deficient sight, and in finding its way (movement) it depends chiefly upon the delicate tactile sense organs in its snout. In cases of this kind the sensory warning might well come too late to save the snout; in fact, instances are often seen in which the snout is almost completely broken off. Stockard (1907) observed a well-conditioned spoonbill that had lost the greater part of its "bill", but that evidently had survived and grown without it.

#### Further Economic Uses

According to Everman (1902) one of the first spoonbill fisheries to develop in this country was that of Louisville, Kentucky, on the Ohio River. In 1898 Everman<sup>3</sup> visited Louisville, where the fishermen were catching considerable numbers every spring. He says they were caught in considerable numbers five to ten feet below the surface of the water. Coker (1930) says they are best found at least ten feet or more below the

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<sup>3</sup>As stated by Hussakoff (1911)

surface. The depth, I believe, at which spoonbills are caught may vary with the abundance of spoonbills, month of the year, and the tide of the river.

As increasing numbers of spoonbills have been caught by the various fisheries, further economic uses have developed. In cutting up the paddlefish the heads and fins are usually discarded but sometimes they are boiled for oil. Roe is removed to be prepared for caviar. It weighs from two to twelve or fifteen pounds in a single fish. It is put on a coarse wire sieve and rubbed by hand across the wires until the eggs are separated from their membranes and dropped into the bucket beneath the sieve. The eggs are greenish black in color, about three times the size of shad eggs, and are very numerous. The raw caviar is then mixed with "German" salt and is ready for shipment. It must undergo still further preparation before it is in the form familiar to us. In its raw state it was valued at fifty cents a pound (1910). During the World War it was valued at three dollars a pound. To date (1934) its value is two dollars a pound. It is said that spoonbill caviar is the best known, having received the highest award at one of the world expositions.

From the figures brought together by Sette

(1925), it appears that the paddlefish, after a marked decline following the census year of 1899, has been holding its own as commercial resource of the Mississippi basin.

In regard to the price of spoonbill meat, Goode (1903) states that "it is generally sold at four cents a pound". To date (1934) the meat of the fish sells at twenty cents a pound. This result in rise of price indicates the spoonbill to be less common or more in demand than in former years.

#### Summary

By way of summary we can say that the paddlefish or spoonbill, though not migrating in as large a number as in former years, is still an important product of the commercial fisheries of the Mississippi basin. Formerly sold under a false name, it has now come to stand on its own merits. Furthermore its roe has a value for the production of caviar. The breeding of spoonbill fish has never been observed but is presumed to occur in early spring.

. . .  
CHAPTER TWO

BRIEF HISTORY AND CLASS-  
IFICATION OF THE OSTRICHTHYES  
WITH SPECIAL EMPHASIS ON THE ORDER  
ACTINOPTERYGII (SARCOIDEI) AND  
THE PLACE OF POLYODONTI-  
DAE AMONG THEM  
. . .  
.

## OSTEICHTHYES IN GENERAL

### Distinctive Characters and Classification

The Osteichthyes or bony fishes are those in which the primary cranium is always complicated by the addition of investing bones, some of which as in sturgeons may secondarily disappear, of which a pair of parietals and one of the frontals above and unpaired vomer and parasphenoid below are the most constant. The chondocranium is always more or less ossified by replacing bones, including a supra-occipital; and upper and lower are both bounded by investing bones.

Lankester (1909) indicates that the jaws are connected with the cranium through the intermediation of a hyomandibular which is probably not homologous with the similarly named elements of the Elasmobranchs. The dermal finned rays are formed of bones, and are supported by pterygiophores<sup>4</sup> which may be either cartilaginous or bony but which always show a great reduction in number as compared with the homologous structures in Elasmobranchs.

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<sup>4</sup>One of the cartilaginous or bony elements by which the rays of the fin of the fish are supported: radial, an actinost.

The primary shoulder girdle is complicated by the addition of investing bones, of which a large clavicle is the most constant. The pelvic girdle is vestigial or absent. The pelvic fins usually undergo a forward displacement, their position being either abdominal, i. e., between the anus and pectoral region, or thoracic, i. e., in the pectoral region, or jugular, i. e., under the throat. A dermal exoskeleton is usually present. The intestine may or may not have a spiral valve; the anus is separate from, and placed in front of, the urinary and genital apertures. The gills are covered by an operculum supported by investing bones, and the inter-brachial septa are reduced or absent, so that the gill-filaments are partially or wholly free; the hyoidean gill is reduced or absent. The conus arteriosus is sometimes present, sometimes absent; when it is absent there is a large bulbus aortae formed as a dilatation of the ventral aorta. The prosencephalon has usually a non-nervous roof; the optic nerves either form a chiasma or simply decussate. The ova are small; the gonoducts are continuous with the gonads or open anteriorly into the coelom or are absent; in the last instance the sexual products pass out by genital pores;

true abdominal pores may be present in addition. Segmentation of the egg is either entire or discoidal; development is sometimes accompanied by a metamorphosis.

Since my topic deals specifically with Polyodon, I shall discuss the special group Actinopterygii including the family Chondrosteidae and sub-orders Palaeoniscoidei and Acipenseioidei. The sub-order Palaeoniscoidei includes the families Platysomidae and Catepteridae and sub-order Acipenseroides includes the families Chondrosteidae and Polyodontidae.

These specific types can serve to show evolutionary changes in the order Actinopterygii as well as to place the particular family Polyodon at the height of the evolutionary scale preceding the Holostei or next higher evolutionary species.

Briefly the following classification can be used:

Group or Order:	Actinopterygii
Sub order 1:	Palaeoniscoidae
a. family:	Platysomidae
b. family:	Catepteridae

- Sub order 2:           Acipenseroidae  
 a. family:           Chondrosteidae  
 b. family:           Polyodontidae (spoonbill)

To follow the brief classification outlined above:

- Order:                Actinopterygii  
 Sub order:       Palaeoniscidae

These are the most primitive and the earliest of the Actinopterygii. They appear in the Lower Devonian period, and are abundant in the Carboniferous and Permian periods, and die out in the Jurassic period. The dermal skeleton is covered with ganoinae. The scales are usually rhomboid, with articulating pegs; but in some (*Coccolepis*, *Cryphiolepis*) the scales are cycloid and deeply imbricating on the trunk, and in *Phanerostrum* the trunk is almost scaleless.

The orbits are far forward and the snout blunt, so that the nostrils are lateral or even ventral, rather than dorsal. The superficial cranial bones differ but little in plan from those of the normal Teleostomi. The opercular, subopercular, and gulars form a continuous series. The orbit is surrounded by a narrow ring of few bones. The hyomandibular is elongated backwards and connected with a broad



pterygoid plate. The lower jaw has dentary, angular, splenial, and articular bones.

#### Family Platysomidae

In everything but the shape of the head and trunk, which becomes very much compressed and deepened, and the accompanying extension of the dorsal and anal fin, the Platysomidae closely resemble the Palaeoniscidae. *Xurynotus*, *Mesolepis*, and the *Platysomus* are three stages in change of form. As the body deepens, the scales become transversely elongated. The jaws become more pointed, and pelvic fins become reduced in size (*Platysomus*), or disappear altogether as in *Cheirodus*. The hyomandibular becomes nearly vertical, and the mouth is diminished. The teeth may be considerably modified, becoming swollen and tritoral.<sup>5</sup> In *Cheirodus* and *Cheirodopsis* the palatal and splenial<sup>6</sup> teeth fuse to grinding plates. This family is found in the Carboniferous and Permian strata.

#### Family Catopteridae

This type comes from a triassic family of fusiform

---

<sup>5</sup>Tritor - The flat surface of a tooth developed for purposes of trituration, or grinding.

<sup>6</sup>Splenial - A thin elongated membrane bone of the lower jaw of some reptiles and ganoid fishes, between the articular and dentary (called "teeth" in ganoids).

fish resembling the Palaeoniscidae in general structure, but with an abbreviate heterocercal tail. The head and shoulder girdle are Palaeoniscid. The ganoid scales are rhombic; the teeth slender and conical.

#### SUB ORDER 2

#### ACIPENSEROIDEI

Lankester (1909) says that according to the researches of Traquair and A. S. Woodward, the families in this group form a degenerating series starting from a type similar to the Palaeoniscidae; they reach the highest degree of differentiation in the Acipenseroides.

The body remains fusiform with a typical bifurcated heterocercal tail. The dorsal and anal fins are moderately short. The orbits are far forward, near the olfactory capsules, but the snout becomes greatly prolonged from the mouth.

#### Family Chondrosteidae

The Chondrosteidae contain the most ancient known Actinopterygii. The definite association of the Palaeoniscidae and Platysomidae with the Acipenseroides is due to Traquair. One of the Palaeoniscids, *Cheirolepis*, is found as the first

representative in Lower and Upper Devonian rocks. They seem to have diverged in three principal directions leading to the Platysomidae, Chondrosteidae, and Catepteryidae. The degenerate Chondrostei are considered to be the only direct survivors of the sub-order at the present day. It should be remembered that the belief in their close affinity to the Palaeoniscids rests on slender evidence. The whole endoskeleton is incompletely ossified, remaining for the most part cartilaginous, and in consequence is very incompletely known in the extinct species.

The trunk appears to be scaleless; rhombic ganoid scales are found on the tail only. The paired frontals, parietals, postfrontals, and pterotics (squamosal) are still normally developed and not separated by a median series.

In this family the pectoral fin has a fairly normal skeleton, conforming to the rhipidostychous plan, with a remarkable structure, differing from all other Osteichthyes. There is no definite line of demarkation existing between the pelvic girdle and the skeleton of the fin itself.

The radials, forming a single series, are

articulated to basals which are more or less independent posteriorly, but which are fused to the girdle in front.

Dorsal processes, analogous if not homologous with the iliac process, are developed along the basal region of the fin of the Polyodon. In the Scaphirhynchus cataphractus the internal end of the pelvic cartilage may be segmented off as a separate element.

#### Family Polyodontidae

Polyodon is from the Greek meaning "many and tooth"; but the name is a misnomer, for when grown, the spoonbill has not a tooth in its head. Spathula is Latin "spatula", appropriately referring to the blade-like snout.

Gowanlach (1933) says, "Today the paddlefish stands a single North American member, not only of its family (Polyodontidae) but also the single surviving North American Selachostome."

These fish have minute scales on the trunk; small and separate in Crossophilis, quite vestigial in Polyodon. A Cretaceous genus, Pholidurus, alone retains the ganoin (A. S. Woodward). An enormous flattened rostrum with

very small barbels is developed in the Polyodon.

Jordan (1925) states that the second species of Polyodontidae namely Psephurus gladius found in the rivers of China, possess a narrower snout, fewer gill rakers, and much coarser fulcra on the tail than does the American species Polyodon spathula. Goode (1903) says that Chinese species occasionally attain a length of at least twenty feet. According to Jordan, the habits as far as known are much the same in the two species. However, Kyle (1926) points out a difference. He says that the long, spade-like snout of the spoon-bill is supposed to be of use in stirring up mud when the fish is searching for its food. But the species that lives in the Chinese rivers is said not to use its snout in this way; in fact, the fish seems to be greatly inconvenienced by it. Jordan reports the carps can stir up the mud without a snout.

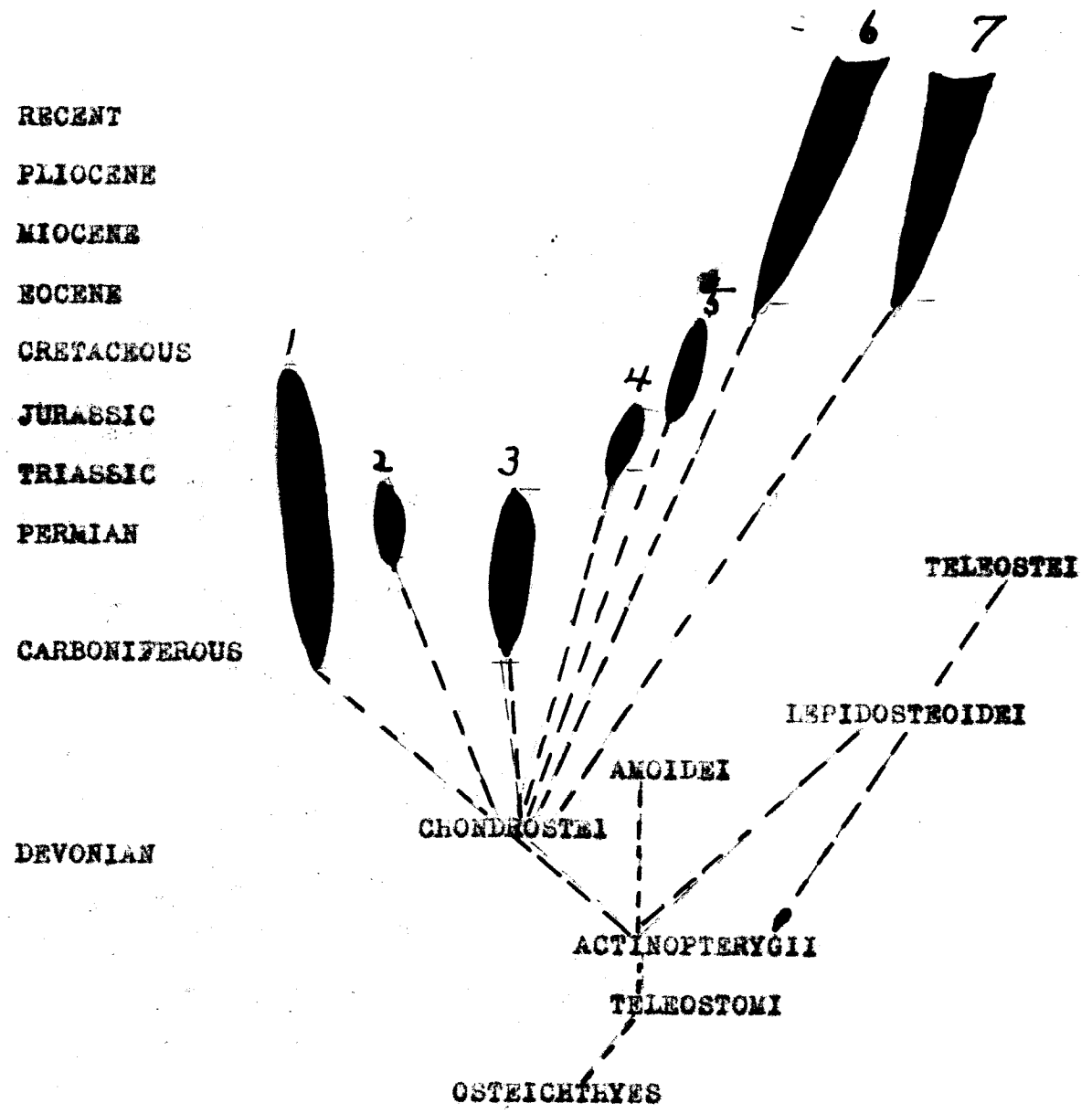
It may be that through disuse the bill of the Psephurus gladius will eventually disappear. Perhaps the same will also be true of the American spoonbill because many forms are found that apparently live just as conveniently without the bill.

The Actinopterygii first appear in the

early Devonian strata and have since survived as the dominant group of fish. Modern advances in knowledge of structure and classification of the more primitive fossils which formerly included the Gascoidei are due to Wagner (1908).

The following table shows geologically the phylogeny of the Osteichthyes from which the Actinopterygii have advanced.

