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The Swim Bladder in the Serrasalminae

With Notes on Additional Morphological Features

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INTRODUCTION

The Serrasalminae is a subfamily of the teleost fishes belonging to the family Characidae of the order Ostariophysi (see Tables I and II). This group includes the carnivorous "piranhas" and the vegetarian "pacus." All members of this subfamily are limited to the fresh waters of South America.

As a group these fishes are deep-bodied and laterally compressed. Both the nuchal and ventral margins continue the slope of the head, thereby forming portions of the anterior border of the fish as it swims through the water. The mouth is relatively heavy but not particularly large. A common characteristic is a series of scutes along the ventral margin that produce a saw-like edge from which the group derives its name, the "serrated salmons." (Since early times the systematists—Linnaeus, Cuvier, etc.—have listed these fishes in the salmon family because of the possession of an adipose fin. Lacépède, in 1803, was the first to use the term "serrasalmes.")

The most recent comprehensive treatment of this subfamily is that of Gosline (1951). In that paper he brought together the systematic information available through the use of external characters. The present paper is concerned in the main with a re-examination of this group from the point of view of internal characters. A few other morphological features are also examined in view of their individual interest.

Table III lists the various specimens of serrasalmids used in this study. Representatives of the type species of all of the accepted genera and about half of the genera in synonymy were examined in

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one fashion or another. The accepted genera, *Acnodon, Mylesinus* and *Utiaritichthys,* are not considered to have been studied adequately because of a lack of specimens, and therefore references to them must be tentative. The number of specimens per genus and their varied distribution in time and geographic locale are such as to give an "average" picture of the condition of the structures under consideration rather than the possibility of an unusual specimen or a population variation.

TABLE I.—GENERA OF SERRASALMIDS

Family Characidae; Subfamily Serrasalminae