PHYLOGENY OF THE OSTEICHTHYES FROM WHICH  
THE ACTINOPTERYGII HAVE ADVANCED



- 1. PALEONISCIDAE
- 2. THRISSOLEPIDAE
- 3. PLATYSOMIDAE
- 4. CATOPTERIDAE
- 5. CHONDROSTEIDAE
- 6. POLYODONTIDAE (Speonbill)
- 7. ACIPENSERIDAE

(From Lankester (1909) but  
in 1880)

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**CHAPTER THREE**

**EXTERNAL ANATOMY AND  
INTEGUMENT OF POLYODON SPATHULA  
INCLUDING AN ACCOUNT OF  
RELATED FORMS OF  
GANOIDS**

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### Introduction

The body may be divided into three regions: the head, trunk, and tail, the boundary between the latter two being the anus.

Vertebrates which live in the water differ from those living on land in the arrangement of the body regions. Aquatic animals must force their way through a denser medium and hence the forward position of the body is rigid and more or less wedge-shaped. A true neck region is absent. Even in those mammals which have adapted themselves to a wholly aquatic life, as in the Cetaceans, the neck region is so much reduced that the head and trunk are in direct contact with one another. In every animal which moves rapidly, however, at least one flexible body region must be present where the body can turn when the direction of movement is to be changed. In the fish this is accomplished in the caudal region; in most land animals in the lumbar region.

## A SKIN AND SCALES IN GENERAL

Although it is a popular belief that all fishes have scales, in reality this is not true. In general, scales seem to be a pre-requisite of the higher or bony fishes, though by no means all of these fishes have scales. Their chief purpose, is no doubt, protective and this is only one of the several ways which nature has found for achieving that purpose for different fishes. Bony plates, spines, and shagreen are all made use of, and when all these are wanting the usually tender skin becomes hard and leathery in composition as can be observed in the dogfish in contrast with the smooth skin of the Polyodon spathula. The evidence leads us to believe that all true fishes have an outer covering of some sort and that those which appear naked have lost it.

Whichever one of these extra protective devices nature employs, they all grow out of the skin itself. As in other vertebrates, the skin of the fish consists of two layers. On the outside is the epidermis, made up of several layers of cells without blood vessels, and on the inside the thicker dermis, composed of fibers and supplied with blood vessels and nerves. The epidermis is almost transparent, and so soft that friction will remove it. Hildebrand (1930)<sup>7</sup> says, "In the dermis,

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<sup>7</sup>Director of United States Fisheries Biological Station--North Carolina.

incidentally we find the explanation of the distinctive beauty of fishes, their silvery iridescence. This results from the presence of elements with a remarkable power of reflecting light called iridocytes. When they occur in a thick and dense layer, called argenteum, on the inner surface of the skin, they give to the fish its silvery appearance."

Incidentally, as already mentioned, the integument of the Polyodon spathula is devoid of scales but is more or less smooth (smooth in young specimens, rougher in old specimens) and very little silvery appearance is shown. It presents a rather dull grey or brownish grey color. From this fact we conclude that Polyodon spathula has very few of the elements called iridocytes. The pigment cells of Polyodon spathula seem to be actively functional by color reflection, variation, and intensity of color, both externally and in the dermis. When the iridocytes are scattered singly they are said to cause an iridescence or play of colors. This fact also leads us to conclude that there are only few iridocytes in Polyodon spathula. In general, the dermis in fishes contains iridocytes (if silvery scaled or many colored) and pigment cells. Some pigment cells are

black and others colored.

Scales grow out of the dermis beneath the epidermis, but the posterior edge may project to some extent through the latter. They are thin calcified plates, being more horn-like in composition than bones and comparable to human finger nails. True scales in the adult fish also overlap one another like shingles on a roof, the outer edges always being directed toward the tail of the fish, and the scale in front covering three-fourths of the one behind it.

Once a race of fishes have developed a complete body covering of scales they may for some reason lose it wholly or in part, or they may retain it only in a degenerate form as oblong plates partly embedded in the skin or as small spines or prickles. The carp (Cyprinus carpio) offers an example of a single species some members of which may be completely scaled; others, such as the mirror carp, only partly scaled; and still others, such as the leather carp, wholly naked. The fresh water eels have degenerated scales consisting of oblong plates arranged in groups, set at right angles to each other, and partly buried in the skin. Only very close examination will show these structures in the eel. The file-fishes, some of the puffers, and certain sculpine all

show degenerate or modified scales in the form of small spines; the porcupine fish (*Diodon hystrix*) is an outstanding example. Besides having spines, this fish fills itself with air or water for protection.

### The Substance Ganoid

The word ganoid refers to the substance which covers the outer surface of the bony plates protecting members of this great group of fishes (ray-fins). This substance resembles dentine and is called ganoin. The ganoid plates on the American gar-pike may be taken as the most typical example of this kind of covering. These are large, bony, rectangular plates arranged in rows and placed edge to edge, in contrast to the overlapping scales already described. These plates are very hard and form an excellent armor. Although interlocked for additional strength, they do not make the body rigid, as they may separate or partly slide over each other when the fish moves its body from side to side. The free edges of the plates are so sharp that a live fish, when held in the hands, can cut deep wounds by throwing its body from side to side in an effort to escape, thereby pinching the hands and fingers between

the margins of the plates.

In the sturgeons - among the largest fishes of our seashores, rivers, and lakes - the ganoid plates only partly cover the body. Generally two rows of plates lie on the back: one along the side, and another along the edge of the abdomen. Those parts unprotected by shields are covered with rough leathery skin. Finally in the paddlefishes, Polyodon spathula, the ganoid plates have disappeared entirely, leaving the skin almost smooth. The Polyodon spathula with its rather delicate bill and smooth skin, appears, as compared to other ganoid fishes, to have very little protective adaptation.

## B External Anatomy of *Polyodon spathula*

### Form

The body of the spoonbill is compressed laterally and is in general elongate. Its maximum width is that region of the trunk just anterior to the pelvic fins; this body region is approximately one-sixth its entire length. The head is depressed and elongated, terminating anteriorly in a spathula-shaped snout.

The snout is paddle-shaped as can be seen in the photograph (Fig. 1). The greatest width of the bill is its anterior portion. The snout is believed to have a sensory function. Protruding from the head into the bill, the cartilaginous rostrum can be felt extending to the tip end of the snout. The rostrum is thickest at the posterior portion of the bill and thins out as it goes anteriorly along the mid region of the bill. The lateral portions of the bill are soft and present the feeling of a thick rubber membrane when pressed from the sides.

### Function

Although no reference has been found pertaining to the relation of bill to pressure, we suggest that since the snout is a sensory organ, pressure may

have an effect on it. When pressure becomes too great, the bill may warn the fish to seek a higher level. The chief function of the long spatula, however, is to stir up the mud, in which are found the minute organisms on which the fish feeds. Under the paddle are two pairs of minute barbels corresponding to those of the sturgeon. The long and slender gill rakers serve to strain the food (worms, leeches, water beetles, crustaceans, and algae from the muddy waters from which they are taken). According to Jordan (1907) the most important part of their diet consist of Xtomestracans (small crustaceans).

### Color

The color of the spoonbill varies on its different surfaces. The dorsal surface is dark grey, the lateral, a variation to a grayish brown color, and the ventral surface, a light brown except for the belly surface which is white (Fig. 2).

### Fins

The fins are flattened outgrowths of the body. They are supported by internal cartilaginous rods and the dermal fin-rays. Both the cartilaginous and dermal structures are visible on external examination.



The fins are of two types: median and paired. The paired fins are homologous to the paired limbs of higher vertebrates, although the skeletal elements characteristic of higher vertebrates are lacking in Polyodon spathula. All the fins are non-lobate. The median fins will be described first. There is only one dorsal fin, the posterior dorsal fin, located on the mid-dorsal line of the body.

The tail or caudal fin is of the heterocercal type. The lobes of the tail are of unequal size, the dorsal lobe being larger. The skeletal axis of the tail bends upward and enters the dorsal lobe. The caudal fin helps propel the fish forward and aids it in sudden changes of direction.

A camera lucida drawing (28 x) is shown of the caudal fin of Polyodon spathula (Fig. 3). It shows the cartilaginous and dermal portions of the caudal fin. The spiny structures, the fulcra, are seen anterior to the dorsal lobe of the tail.

The anal fin lies immediately posterior to the anal aperture; it is median and projects in a caudal direction. It ends in a convex fan-shaped structure.

#### The paired fins

The pectoral fins are paired and ventrally

located. They are fan-shaped and attached to the ventral surface of the body just posterior to the operculum. The pectoral fins function in controlling the horizontal position of the body in the water. The pelvic fins are broad and convex shaped at the end. They are attached to the ventral surface of the body, about an inch anterior to the anal aperture. They are horizontally attached and point in a ventro-lateral direction. In function they work in conjunction with the pectoral fins. The anatomical make up is more or less similar in all the fins of the spoonbill.

#### Apertures

The mouth, as in Elasmobranchs, is located on the ventral side of the head. It lies immediately ventral and posterior to the bill. It is large and horseshoe shaped (Fig. 4). In the adult Polyodon spathula teeth are lacking entirely. However, in young specimens small bony teeth are present.

The anal aperture is large and about an inch posterior to the pelvic fins. It is the outlet of the products of the digestive tract. The urino-genital opening lies immediately posterior to the anal aperture. Through it the products of the renal and genital organs are discharged. Laterally

the eye is found just posterior to the snout. It is comparatively small, spherical, and degenerate. It fully occupies the spherical socket. The eyelids are not movable.

### Nares

The spiracles are located about an inch posterior to the eye on the dorso-lateral margin of the head. They are narrow slit-like openings.

There is a pair of openings leading to each nasal cavity. These are anterior to the eye and about an inch apart and obviously assist in the circulation of the water through these cavities.

On the dorsal surface the larger pair of external nares are located as elevated structures, dorsal and anterior to the eyes. Bony ray-like structures are present dorsally across the head region, which feature distinguishes it from the surrounding pigmented skin area. This ray-like structure is due to the close contact of the endoskeleton with the integument.

### The Lateral Line

This will be discussed under integument. Externally the canal is visible just posterior to the nostril and extends across the body up into the dorsal

lobe of the tail. Minute pores can be seen leading directly into the lateral line canal itself.

### The Operculum

The operculum is fleshy and forms a pouch-like fold ventrally. The outer surface of the operculum is pigmented with cluster-like spots. Forbes and Richardson (1909) say these cluster-like spots or patches on the opercular flap are believed to be sensory (Fig. 5). Under the opercular flap, margins of gill openings, with numerous corneous shagreen-like denticles are seen. The under surface of the operculum is smooth and unpigmented. Blood vessels can be seen from the inner surface of the operculum. Merely by pulling the pouch-like operculum upwards when the fish is laterally placed, the gill structures beneath are clearly demonstrated (Fig. 6). The operculum contains no opercular bones and is extended into a pointed process; the branchiostegal membrane is continuous with the opercular and has no branchiostegal rays.

### The Integument

The skin is devoid of scales. However, a few degenerate calcified structures may occasionally

be seen on the dorsal part of the trunk, and caudal regions, but these are degenerate forms of rhombic scales. Chromatophores (brown pigment cells) are present on the flank and operculum and are especially numerous on the back. They are absent on the belly region. Occasional orange-colored spots are seen among the chromatophores. These may be large chromatophores and of different color. Numerous chromatophores are found on the spatula especially dorsally. The snout also has sensory pores. We have sectioned a part of the bill and made it transparent by treatment in 70% alcohol, followed by immersing in Beechwood creosote. A camera lucida drawing (28x) was made (Fig. 7). The same procedure was followed for sections of integument from the dorsal surface, belly surface, and flank of the fish (Fig. 8, three views).

A section of integument was taken from the trunk region including the lateral line canal. Dorsal and especially ventral to the lateral line are finger-like lobes which lead to the main canal of the lateral line system (Fig. 9). These lobe-like projections are sensory in function, being connected to the lateral line system. They are distributed along the lateral line canal and can

be followed to the dorsal surface of the head, ending in a definite path at the nostril region. These structures are less numerous in the caudal part of the spoonbill. A few of these sensory structures can be traced forward on the surface of the bill (ventral and dorsal) in large spoonbills.

#### Microscopic Examination of Chromatophores<sup>8</sup>

Celloidin cross sections, 40 microns, of the integument of the anterior trunk region (excluding the lateral line canal) were made, and stained by the hematoxylin and eosin method, as outlined by Guyer (1932). The chromatophores were of a brownish color and arranged in two rows for the most part, although a few chromatophores were seen scattered between these two rows. In the epidermis the chromatophores appeared small, spherical and light brown. In the dermis the chromatophores were more or less stellate-shaped, large and dark brown.

Celloidin cross sections (40 microns) from the mid-dorsal body wall, including the integument, muscle, and connective tissue were prepared as above. It was observed that in the epidermis

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<sup>8</sup> Magnification: 100 diameters

the chromatophores were small and spherical-shaped, but the color varied, that is, alternating from a light to dark brown. The larger stellate-shaped chromatophores were more or less equally distributed in the dermis, extending down adjacent to the muscle and connective tissue, but not arranged in any definite row.

Sections of integument (40 microns) from the mid-trunk region, including the lateral-line canal, were also prepared. Numerous small spherical brownish chromatophores were seen in the epidermis and a few in the dermis. The large stellate-shaped chromatophores were absent, except for a few that appeared around the lateral line canal.

The unusual features of the external anatomy of the spoonbill may be demonstrated by a comparison with another ganoid, the needlefish, Tylosurus longirostrus. The following ten points will serve to emphasize these differences (Fig. 10):

Polyodon spathula

(spoonbill)

1. Bill ends horse-shoe shaped and extends beyond the mouth. Mouth is posterior and ventral to the bill.
2. Bill considered sensory in function.
3. Small, rather degenerate eyes, spherical and ventral to nasal aperture.
4. Large posterior projecting fleshy operculum

Tylosurus longirostrus

(needlefish)

1. Narrow bill composed of ganoin. Upper and lower bills include the mouth.
2. Bill is not sensory in function.
3. Very large, efficient spherical eyes, ventral to the nasal aperture.
4. Rounded operculum.



Polyodon spathula

(spoonbill)

5. Pectoral fins ventrally located and non-lobate.
6. Nasal apertures paired and small (two pairs).
7. Smooth skin (except a few degenerate scales in caudal region).
8. Body compressed laterally as in the perch.
9. Heterocercal tail.
10. Absence of true teeth in adult state.

Tylosurus longirostrus

(needlefish)

5. Pectoral fins laterally located and non-lobate.
6. Nasal apertures large and single (one pair).
7. Smooth skin but rougher than the spoonbill.
8. Cylinder-shaped body and elongated as in the eel.
9. Homocercal tail.
10. Numerous needle-like teeth present.

C           EXTERNAL APPEARANCE OF THE YOUNGEST SPOON-  
              BILL EVER RECORDED   (MISSISSIPPI RIVER)

Thompson (1933) reports to have obtained seven small ganoid fishes ranging in size from 17 to 20 millimeters collected from the Mississippi River near Grand Towers, Illinois. These have been identified as young of Polyodon spathula. These post-larvae of Polyodon were reported to be pale and translucent and so small that most of them fell through the meshes of the seine and into the sand as it was hauled from the water. The water temperature was about 55° F. Four of the specimens were preserved immediately in 80% alcohol and the other three preserved in formalin. Drawings of the smallest of the latter (17 mm.) and of a 200 mm. specimen made by Mr. Mohr, are shown in Figure 11, in order to suggest the striking change in external appearance of the fish.

The reader may wonder why it has taken a century to secure a few small specimens of this conspicuous and common fish of the Mississippi River. Thompson (1933) explains that this scanty yield seems to be associated with the fact that the spawning takes place, and the young grow up in the swift and turbid

portions of the main channel of the Mississippi, where biological phenomena of all sorts are largely "sights unseen". The evidence indicates that the spoonbill migrates extensively through a wide variety of large rivers and bottomland lakes, habitats all of which are more or less inaccessible to tackle used for collecting such material. It also seems likely that the most desirable stages are passed within a few days or weeks time.

## D SEX

It should be mentioned at this time that from all external appearances the male and female spoonbill cannot be distinguished from each other. Even in the spawning season one cannot differentiate the male from the female. The similarity between the two sexes during the spawning season is because of the great abdominal distension in the male due to the fat that collects about the testes at this time.

Stockard (1907) discusses this point. "No indication of sexual dimorphism could be detected, the males and females being indistinguishable in their color, size, and shape, and in the proportion of their external body appendages. A female with her ovaries filled with eggs of the season was usually recognized by the distended condition of the abdomen, and yet even this distended condition of the abdomen was not always valid since the males when fat and in good condition have so extensive a mass of adipose tissue about the testes that their abdomen is almost equally swollen. The fat about the testes

of one male was found to weigh three and three-quarters pounds."

We should also take into account that a poorly fed female spoonbill may be mistaken for a male. The only way to definitely determine the sex of a spoonbill is to study its reproductive system, and look for the presence of ova in the mature specimen.

Allen (1911) says he has never seen sexually mature *Polyodon* weighing less than fifteen or twenty pounds.

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CHAPTER FOUR

GENERAL INTERNAL ANATOMY  
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## A Pericardial Coelem

The coelem or body cavity is large and well developed even in the lowest of vertebrates. In the spoonbill as in other fish the coelem is divided into two parts: the pericardial cavity containing the heart, and the abdominal or peritoneal cavity containing the viscera. The pericardial cavity, which lies just anterior to the pectoral girdle, is triangular in shape with its apex at the anterior end. The shape of the pericardial cavity of the spoonbill differs from that of mammals because of the shape of the heart. The heart is widest at the base and narrows slightly at the apex, the opposite to the mammalian heart. The heart is covered with the visceral pericardium. The parietal pericardium which lines the cavity is a smooth and rather tough membrane.

There are no mesocardia in the adult spoonbill. The heart is attached to the wall of the pericardial cavity at the anterior end by the conus arteriosus and at the posterior end by the sinus venosus. At these two points only are the visceral and parietal pericardia continuous.

## B The Abdominal Coelen

The abdominal cavity is bounded anteriorly by the transverse septum just posterior to the pericardial sac. The transverse septum separates the abdominal from the pericardial cavity. The abdominal cavity extends to a point just posterior to the anal aperture. It is lined throughout by a membrane, the parietal peritoneum, which forms the smooth wall of the cavity, adhering very closely to the muscles of the body wall. It is morphologically equivalent to the parietal pericardium. The parietal peritoneum is a tougher membrane than the parietal pericardium. In studying the relative sizes of the abdominal and pericardial cavities, we found during the dissection that the pericardial cavity measured approximately one-half inch in length whereas the abdominal cavity measured six inches in length, giving a proportion of one to twelve.

## C The Abdominal Viscera

The viscera will be discussed under individual systems. However, the following organs are



exposed when the abdominal cavity is opened. The liver is a large brownish gland in the anterior region of the coelom. It is composed of a long right and left lobe and a much divided median lobe. Between the margins of the right and median lobes the gall bladder is located. It is thin walled and almost completely spherical. If the caecum is raised the stomach is seen. It is shaped like an inverted letter "J". The curved portion lies below the liver and the straightened portion along the body wall. The large fanshaped caecum is divided into several lobes. It is attached to the short duodenum. Posterior to the duodenum is the ileum or valvular intestine. The ileum narrows into the short, rather wide rectum. The rectum leads to the exterior or anal aperture.

The triangular shaped spleen elongates posteriorly ending at the mid portion of the ileum. It lies between the curvature of the short duodenum and the ileum. Large blood vessels run to the spleen. The dorsal aorta also crosses the body cavity and enters the mesenteries near the liver.

The reproductive organs in the specimens available were immature and therefore small and con-

cealed by the other abdominal viscera.

The kidneys are retro-peritoneal and elongate.

#### D The Mesenteries

The viscera are held in place by a number of folds of the peritoneum, the mesenteries. These membranes are delicate. The dorsal mesentery does not attach itself to the entire digestive tract. It is attached to the stomach, duodenum and caecum, but not attached to the oesophagus, ileum, and rectum. A membrane connects the spleen and ileum; this is the lieno-mesenteric ligament. The liver is connected to the loop of the stomach by the gastro-hepatic ligament, and to the oesophagus by the hepato-oesophageal ligament. At the junction of the stomach and duodenum a membrane is attached to the liver. This is the hepato-duodenal omentum. The portion of the dorsal mesentery supporting the valvular intestine (ileum) is the mesentery proper. The anterior end of the liver is attached to the ventral body wall by the suspensory or falciform ligament, which is only one centimeter long. This is a short remnant of a ventral mesentery extending from the mid-ventral wall of the coelom to the mid-ventral surface of the liver.

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CHAPTER FIVE  
DIGESTIVE AND RESPIRATORY  
SYSTEMS  
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## A. REGIONS OF THE ALIMENTARY TRACT

The ventral mouth is the region extending from the lips to the pharynx. It is more or less fleshy. Enormous of mouth but weak of jaw, the paddlefish when adult loses all of its teeth (Fig. 12).

It is interesting to note that the ganoid *Rhizodus* of the Carboniferous period had more powerful teeth than any animal ever known, sharper than and four times as large as the largest living crocodile possesses.<sup>9</sup>

Since the spoonbill supports itself entirely by straining minute plants and animals (plankton) from the surrounding medium, it is not surprising to find that the pharynx contains an elaborate system of structures. The pharynx is the region surrounded and supported by the five pairs of branchial arches. It is pierced by the spiracles dorsally, and by the five nearly semi-circularly pharyngeal clefts laterally. The branchial arches extend forward in an antero-medial direction on both the dorsal and ventral sides of the pharynx. Dorsally the gill arches fuse in a mid-dorsal cartilaginous bar, part of the visceral arch. Posterior to the visceral arch the

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<sup>9</sup>The American Encyclopedia (1879), Vol. 7, p. 614

pharynx broadens into a triangular fleshy mass. On the ventral side of the pharynx the five pairs of branchial arches also fuse in a mid-ventral cartilaginous rod, the basi-branchial cartilage, part of the visceral arch. On each gill arch there is a double series of fine, comb-like gill-rakers, which are long, slender and exceedingly numerous. A more complete description of the structures connected with the gill arches appears below in connection with the respiratory organs and the visceral skeleton. The fifth visceral arch, which is much reduced in size and bears no gill filaments, extends down to the beginning of the oesophagus.

The oesophagus is the first tube-like structure of the digestive system through which the food passes. To the mid-dorsal surface of the oesophagus the large cucumber-shaped swim-bladder is attached by the dorsal mesentery; and posteriorly the swim-bladder is directly connected to the oesophagus by the pneumatic duct. Another duct at the anterior part of the swim-bladder is present but vestigial, or at any rate is not nearly so large as the posterior pneumatic duct. It can be said, then, that the swim-bladder of the spoonbill possesses two pneumatic ducts: the posterior duct clearly shown and the anterior duct, which is vestigial.

This species has a particularly large swim-bladder as compared with other ganoids. The swim-bladder is a hydrostatic organ. Since the swim-bladder opens directly into the oesophagus, air can be taken in directly through the mouth. This classes the spoon-bill with the physostomous group of fishes.<sup>10</sup> While the swim-bladder of fishes (pneumatocyst) is not ordinarily considered a respiratory organ, its possible relations to the lungs of higher vertebrates makes it possible to consider it a respiratory as well as a hydrostatic organ. Dorsally it is attached to the dorsal body wall.

The American gar-pike of the family Lepidostidae has a subdivided swim-bladder used in respiration.

"The swim-bladder of the gar-pike is muscular, freely supplied with blood from the aorta, divided into cells like the lung of a reptile by muscular bundles and opening into the throat by a wide duct (pneumatic) and long slit guarded by sphincter muscles."<sup>11</sup>

In the spoonbill, the swim-bladder is more membranous than muscular and has a comparatively poor blood supply. This fact indicates that the spoonbill has very little use of the swim-bladder in respiration.

The soft fleshy oesophagus leads to the hard

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<sup>10</sup>Walter (1929), (p. 371), includes the bony ganoids, Dipnoi and soft rayed Teleosts in the Physostomi group of fishes. Polyodon is a cartilaginous ganoid and from the above evidence also belongs to the group Physostomi.

<sup>11</sup>The Encyclopedia Americana (1932) Vol. 12, p. 277

and widened portion of the digestive tract, the stomach. The cardiac portion of the stomach is straight and curves to become the fundic portion of the stomach. The stomach becomes knob-like in structure at its pyloric portion just before it constricts to form the pyloric sphincter. Posterior to the pyloric sphincter is the short duodenum, or small intestine (3 inches long), which leads to the ileum or valvular intestine, which ends in the short, wide rectum, followed by an opening the anal aperture. Figures 13 and 14 show digestive tract.

The spiral valve in *Polyodon* consists of about seven folds or spirals but are not nearly as well developed as they are in *Blasmodrancha*. Surface absorption is aided by the pyloric caecum in *Polyodon* as well as by the valvular intestine. The pyloric caecum will be discussed under the topic pertaining to glands.

Nodular markings were present on the caecum, stomach, and duodenum, but absent on the oesophagus, ileum, and rectum. When these nodular structures on the stomach, caecum, and duodenum were cut open, small nematode worms were removed. These nematodes showed parasitic infection of parts of the digestive tract. These nodular structures were seen on other

speenbills and on the same organs; namely, the oesophagus, caecum, and duodenum. In one instance, two tape-worms were lodged in the abdominal cavity, and not in any particular organ. These cestode parasites, *Dibethruim hastatum*,<sup>12</sup> were three to four inches long.

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<sup>12</sup>Steckard (1907) quotes Linton for the above classification of the tape-worm.



## B INTERNAL STRUCTURE OF THE DIGESTIVE TRACT

The mucous lining of the oesophagus, when exposed presents numerous large fluffy papillae at its anterior portion. Posterior to the papillae many long, slender folds called rugae are present. These rugae become larger and fewer at the point where the cardiac end of the stomach begins. The muscular walls of the elongated stomach thicken posteriorly and the gastric cavity becomes smaller. The short duodenal portion also has a thick muscular wall and a small cavity leading to the ileum. The ileum or colon has a spiral valve which enlarges the surface of the intestine for absorption. Along the rectum a few folds can be seen that extend in a longitudinal direction; these are the rectal folds. The caecum when cut open presents a soft spongy mass; this is glandular tissue.

Numerous nematodes were taken from the mucous layer of the stomach and from the partially digested food material. In one specimen forty-three nematodes were lodged in the stomach, ten in the duodenum and five in the caecum. This large number of nematodes shows that the stomach of the spoonbill is the favorable place for nematode infection.

## C GLANDS

Caecum

An evolutionary significance can be observed in the pyloric caeca of ganoids. This is discussed by Walter (1929). "The ganoids in general show a transitional condition by the presence of a degenerating spiral valve, along with the introduction at the same time of 'pyloric caeca', which in higher fishes take the place of an elasmobranchian spiral valve as a device for enlarging the internal surface of the food tube."

Attached to the duodenum is the large pyloric caecum. It is divided into several lobe-like portions ridged at the ends. The number of lobes varies in different specimens of the same species. The pyloric caecum is part of the digestive tract and is used as an organ of digestion in the spoonbill. It is not a rudimentary organ as is the appendix in man. By cutting away a piece of caecum and squeezing the remainder, one can see partially digested food oozing out.

Alexander (1915) says the pyloric caecum of the spoonbill has been formed phylogenetically by several small pyloric caeca becoming confluent at the base.

### Liver

The liver attaches itself to the ventral and anterior portion of the oesophagus by means of a ligament, the hepato-oesophageal ligament. As stated, the liver consists of three lobes. The right lobe ends at the pyloric portion of the stomach. The left lobe terminates at the fundic portion of the stomach. The large spherical gall bladder, almost equal in size to the human gall bladder (one and one-half inches in diameter), is found attached to the ventral surface of the right lobe of the liver. It touches the margin of the caudate lobe of the liver. Bile secretion by the liver is collected by a series of tubules, some of which empty into the gall bladder. The gall bladder is drained by the ductus choledochus or common bile duct, which leads from the gall bladder to the duodenum.

### Pancreas

A light yellowish gland is seen when the caecum is raised; this is the pancreas. Alexander (1915) says the duodenum receives the duct of the pancreas, but the pancreatic duct leading to the duodenum could not be traced.

### Spleen

The red triangular spleen is not connected by any ducts to the digestive system, but is attached to

the dorsal anterior portion of the ileum by a highly vascular mesentery, the lieno-mesenteric ligament.

Although not a digestive organ, the position of the spleen on the ileum makes it more convenient to include its description here.

## D RESPIRATORY STRUCTURES

### Gill Rakers

On the pharyngeal walls of the branchial arches in *Polyodon* there have developed rows of gill rakers. These gill rakers evidently serve as strainers to prevent food from passing out with the respiratory current. The gill rakers in the spoonbill are especially adapted for separating the food from the mud. They are large, brittle, comb-like in arrangement, and curve in an opposite direction to the gill filaments. The rakers arise from the base of the branchial arches and extend into the pharynx as slender rods in a densely packed layer close to the branchial gill arch. They extend into the pharynx for a distance of about one centimeter. There are nine sets of gill rakers. There are 46 gill rakers to an inch and a rough estimate totals about 598 gill rakers on one surface of the first gill. The gill rakers on the anterior surface are larger posteriorly than are the gill rakers on the posterior surface of the branchial arch, but their number is about the same. On the middle part of the arch the filaments and rakers are longest.

Figure 15 shows the arrangement of gill rakers and gill filaments. Most of the gill rakers average one and a half inches in length and are curved at the base, giving the appearance of a small fish-hook. The gill rakers on the more posterior gills become progressively reduced in number. The gill rakers on the seventh visceral arch are more uniform in size than in any of the other branchial arches. They measured 0.75 inches on a typical specimen. The following table shows the length of both surfaces of each visceral arch at the point where the gill rakers are attached to the respective visceral arch, and the total number of gill rakers per visceral arch.

Gill	Visceral arch	Inches on anterior and posterior surface of visceral arch	Number of gill rakers on entire gill arch (46 gill rakers per inch)
1.	3	26.0	1196
2	4	24.6	1132
3	5	20.4	938
4	6	18.4	846
5	7	5.0 (measurement taken on one side)	230

Total 4342

From the above table we see that there are 4342 gill rakers on four gills and the seventh visceral arch. In the entire respiratory system we would then have 4342 times 2 or a total of 8684 gill rakers in the spoonbill. This number should be considered as only approximate. The very large number of gill rakers in Polyodon emphasizes their functional importance to the fish. They are more numerous in the spoonbill than in other fishes because the spoonbill obtains its food by straining it from the water by means of their tremendous number of gill rakers.

The interbranchial septum is reduced in size as in other ganoids. The filaments are firmly attached to the septum except the distal ends, which project freely about one centimeter. In studying the gill structures of lower and higher forms of fishes we find that the more primitive fishes possess the best developed interbranchial septa. In Elasmobranchs the interbranchial septa are well developed, in Ganoids they are reduced, (Polyodon) and in Teleosts, which include ninety percent of the fishes, there are no interbranchial septa present.

Four sets of demibranchs are present in Polyodon,

one set on each of visceral arches three to six. There are no demibranchs on arch seven or on the hyoid arch. There is no pseudobranch or false gill around the spiracle. The seventh visceral arch is incomplete and extends as a finger-like projection posteriorly. Further discussion of the visceral arches will be dealt with under the skeletal system.



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**CHAPTER SIX**  
**THE CIRCULATORY SYSTEM**  
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## A INJECTION OF BLOOD VESSELS

### Red Mass Injection<sup>13</sup>

We mixed four grams of carmine thoroughly with eight cubic centimeters of distilled water in a mortar and added concentrated sodium hydroxide drop by drop until a transparent red color resulted. Ten grams of Knox's gelatine (instead of French gelatine as Guyer suggests) was soaked in distilled water until the gelatine was swollen and soft; then it was removed to a porcelain evaporating-dish and melted at a temperature of about 45 degrees C. While the gelatine was yet fluid we slowly added the coloring matter, stirring constantly until a homogeneous mixture was obtained. Before the mass was allowed to cool a 25 percent acetic acid solution was added drop by drop, stirring thoroughly until the mass became slightly opaque and the odor of ammonia gave place to a faint acid smell. This change must be carefully watched, for a few drops too much of the acid will spoil the entire mass by precipitating the carmine. If the ammonia is not completely neutralized, on the other hand, the coloring matter will diffuse through the walls of the injected vessels

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<sup>13</sup>Guyer (1932), p. 85.

and stain the surrounding tissues.

Walker<sup>14</sup> makes results more certain by mixing one part of laboratory water with four parts of distilled water, and then determining the exact amount of the laboratory acetic acid which will neutralize it. Just before using, the mass should be heated and strained through clean flannel wrung out of hot water.

Three spoonbills were injected: one was injected through the heart and the red mass was forced anteriorly through the ventral aorta and afferent branchial arteries. The second injection was through the dorsal aorta at a point where it lies free in the abdominal cavity. This second injection was forced anteriorly into the efferent branchials and posteriorly into the distal portion of the aorta. The third injection was through the caudal artery. The spoonbill injected through the dorsal aorta took the best injection, as was observed during the course of dissection. The injection through the heart and ventral aorta also was successful, but the injection through the caudal artery did not yield satisfactory results. The melted gelatine cools within the blood vessels forming a gel which shows up very well because it swells the vessels to their full extent.

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<sup>14</sup>Walker, as quoted by Guyer (1932) p. 85.

Blue Mass Injection

A gelatine was prepared as above. To the warm mass a sufficient quantity of saturated aqueous solution of Berlin blue was added to give the desired blue color to the veins. This was injected into the hepatic portal vein at the point where it enters the liver.

## B THE HEART

The heart of the spoonbill is composed of four chambers: the sinus venosus, auricle, ventricle, and conus arteriosus. The heart does not undergo the differentiation characteristic of the more complex heart of higher animals. The auricle and sinus venosus are thin-walled. The auricle receives the non-oxygenated blood from the sinus venosus and the ventricle sends it forward through the conus arteriosus (Fig. 16). The ventricle is relatively small in all Elasmobranchs, but in Polyodon spathula it is quite large and thick-walled. It is more or less pyramidal-shaped with the base posteriorly, two faces directed ventrally, and the other dorsally in position. A section through the ventricle shows its greatly thickened walls. The lining, unlike that of the auricle, is rougher and irregular. The tendinous cords, chordae tendinae, present in the ventricle of the spoonbill are muscular at one end and drawn out into tendons at the other. The ends are attached to the opposite walls and prevent the ventricle from spreading beyond its capacity. The base of the ventricle is joined anteriorly to the conus arteriosus, a short tube, the wall of which is muscular. The three rows of semi-lunar valves of the conus have not yet

been mentioned. The valves of the anterior row are best developed and cover practically the entire lining of this section of the conus. The valves in the succeeding tiers decrease in size the farther they are located posteriorly. The coronary arteries are numerous on the dorsal surface of the ventricle. The auricle (atrium) in the spoonbill is thin-walled and is dorsal to the ventricle. Internally the auricle is smooth and possesses no tendinous cords which pass across the cavity from one wall to the other as in the ventricle. Communication between auricle and ventricle takes place through the auricular ventricular valve, a very small pocket-like flap.

The sinus venosus may be described as a large delta-shaped collecting sac, the anterior mid-portion of which leads to the auricle, and the base of which is posterior in position. Dorsally the sinus venosus is fused to the posterior part of the roof of the pericardial cavity. Connecting the sinus venosus with the auricle is the sine-auricular aperture, which is guarded by three sino-auricular valves (Fig. 16). These valves are nothing more than folds of endothelial lining of the auricle projecting into the sinus venosus. They are so arranged as to permit the free passage into the auricle, but a flow in the opposite direction is prevented by their closure.

## C THE VEINS

The following vessels enter the sinus venosus: laterally the posterior cardinal veins unite with the anterior cardinal veins to form the Ducts of Cuvier, which finally enter the sinus venosus. Posteriorly and medially the large hepatic vein enters the sinus venosus. The hepatic vein is the result of the fusion of the two hepatic veins in their course from the liver to the sinus venosus.

Owing to their small size and the fact that they were not injected, the small branches of the systemic veins have not as yet been traced.

### The Renal Portal and Hepatic Portal Systems

In fishes, besides the capillaries which unite the outward distributive system of blood vessels (arteries) with the inward collecting system (veins) there are two notable strainer-like complexes of capillaries or portal systems within the kidneys and liver respectively, that interrupt the stream of blood returning to the heart. The former is the renal portal system, an additional capillary complex involving the kidneys. The renal portal system is a device for the return of blood from the caudal region through a capillary network in

the kidneys. The renal portal system joins the main blood stream secondarily.

The extra capillary network of the digestive system comprises the Hepatic portal system. The Hepatic portal system consists of a system of veins from the spleen, stomach, ileum, duodenum, and caecum which enter the liver and there break up into capillaries. Fig. 17 shows plan of circulation in a fish (after Walter (1929)).



D VENTRAL AORTA AND AFFERENT BRANCHIAL  
ARTERIES

Emerging from the ventricle is the conus arteriosus. It is not so conspicuous externally as it is in Elasmobranchs; but careful study indicated that it is about half an inch in length. When we cut open the wall of the conus arteriosus, we observed nine semi-lunar valves, three in a row, one close to the other (Fig. 18). These valves appear as large crescent-shaped pockets, which are muscular at the base and membranous at the apex. The conus arteriosus narrows slightly at its anterior end and becomes the ventral aorta. The ventral aorta lies in a deep groove, the groove being formed in an anterior projection of the pectoral girdle. The ventral aorta passes forward several inches unbranched until it reaches the anterior end of the groove. When the ventral aorta was first exposed only a single pair of afferent branchials at the extreme anterior end could be seen. This pair of afferent branchial arteries supplies blood to the first pair of gills which are located on the third visceral arch (Fig. 19). The second pair of afferent branchial arteries loops off

the ventral aorta dorsal and posterior to the first pair and can be seen only by dissecting dorsal to the ventral aorta. This pair supplies blood to the second pair of gills on the fourth visceral arch. From the dorsal surface and posterior to the second pair of afferent branchial arteries a pair of arteries are given off, one to the left and one to the right. These arteries bifurcate on both sides to become the third and fourth afferent branchials. The third pair is more anterior; the fourth pair rise dorsally and then pierce the cartilage of the sixth visceral arch posteriorly. These arteries supply blood to the third and fourth pairs of gills respectively, which are on the fifth and sixth visceral arches. The afferent branchial arteries pass along a canal in the visceral arch just internal to the gill filaments. We shall name these canals the afferent branchial canals.

From each of the afferent branchial arteries, minute arterioles are given off to supply the gill filaments. These arterioles are too fine to be traced by gross dissection. However, during the course of dissection, small openings were seen on the afferent branchial arteries, these openings being the points at which the delicate arteriole structures were broken. The afferent branchial arteries carry blood to the gill region to be

oxygenated. The afferent branchial arteries are of uniform size around each gill arch and become smaller as they reach the region of the pharynx, terminating in the dorsal part of the branchial region.

The capillaries to the gill filaments are connecting links between the arterioles of the afferents with the efferent arterioles leaving the gills. The fine structure of the capillary network prevents the tracing of a single capillary by dissection. The wall of each capillary is made up of a single layer of endothelial cells, forming the effective membrane through which the exchange of gases is made.

## E EFFERENT BRANCHIAL ARTERIES AND DORSAL

## AORTA

The dorsal aorta is formed by the union of four pairs of efferent branchial arteries (Fig. 20). They are not so uniform in size as are the afferent arteries. The first pair of efferent branchial arteries is a bifurcation of the dorsal aorta. They are the smallest of the efferent branchial arteries. The first efferent collector gives off a branch, the hyoidean efferent artery. This artery is usually called the common or posterior carotid artery.<sup>15</sup> It goes to supply blood to the head and spiracle region. The other branch to either side, which is a continuation of the first efferent branchial artery, supplies the first pair of gill arches. The second pair joins the dorsal aorta immediately posterior to the first pair and supplies the second pair of gill arches. The third pair is quite large, looping off the dorsal aorta and curving back in a V-shaped manner to supply the third pair of gill arches. The fourth pair of efferent branchial arteries also loop off the dorsal aorta and are quite large. The fourth pair of efferent branchial arteries bifurcate to either side to form the small pre-trematic branch that supplies the fourth gill arch and goes to the third gill slit, and a larger post-

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<sup>15</sup>Daniels (1928), p. 161.

trematic branch that supplies the fourth gill arch and goes to the fourth gill slit.

The dorsal aorta is composed of a short anterior paired part and a long posterior unpaired portion. The paired portion gives rise to the hyoidian arteries; the unpaired part receives the second, third, and fourth pairs of efferent branchial arteries. The unpaired dorsal aorta then passes backwards, where it becomes extremely large. It is enclosed in a cavity dorsal to the wall of the pharynx and enclosed by a thick membrane, a portion of the parietal peritoneum. The unpaired dorsal aorta then passes backward, and in its course through the body gives off arteries to the digestive tract and its appendages, to the extremities, and to the body musculature and deeper structures.

After leaving the canal in the gill region, the dorsal aorta enters the abdominal coelom dorsal to the liver and ventral to the oesophagus. It passes backward through the abdomen unbranched and unsupported by mesenteries for a distance of several inches; it finally comes to the region of the median lobe of the liver where it lies adjacent to the portal vein. The dorsal aorta now gives off a short, broad artery, the gastro-hepatic artery. The arterial supply to the digestive tract is very complicated at this point. The short gastro-hepatic vessel turns to the left and divides into a large

hepatic artery which goes to the dorsal surface of the liver, and a large gastric branch which supplies the anterior and posterior dorsal surface of the stomach. The hepatic artery divides into smaller hepatics and finally into capillaries within the liver. The gastric artery divides into smaller gastric branches and finally into capillaries on the wall of the stomach. At the point where the gastro-hepatic leaves the dorsal aorta, but to the right, the dorsal aorta gives off two arteries; one to the ventral surface of the oesophagus, the oesophageal artery, and the other the gastro-duodenal artery, which bifurcates to form a gastric branch to the ventral cardiac portion of the stomach, and a branch to the duodenum, the duodenal artery. (The large pyloric caecum is very vascular. This structure indicates that the caecum is functional during life.) Underneath the caecum (dorsal surface) a blood sinus is present. From this vascular structure on the dorsal surface of the caecum a short wide caecal artery is given off to the caecum. The caecal artery divides into about five moderately large caecal branches also supplying blood to the caecum. The dorsal aorta continues posteriorly over the spleen enclosed in a thick fibrous sheath. This portion of the aorta is the splenic artery. It passes over the spleen and gives

off splenic branches too small to be dissected. However, by raising the artery at this point, it will break off from the spleen, to which smaller branches pass. Continuing posteriorly, the dorsal aorta passes over the mid-dorsal surface of the valvular intestine or ileum to become the posterior dorsal intestinal artery. Smaller arteries terminate at the rectum; these are rectal arteries. From the dorsal surface of the ileum the posterior intestinal artery gives off about nine small arteries to the kidneys or mesonephroi; these are the renal arteries.

CHAPTER SEVEN  
THE SKELETAL SYSTEM



## INTRODUCTION

Walter (1929) divides the ganoids into two classes on the basis of skeletal development. The first and more primitive class comprises the cartilaginous ganoids, which include the paddlefish, *Polyodon* of the United States; *Psephurus* of China; the sturgeons, *Acipenser* and *Scaphirhynchus*; and the gar-pike *Lepidosteus*. These are called cartilaginous ganoids because their skeletons are partly cartilage and partly bone, and show a transition between Elasmobranchs and bony fishes. The other surviving class includes the bony ganoids, so called because the cartilaginous components of the skeleton have been quite completely replaced by bone. The bony ganoids include the *Polypterus*, *Callimnichthys* of Africa, and the bowfin, *Amia*, found in rivers and lakes of the United States.

The endoskeleton is briefly described by Kingsley (1925). "The endoskeleton is outlined in cartilage, but membrane bones may be added to the primitive framework, especially in the heads of the higher groups. In Cyclostomes and Elasmobranchs, it never passes beyond the cartilage stage, but in all other groups more or less of the cartilage is converted into bone, the amount of this increasing, the higher the animal in the scale. To the cartilage bone thus formed, membrane bones are added,

these being more numerous in the skull, there being none in the vertebral column or ribs and few in the appendicular skeleton."

Since Polyodon is a cartilaginous ganoid, and the ganoid fishes are the next higher group of fishes over the Elasmobranchs, we should expect to find only a few membrane bones and many cartilaginous parts in the skeleton of Polyodon.

## A AXIAL SKELETON

The axial skeleton includes the framework of head, trunk and tail (notochord in *Polyodon* and lower vertebrates).

### The Cranium

The skull of *Polyodon spathula* is composed of a relatively thin-walled cranium or brain case, a series of cartilaginous visceral arches and capsules for the organs of special sense. Figure 21 shows left side view of the skull, jaws, and pectoral girdle and inner view of the right jaw in *Polyodon*. The cranium is dorso-ventrally depressed with the long cartilaginous rostrum protruding anteriorly into the spathula. At the most postero-lateral portion of the rostrum are found the olfactory capsules for the nasal apparatus. The cartilages of the capsules are exceedingly thin-walled and open to the exterior by way of the nasal apertures. The nasal capsules fuse with the cranium. In the nasal fossa are found the lamellae. These are fifteen lamellae in each nasal fossa, arranged in a radial fashion, starting from a point on the dorso-medial wall of the fossa. Fig. 22 shows the arrangement of lamellae in the fossa. These folds or lamellae are called Schneiderian folds in *Acanthias*

according to Daniels (1928). The folds produce accessory folds in which are found the olfactory sense cells. The optic capsule does not fuse with the cranium. On each side at the posterior third of the cranium is the auditory aperture or spiracle in which the organs of hearing are located. Between the auditory and nasal capsules is the comparatively small ellipitical-shaped optic fossa for the eye. Overhanging the fossa is the supra-orbital crest, the anterior projection of which is the pre-orbital and the posterior one the post-orbital process. The ventral portion of the orbit bends downward forming the basal angle of the orbit. Anterior to the basal angle and extending from the margin of the cranium is a projection which is the an-orbital process, which Allis (1923) calls the ectethmoidal process in the dogfish.<sup>16</sup> The wall of the orbit is composed mainly of thin cartilage, except the portion medial to the orbital process, which is composed of a thick-walled cartilage.

Figure 24 shows a dorsal view of the skull of Polyodon spathula. Note that the entire dorsal surface is dermal in composition, except for a small part, the chondocranium, located between the anterior fontonelle and the fessa. The spathula measured approximately 16 cm. in length, whereas the region from the anterior

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<sup>16</sup>Allis as quoted by Daniels (1928), p. 42.

portion of the olfactory fossa to the posterior end of the pteretic measured 8.5 cm. This estimate shows the proportionate length of the snout with the remainder of the skull. The dermal ossicles are numerous on the snout. The cartilaginous rostrum is widest posteriorly and narrows anteriorly within and in the center of the spathula. The olfactory capsules are latero-ventrally located, just anterior to the orbits, but may be partially seen in dorsal view. The portion of bone between the optic fossae is the frontal. The region posterior to the optic fossae, to the point where it fuses with the pteretic, is the parietal bone. Sutures are lacking in *Polyodon* hence a sharp distinction between the different bones is difficult to make. The hyomandibular can be partially seen in dorsal view attached to the mid-ventral portion of the cranium. The widest part of the cranium, the parietal, measured 4.4 cm.; the widest portion of the snout measured 4.2 cm. Attached to the posterior part of the pteretic is the post-temporal bone, which is long and thin and inclines at an angle in a postero-lateral position. The post-temporal is attached to the pectoral girdle at its posterior end and is sometimes considered a part of the girdle.

### Mandibular and Hyoid Arches:

The visceral skeleton is composed of a series of cartilaginous arches which surround the pharynx. The arches may be divided into two groups: the mandibular and hyoid arches, and the five pairs of branchial arches, which support the gill filaments. The mandibular or first arch, upon which the teeth are borne in the young spoonbill, has become most highly specialized of all the visceral arches.

The components of the upper and lower jaw of the spoonbill make *Polyodon* an interesting species for anatomical study from the evolutionary standpoint. In the dogfish the lower jaw consists of a single piece of cartilage Meckel's and the upper jaw also of a single piece of cartilage pterygo-quadrate. This is reduced in *Polyodon* and modified between two portions of dermal bone; externally Meckel's cartilage is covered by the dentary, and internally by the splenial bone. Meckel's cartilage is best developed posteriorly. The pterygo-quadrate cartilage of the upper jaw is modified in a similar manner by being partially covered externally by the maxillary, and internally by the palatine bone.

The mandibular arch is attached to the cranium through the hyomandibular. This is known as the hyostylic type of attachment. The hyomandibular is broad and

flat anteriorly and curves to become less broad and flat posteriorly. Anteriorly the hyomandibular is attached to the mid-ventral third of the cranium and posteriorly it connects to the symplectic cartilage. The symplectic is a boot-shaped piece of cartilage to which many parts of the skull hinge. It is interesting to mention that the symplectics are found only in Teleosts and two ganoids, *Acipenser* and *Spathularia*. The symplectics appear distal to the hyoids, as a part of the hyoid arch.

Fig. 23 shows the attachments to the symplectic cartilage. The postero-ventral surface of the hyomandibular hinges to the dorsal surface of the symplectic, the stylohyal to the posterior surface, and the maxillary and Meckel's cartilage to the antero-ventral surface of the symplectic cartilage respectively. The cerato-hyal ends posteriorly in a knob-shaped structure which is the stylohyal cartilage, and medially as the hypohyal cartilage. In *Polyodon spathula* the stylohyal appears as a partial fusion to the ceratohyal.<sup>17</sup> The sub-opercular is attached to the postero-lateral surface of the stylohyal. Antero-dorsally the symplectic is bound by ligaments, the quadro-symplectic tendons, to the pterygo-quadrate cartilage.

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<sup>17</sup>This structure is not named by Traquair in Figure 21 and appears as a separate structure.

Ossification centers are found in the spoon-bill; as for example in the hyomandibular and ceratohyal cartilages. This is significant in that it shows the transitional stage *Polyodon* holds between the Elasmobranchs and the Teleosts. An additional point of interest in this direction is that the dorsal portion of the skull of *Polyodon* is almost entirely covered with thin plates of dermal bone derived from ganoid scales.

#### Branchial Arches:

The branchial arches consist of a number of segments. The first branchial arch may be taken as a type. It has five segments. The first pair of branchial arches arise from the posterior portion of the buccal cavity just medial and posterior to the hyomandibular, and ends on the ventral visceral arch as the basi-branchial cartilage. The second, third, and fourth branchial arches are similar in structure to the first branchial arch. A typical branchial arch (Fig. 25) shows two large cartilaginous segments constituting the greater portion of the arch, the dorsal segment; the epibranchial, and the ventral segment, the cerato-branchial. These two segments attach laterally by septa of connective tissue. Medially



and attached to the epibranchial cartilage is the small pharyngo-branchial cartilage. Medially and ventrally attached to the ceratobranchial, is the small hypobranchial cartilage. Medial to the hypobranchial is the basibranchial cartilage.

In *Polyodon* the gill rakers are chitinous. Their number and structure have been discussed under digestive and respiratory systems.

Fig. 26 shows the upper side of the ventral visceral arches in a typical 90 cm. specimen.

There are three basibranchial cartilages. The first basibranchial fuses with the basihyal and measured 2.5 cm., the second 1.8 cm., the third 1.8 cm. in length. A pair of basihyal cartilages fuse anteriorly to the mid-ventral portion of the first basibranchial cartilage. Lateral to the basihyals, the hypohyal cartilages are attached to either side. To the first basibranchial are attached the first three pairs of hypobranchial cartilages. The fourth pair of hypobranchials fuse and attach ventral to the second basibranchial. The first four pairs of ceratobranchials are attached to the respective pairs of hypobranchials. The fifth ceratobranchial is attached to the third basibranchial cartilage. The fifth rudimentary branchial arch is fused to the fourth

branchial arch posteriorly and bears only gill rakers. All the branchial arches are approximately the same length.

Since the skull of *Polyodon* is composed of two distinct parts, the cartilaginous chondrocranium and the overlying dermal plates, we shall list these structures separately. The following table shows the dermal and cartilaginous portions of the skull.<sup>18</sup>

<u>Dermal Parts of Skull</u>	<u>Cartilaginous Parts of Skull</u>
1. Pterotic	1. Rostrum
2. Post-temporal	2. Chondrocranium
3. Parietal	3. Pterygoquadrate (palatoquadrate)
4. Frontal	4. Meckel's cartilage
5. Parasphenoid	5. Hyoid arch <ul style="list-style-type: none"> <li>a. Hyomandibular</li> <li>b. Symplectic</li> <li>c. Ceratohyal</li> <li>d. Hypohyal</li> <li>e. Stylohyal</li> </ul>
6. Maxillary	6. Branchial arches <ul style="list-style-type: none"> <li>a. Pharyngo-branchial</li> <li>b. Epibranchial</li> <li>c. Ceratobranchial</li> <li>d. Hypobranchial</li> <li>e. Basibranchial</li> </ul>
7. Palatine	7. Capsules of organs of special sense <ul style="list-style-type: none"> <li>a. Olfactory capsule</li> <li>b. Optic capsule</li> <li>c. Otic capsule</li> </ul>
8. Dentary	

<sup>18</sup>In this use of the word skull the author follows Kingsley (1926) who includes the cranium, capsules of organs of special sense, and the visceral skeleton under this term.

Dermal Parts of SkullCartilaginous Parts of Skull

9. Splenial
10. Ossicles of snout

Foramina, through which nerves and blood vessels pass perforate the cranium. On making a sagittal section through the head and spathula we found that the rostrum contains fat-like material. The brain is small and primitive and surrounded by thick masses of cartilage and dermal bone. The bone is external to the cartilage encasing the brain.

Vertebral Column

The vertebral column in Polyodon spathula, because of its simplicity, is especially interesting. It consists of a long central column which is essentially the enlarged sheath of the notochord, or notochordal sheath, and the jelly-like substance, the notochord, within the sheath. Anteriorly the central column is continuous with the occipital region of the cranium, at which point the column becomes larger and firmer whereas posteriorly it is observed to extend to the dorsal lobe of the caudal fin. According to Forbes and Richardson (1909) the vertebrae are imperfectly formed and the anterior vertebrae are single.

My investigations confirm their statement. Above the central column there is a series of neural arches, best developed in the trunk region, less developed in the caudal region. There are both neural and haemal arches in the caudal region. The neural arches protect the spinal cord, the haemal arches protect the caudal blood vessels. In the trunk region the dorsal skeletogenous septum is best developed and firmly attached to the vertebral column. A lateral view of the vertebral column in the mid-trunk region is shown in Fig. 27. The soft notochord is very primitive, and only partially surrounded by acentrous vertebrae consisting of separate arcualia. Note that the dorsal and ventral surfaces of the notochord are covered by cartilaginous arcualia, whereas the lateral surfaces are exposed. On the dorsal surface are the large basidorsals, united from either side to form a neural arch continued by a neural spine. Between the bases of the basidorsals are the small triangular interdorsals. The ventro-lateral regions of the notochord are covered on each side by the basiventrals from which a vestigial rib projects. The basiventrals do not meet below the notochord. Between the basiventrals are the small interventrals. In the caudal region the neural arches are least developed and the haemal arches are most marked, as in the region of the fulcra. The haemal arches protect the caudal artery and

vein; hence we can account for the greatest development of the haemal arches in this region. The central column is best developed in the trunk region. Dorsal to the central column and to either side are the neural plates that fuse dorsally and make up the neural spines. These cartilaginous plates are more or less rectangular in shape at the anterior and trunk regions of the column, and triangular in shape in the caudal region of the column. The neural plates have their base on the notochordal sheath. The neural spines are large and project in a dorso-posterior direction. The neural spines, neural arches, and central column are covered by the axial membrane from the head to the tip of the tail region. Fifty-eight neural arches are present on the notochordal sheath. The neural plates are perforated by the roots of the spinal nerve. This is more clearly shown in the anterior and trunk regions. The ventral foramina are not clearly shown in dissection, however Kingsley (1926) states that they appear during vertebral development of *Polyodon*.

With reference to Chondrostei in general, my investigations show that the notochord in living forms is quite unstricted, and surrounded by a very thick sheath outside which are no true centra. Only pleural

ribs occur in living Chondrostei, but they are unknown in extinct families. Dorsal ribs are absent. In Polyodon spathula the ribs are of the pleural type, but vestigial.

## B APPENDICULAR SKELETON

The appendicular skeleton is the framework for the girdles and fins, the latter being attached to the girdles.

### Skeleton of the Paired Fins

Fig. 28 shows a lateral view of the pectoral girdle. The pectoral girdle of the spoonbill is complicated by the addition of membrane bones to the cartilage bones. Such membrane bones are homologous with the dermal plates of the exoskeleton. The dermal portions of Polyodon consist of the clavicle, cleithrum, and postclavicle whereas the cartilaginous portions consist of the coracoid and scapular regions. The branchial artery and nerve pass through the scapular foramen to supply the fin. The post-temporal bone as previously stated may be included as a dermal portion of the pectoral girdle, serving as a bone attachment between the girdle and the skull. The homologies of the pectoral girdle of Polyodon and other Chondrostei have been discussed by Homer (1924).

Fig. 29 shows the medial view of part of the pectoral girdle with pectoral fin attachment. The pectoral fin is fan-shaped, the proximal portion of which consists of four basal pieces of cartilage. The first two pieces (anterior) of basal cartilages fuse as they touch the surface of the girdle. This portion of cartilage is called the propterygium. The third single piece posterior to the propterygium is the mesopterygium. The fourth single and smallest piece of cartilage is posterior to the mesopterygium and is called the metopterygium. Several radials are found between the propterygium and mesopterygium and fuse with them. The dermal portion of the pectoral fin shows radial arrangement (dermotrichia) but not so marked as in the post-dorsal, caudal or anal fins.

#### Pelvic Girdle and Fin

The framework of the pelvic girdle and fin consists of a thin segmented cartilaginous plate, (8 pieces), the basipterygium, and 11 cartilaginous radials which are ventral to the basipterygium. These radials are unsegmented and extend in a postero-ventral direction. The dermal portion of the pelvic fins is similar in structure and arrangement to the pectoral fins.

Skeleton of the Unpaired Fins:    The Posterior

Dorsal Fin

The cartilaginous radials of the dorsal fin are thin and not well marked. They are unsegmented. The dermal portion consists of radials that extend in a postero-dorsal direction. Richardson (1909) says there are fifty to sixty-five dorsal rays present. My estimation showed forty to fifty dorsal rays present in three specimens.

Caudal Fin

The cartilaginous radials of the caudal fin are prolongations of the haemal spines of the haemal arches. The radials extend in a posterior direction and continue backward as the dermal fin rays, which extend in a posterior direction.

Anal Fin

The cartilaginous radials in the anal fin are more marked than in any of the other fins. They are largest anteriorly and become smaller posteriorly. There are two rows of radials, the distal row, as in the pelvic girdle, are the better developed. There are eighteen distal radials in the anal fin. The dermal portion consists of dermatrichia. The dermo-



trichia extend in a postero-ventral direction. According to Forbes and Richardson (1909), about sixty anal rays are present. This number is approximately correct.

#### The Fulcra

Just anterior to the dorsal lobe of the caudal fin are large spines (modified scales) called fulcra. They consist of the hardest material that can be found in the spoonbill. The fulcra are considered a part of the exoskeleton since they arise as direct ossifications in the corium, no cartilage appearing in their development. (Kingsley 1925).

**ORIGINAL CONTRIBUTION**

### Summary of Original Contributions

In dissecting the integument, branched canals passing out from the lateral line canal were observed (Fig. 9). Histological sections of integument showed variations in pigmentation due to the differences in size, shape, and amount of chromatophores present.

The large swim bladder was found to be permanently connected with the oesophagus by a pneumatic duct, thus placing the spoonbill in the Physostomous group of fishes. From its poor blood supply the swim bladder is not considered to have much respiratory function in *Polyodon*.

From the presence of partly digested food in the pyloric caecum and its rich blood supply, it is believed that this organ takes an active part in digestion in the spoonbill. The liver was found to have a very large spherical gall bladder one and one-half inches in diameter.

There were found to be nine sets of gill rakers on each side of the pharynx. Each set except the most posterior one contained about 500 individual rakers, and the entire respiratory system was found to contain approximately 8684 gill rakers. The spiracle was devoid of a pseudobranch or false gill.

Three rows of semilunar valves were found in the conus arteriosus of which the more posterior are

best developed. The sino-auricular opening was found to be guarded by a set of three valves. The walls of the ventricle were found to have ridges, the corda tendinae. The ventral aorta gives rise to three pairs of afferent arteries, the third pair again bifurcating to produce a total of four pairs of arteries which supply blood to gill arches one to four respectively. The dorsal aorta is formed by the union of four pairs of efferent branchial arteries. The remarkable condition of the dorsal aorta which lies free in the abdominal coelom, unsupported by mesenteries, for a distance of several inches, is an unusual feature.

The attachment of the upper jaw to the cranium is of the hyostylic type, that is by means of the hyoid arch.

There is a symplectic cartilage on the mandibular arch, a cartilage which has been reported in only two genera of ganoids. Ossification centers were found in the hyomandibular and ceratohyal cartilages. Meckel's cartilage is surrounded externally by the dentary bone, and internally by the splenial bone. The pterygo-quadrato cartilage of the upper jaw is likewise surrounded by bone, externally by the maxillary and internally by the palatine bone. The above points indicate the transitional stage *Polyodon*

holds between Elasmobranchs and Teleosts.

The dorsal surface and the ventral surface of the skull is covered with dermal plates of bone except for a small part where the chondrocranium is exposed (Fig. 24).

It was found that the basihyal and first basibranchial fuse, and that the fourth hypobranchials fuse together ventral to the second and third basibranchials.

The cartilaginous branchial arches are segmented. Dorsally the arch consists of a large epibranchial and a small pharyngo-branchial cartilage; ventrally of a long ceratobranchial and two small cartilages; the hypobranchial and medially the basibranchial cartilage.

The vertebral column is primitive, acentrous, and consisting of separate arcualia surrounding the notochord. The notochord is not constricted by centra. Vestigial ribs project from the basiventrals. Small interdorsals are found between the bases of the large basidorsals and small interventrals are present between the basiventrals.

The pectoral girdle consists of membrane bones and cartilage bones, showing a further evolutionary

significance in *Polyodon* as a linking genus between Elasmobranchs and Teleosts. The membrane bones are the post-temporal, post-clavicle, clavicle and cleithrum; the cartilagenous portions of the girdle consist of the fused scapula and coracoid cartilages.

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## BIBLIOGRAPHY

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**I L L U S T R A T I O N S**



Figure 1. Dorsal view of Polyodon  
spathula showing large paddle-shaped  
snout

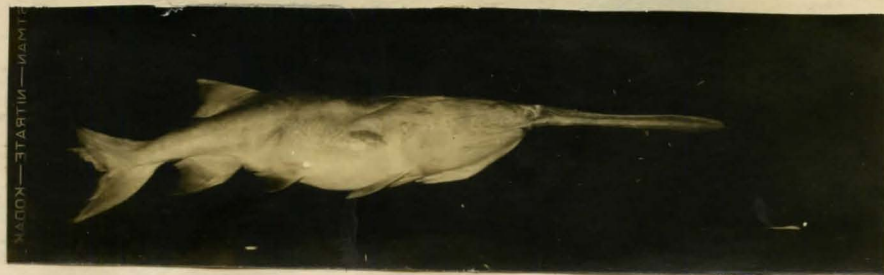


Figure 2. Lateral view showing color  
variation from dorsal surface of body



Figure 1. Dorsal view of Polyodon  
spathula showing large paddle-shaped  
snout

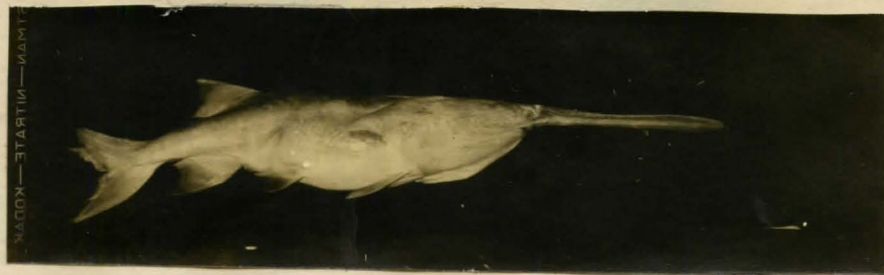


Figure 2. Lateral view showing color  
variation from dorsal surface of body

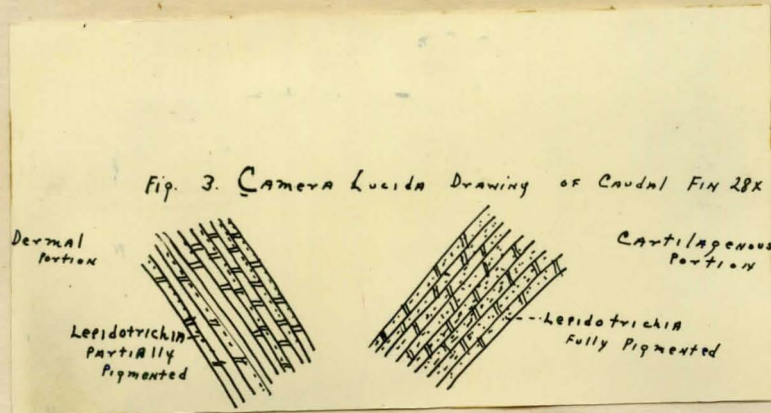


Figure 3.



Figure 4. Note large, ventral, horse-shoe shaped mouth



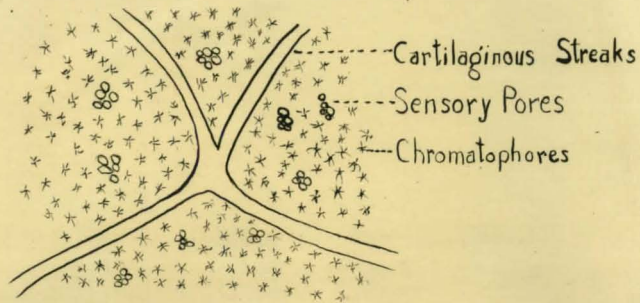


Figure 5. Shows cluster-like patches containing sensory pits on the operculum



Figure 6. Note fleshy operculum and gill structures beneath

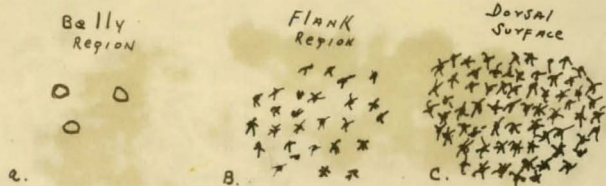
Fig 7 Camera Lucida Drawing of Snout 28 X



The sensory pores are found in grape-like clusters scattered throughout the bill between which are found the chromatophores.

Figure 7.

Fig. 8 Distribution of Chromatophores ON VARIOUS SURFACES OF THE Spoonbill. C.L.D. 28X



- a. Absence of Chromatophores (Few yellow pigment spots)
- B. Moderate Number of Chromatophores
- C. Numerous Chromatophores

Figure 8.

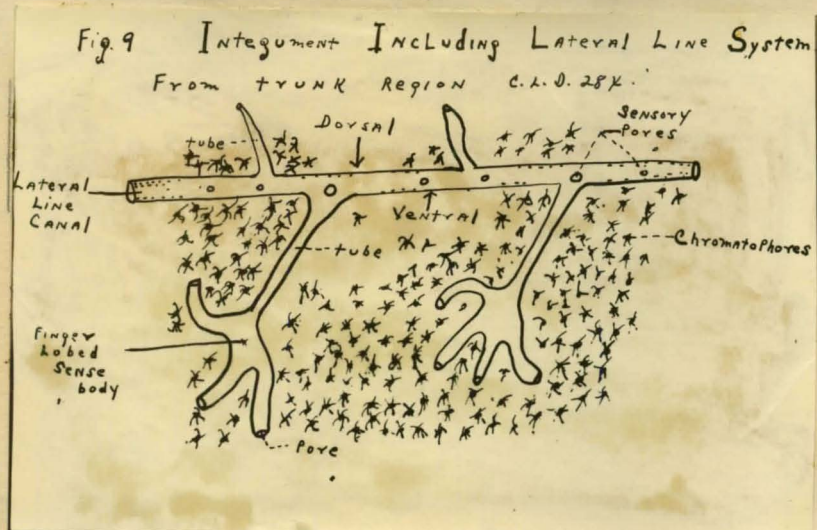


Figure 9. Note that sensory pores lead directly into lateral line canal



Figure 10. Note the many different external features of two ganoids, the spoonbill and the needlefish

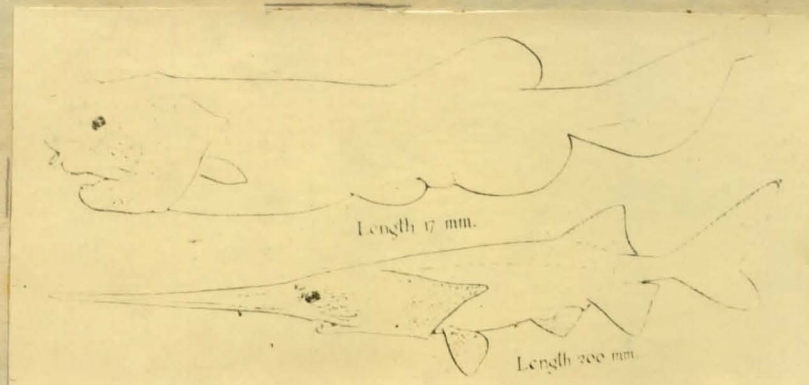


Figure 11. Postlarva and young of Polyodon spathula from Thompson (1933).

Note large head, absence of complete fin formation and proportion of depth to length of body in 17 mm specimen; also the formation of the snout, complete fin formation, lateral line canal, and elongation of the head and body in general in the 200 mm specimen.



Figure 12. Large fleshy mouth and absence of teeth

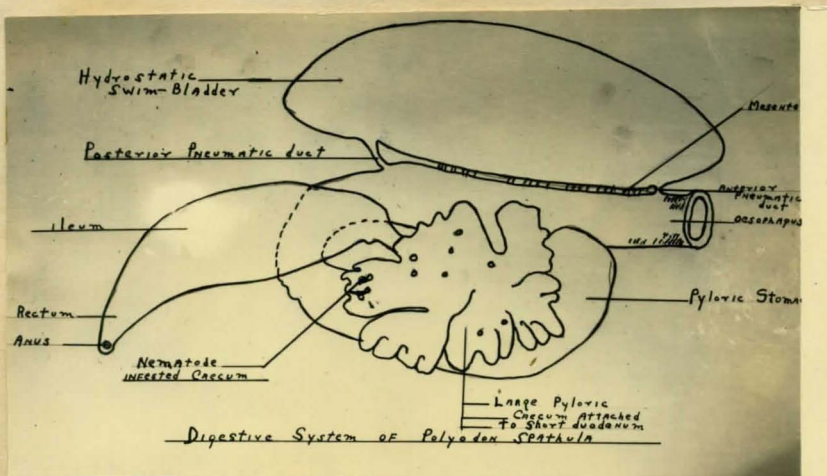


Figure 13. Digestive system of Polyodon spathula. Note large pyloric caecum confluent at the base

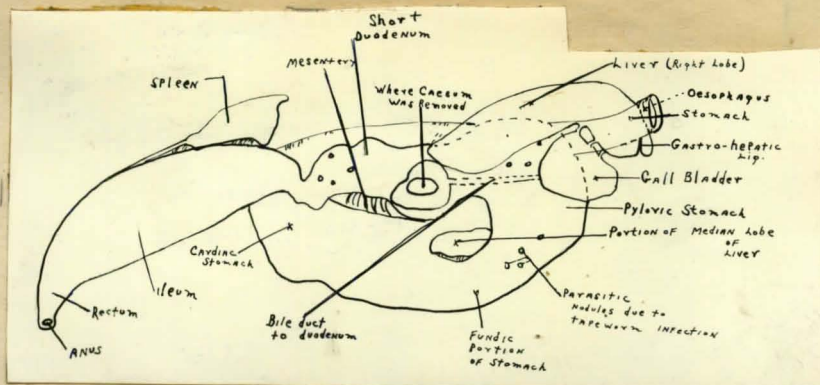


Figure 14. Digestive system with caecum removed

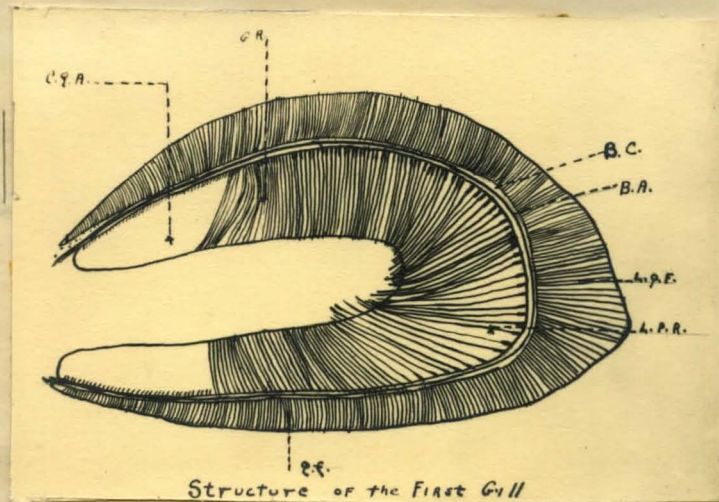


Figure 15. Note tremendous number of gill rakers and filaments

C.G.A. Cartilaginous gill arch    B.A. Branchial artery  
 G.R. Gill rakers    B.C. Branchial canal  
 L.P.R. Large posterior rakers    G.F. Gill filaments  
 L.C.F. Large fill filaments (posteriorly)

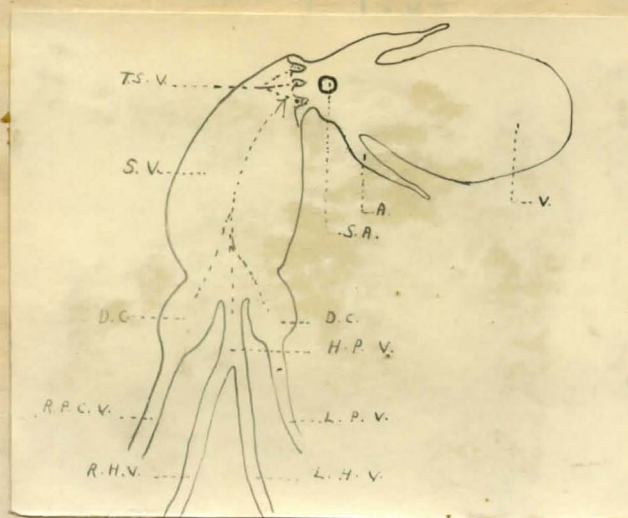


Figure 16. Relationship of sinus venosus to heart.

S.V. dorsal to heart in normal position  
 T.S.V. Three sino-auricular valves    S.V. sinus venosus  
 R.P.C.V. Right post-cardinal vein    D.C. Duct of Cuvier  
 R.H.V. Right hepatic vein    L.H.V. Left hepatic vein  
 L.P.V. Left post-cardinal vein    H.P.V. Hepatic vein (large)  
 S.A. Sino auricular aperture    A. Auricle  
 V. Ventricle

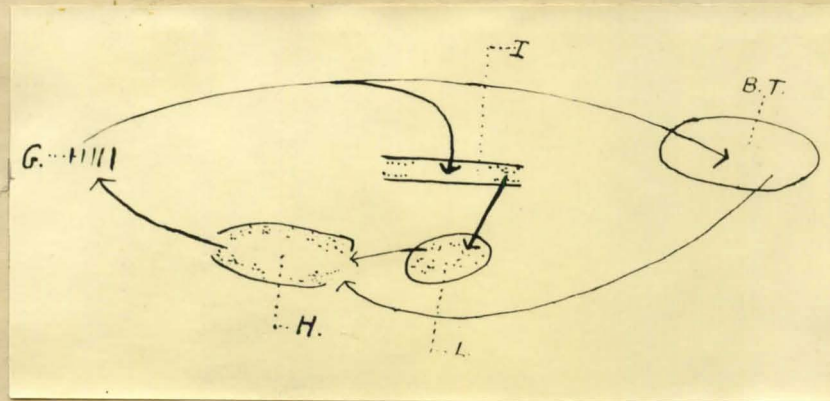


Figure 17. Plan of circulation in a fish  
(after Walter)

G. Gills

I. Intestine

B.T. Body tissues

L. Liver

H. Heart

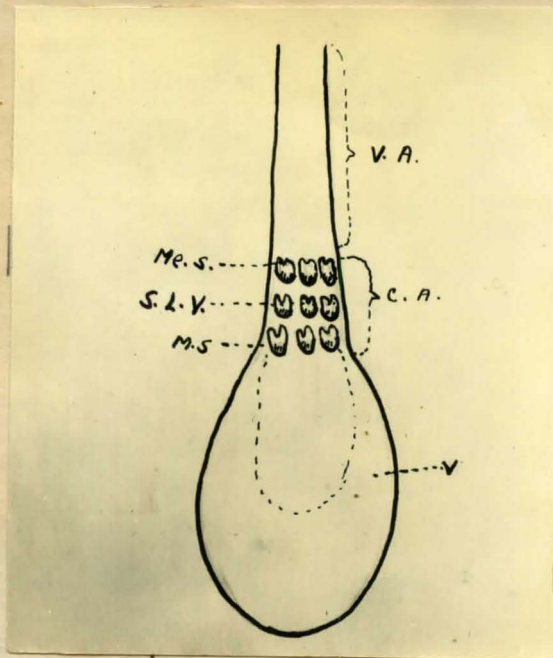


Figure 18. Conus exposed to show arrangement of  
semi-lunar valves

V.A. Ventral aorta      C.A. Conus arteriosus

S.L.V. Semi-lunar valve      V. Ventricle

Me.S. Membranous part of semi-lunar valve

M.S. Muscular part of S.L.V. at base



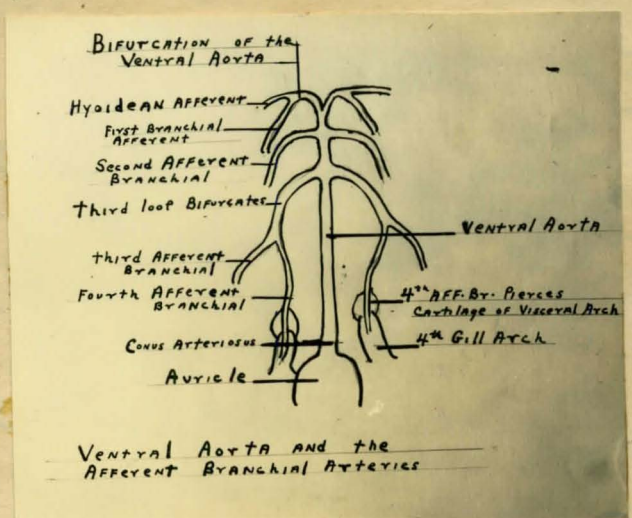


Figure 19.

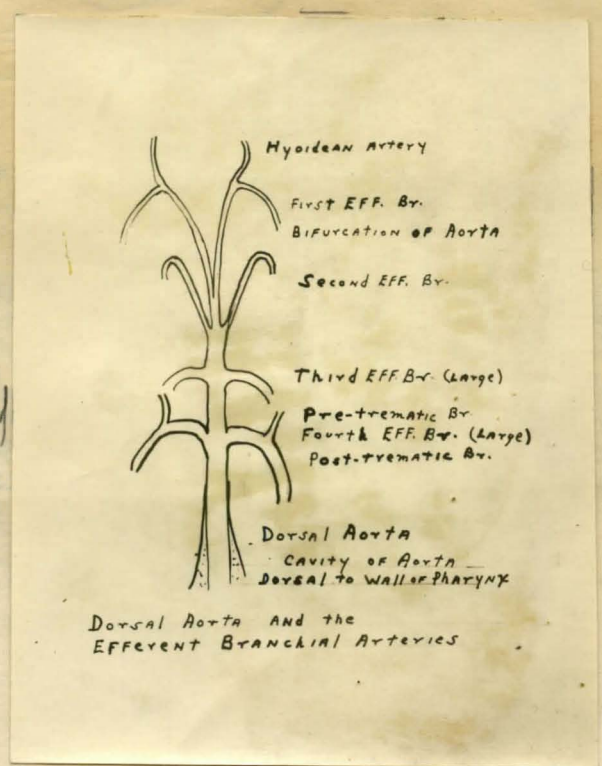
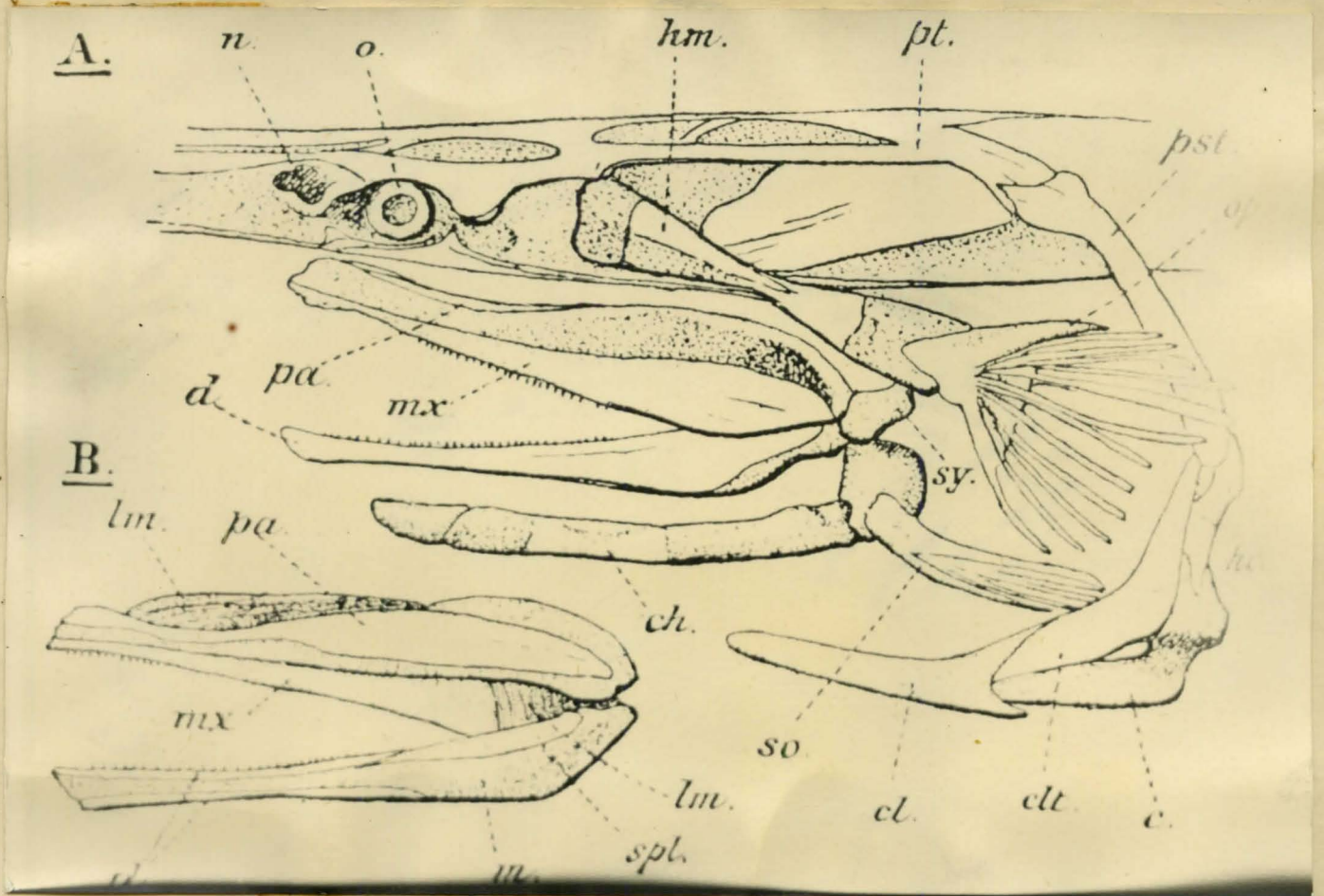


Figure 20

Figure 21



*Polyodon folium*, Lac. (After Traquair.) **A.** Left-side view of skull, jaws, and pectoral girdle; **B.** inner view of right jaws. *c*, Coracoid; *ch*, ceratohyal; *cl*, clavicle; *clt*, cleithrum; *d*, dentary; *hc*, postclavicle; *hm*, hyomandibular; *lm*, levator muscle; *m*, Meckel's cartilage; *mx*, maxilla; *n*, olfactory capsule; *o*, optic capsule; *op*, opercular; *pa*, palatine; *pst*, post-temporal; *pt*, pterotic; *so*, subopercular; *spl*, splenial; *sy*, symplectic,

(From Goodrich, Vert.  
Craniata, 1909)

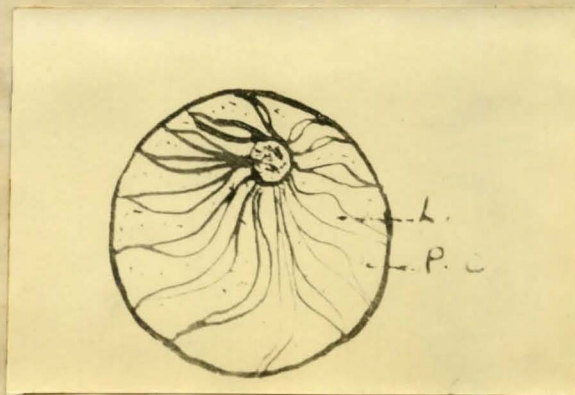


Figure 22. Arrangement of lamellae in nasal fossa.

L. Lamellae has olfactory sense cells  
P.C. Pigmented sensory cells

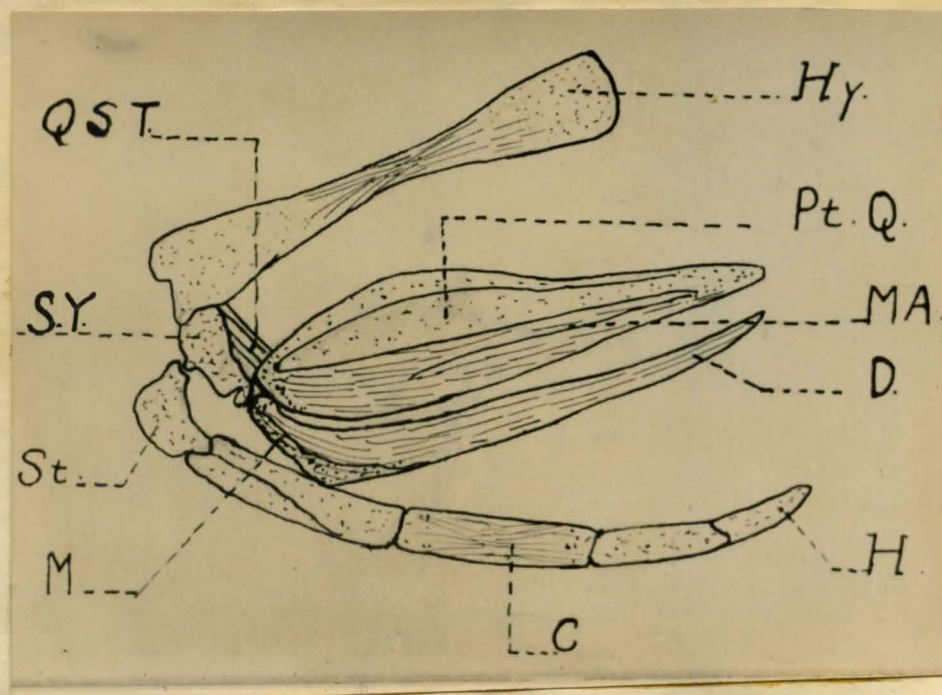


Figure 23. Part of skull showing relationship and attachments to the symplectic cartilage. Nat. size of small specimen (60 cm.)

C. ceratohyal    D. dentary    H. hypohyal  
Hy. Hyomandibular    M. Meckel's cartilage    MA. Maxillary  
Pt.Q. pterygo-quadrate    QST. quadro-symplectic tendons  
St. stylohyal    Sy. symplectic

Figure 24. Dorsal view of the skull of Polyodon spathula

C. chondrocranium  
F. fontonelle  
F', fossa  
Fr. frontal  
H. hyomandibular  
OC. olfactory capsule

Of. optic fossa  
P. parietal  
Pt. pterotic  
S. snout  
O. ossicle  
R. rostrum

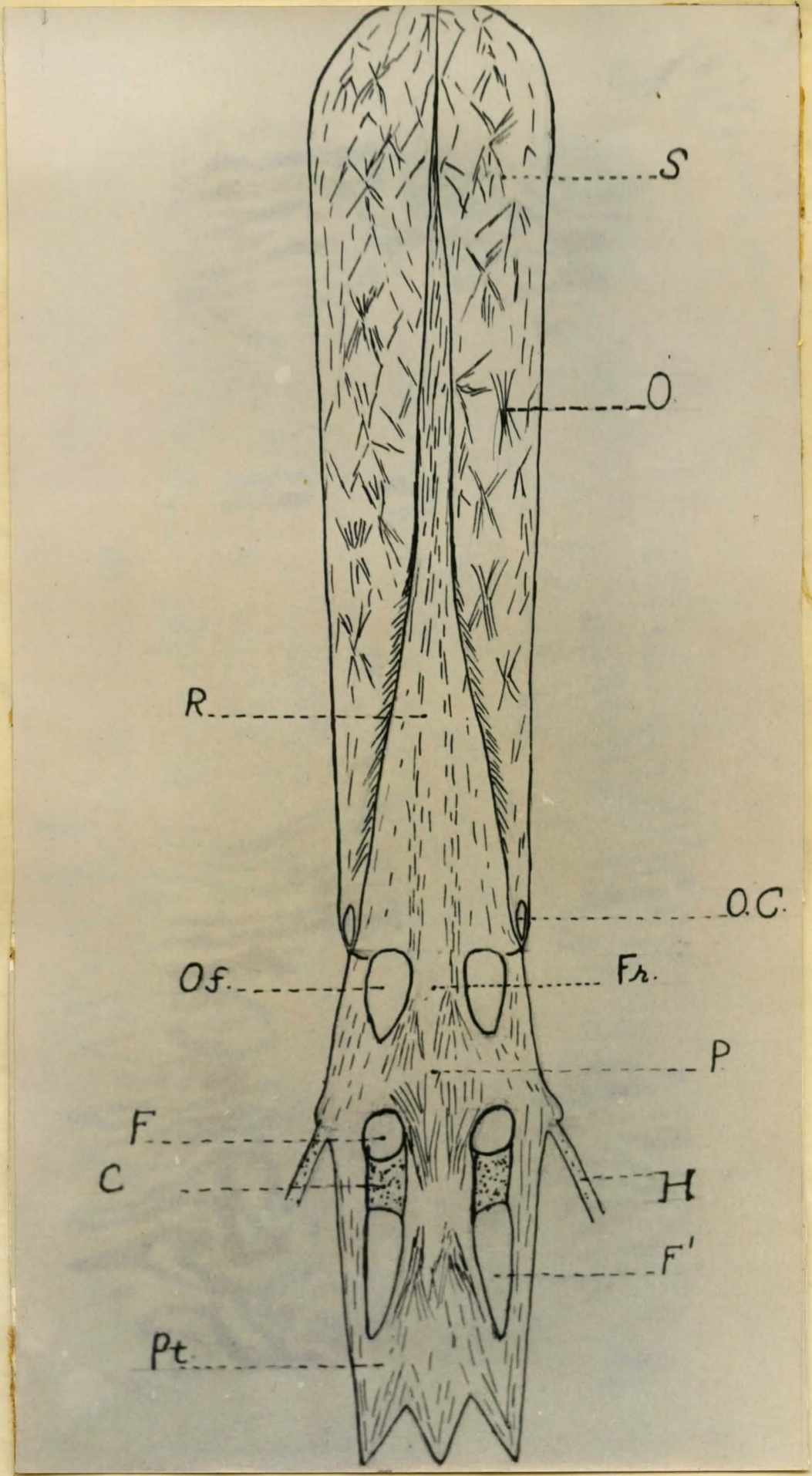


Figure 24.

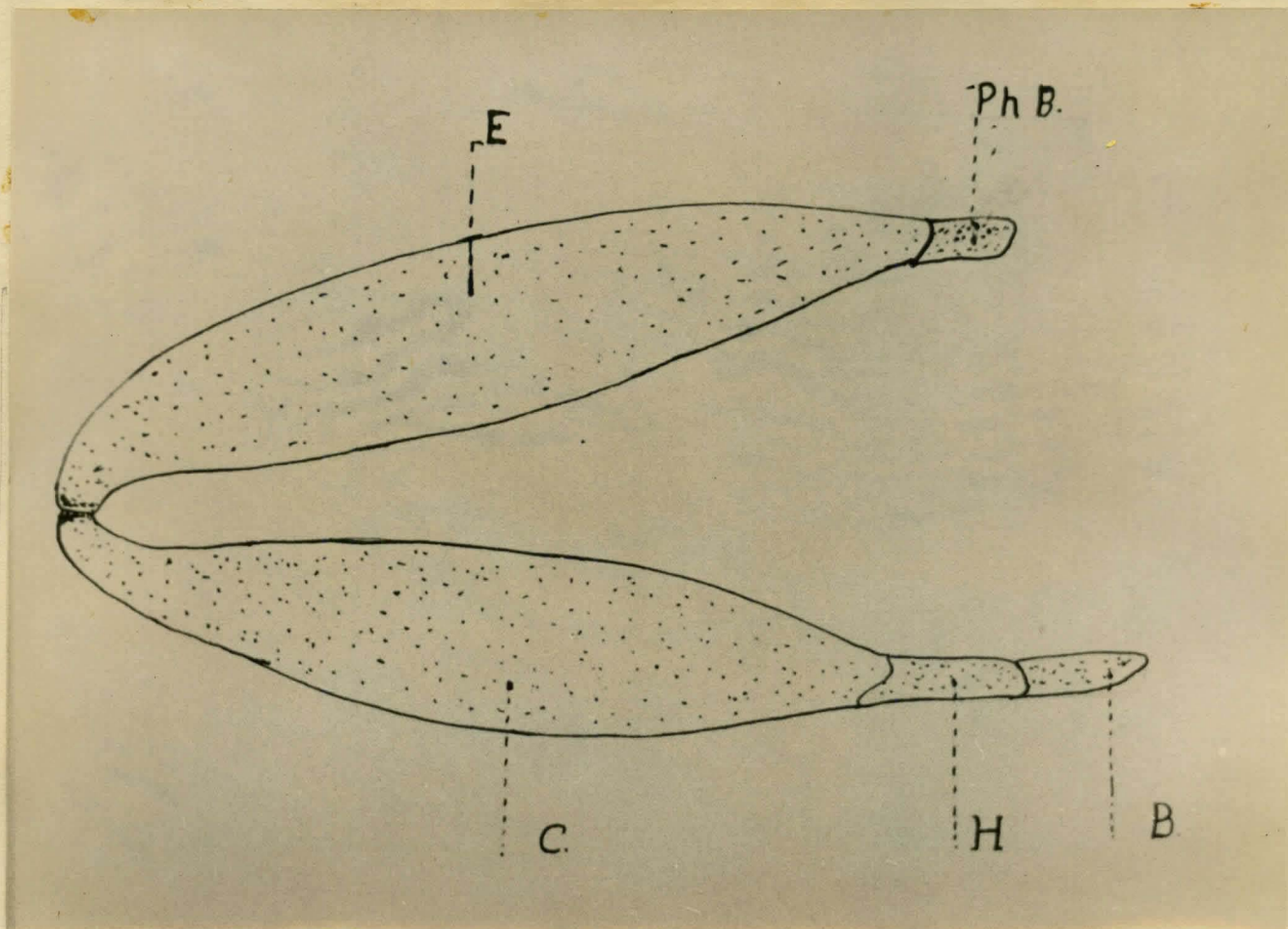


Figure 25. A typical branchial arch of 90 cm.  
specimen (nat. size)

- E. Epibranchial
- PhB. Pharyngo-branchial
- C. Cerato-branchial
- H. Hypo-branchial
- B. Basibranchial

Figure 26. Upper side of the ventral visceral arches in a  
typical 90 cm. specimen

Bb1. basihyal fused to first basibranchial  
H.H. hypohyal joins basihyal  
H1. first hypobranchial  
C. ceratohyal  
Cb1. ceratobranchial  
Hf4. fused hypobranchial 4th

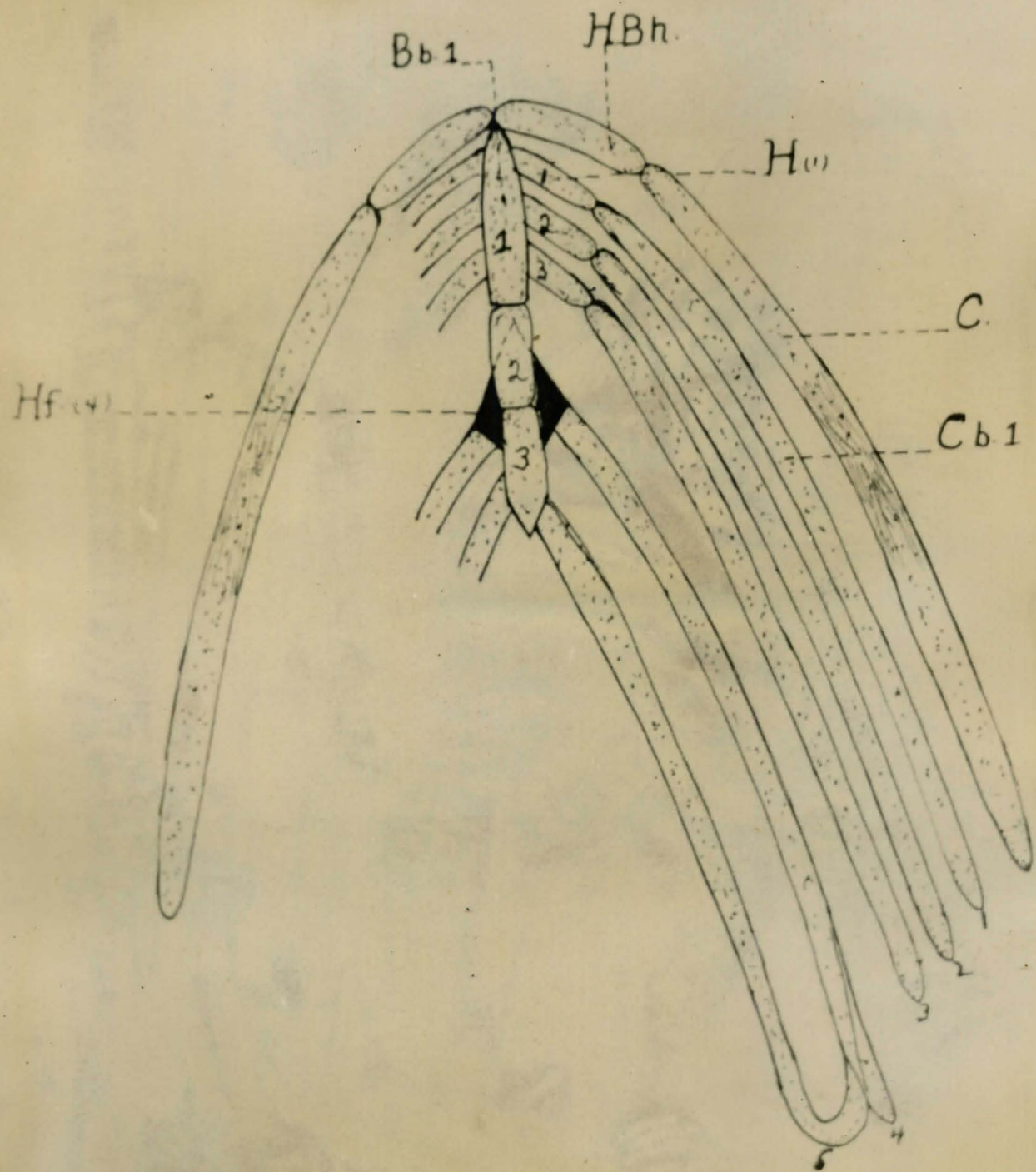


Figure 26.



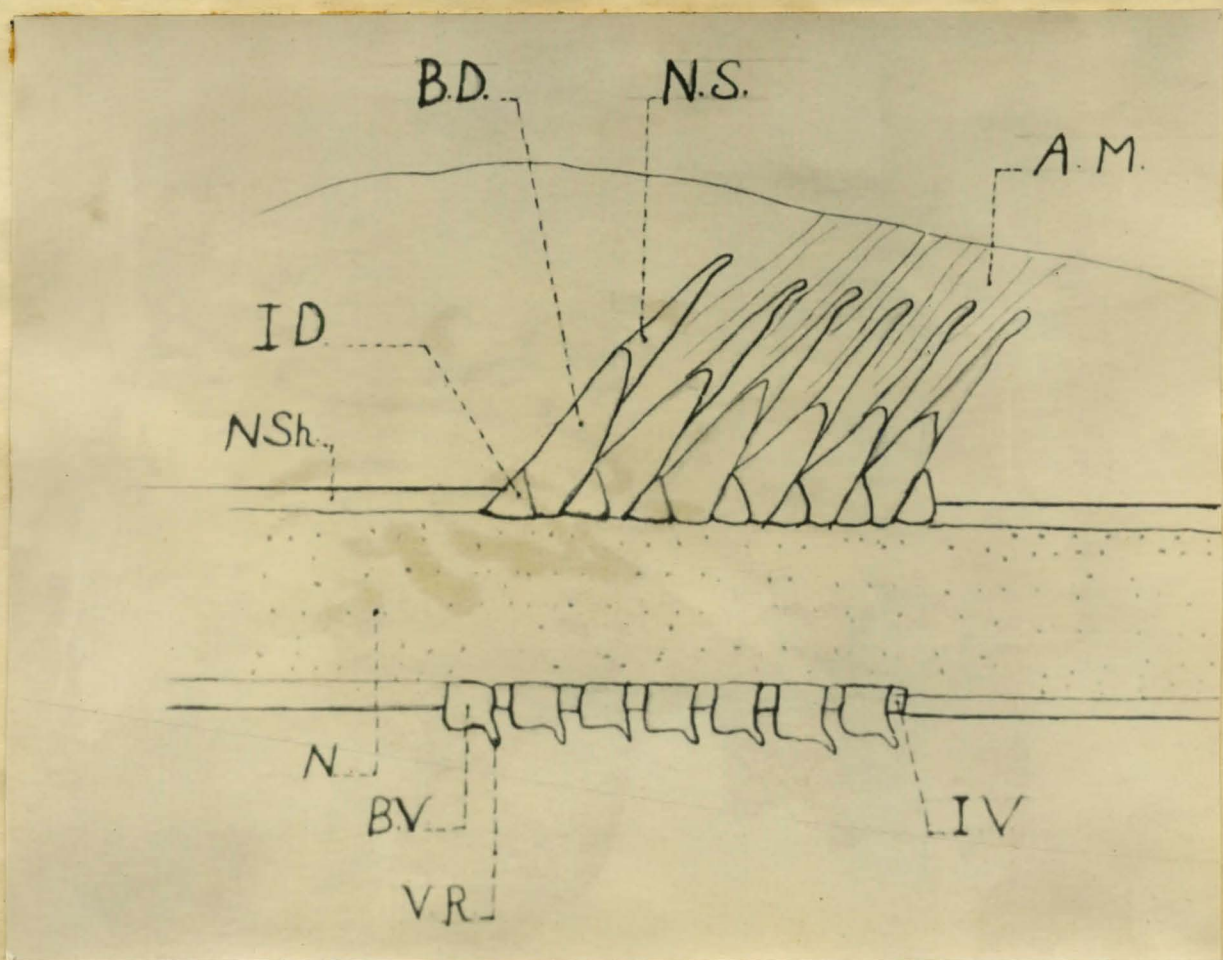


Figure 27. Lateral view of vertebral column from mid-trunk region (2X)

- |            |                |              |                    |
|------------|----------------|--------------|--------------------|
| <u>AM.</u> | Axial membrane | <u>Iv.</u>   | Intervertebral     |
| <u>BD.</u> | Basidorsal     | <u>N.</u>    | Notochord          |
| <u>BV.</u> | Basiventral    | <u>NS.</u>   | Neural spine       |
| <u>Id.</u> | Interdorsal    | <u>N Sh.</u> | Notochordal sheath |
|            | <u>VR.</u>     |              | vestigial rib      |

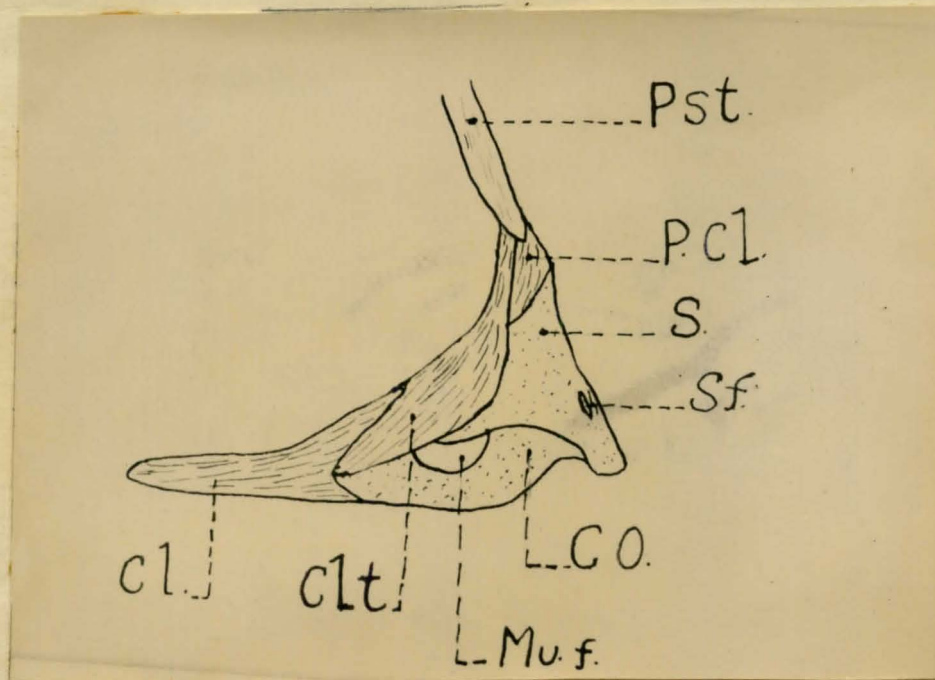


Figure 28. Pectoral girdle of a 60 cm. specimen nat. size.

Cl. clavicle      Clt. cleithrum      CO. coracoid  
Muf. muscular foramen      P.Cl. post-clavicle  
Pst. post-temporal      S. scapula      Sf. scapula foramen

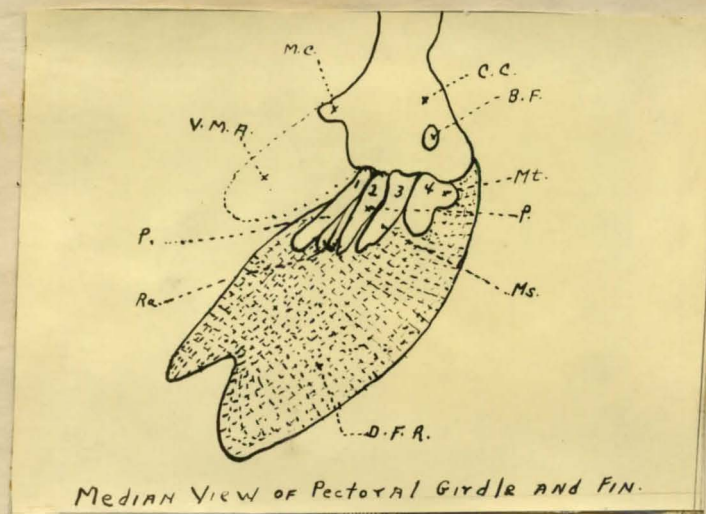


Figure 29. Median view of pectoral girdle and fin

M.C. median cartilage      V.M.A. ventral muscle attachment  
P. propterygium      R.A. radials (2)  
D.F.R. dermal fin rays      M.S. mesopterygium  
M.T. metapterygium      B.F. branchial foramen  
C.C. coracoid cartilage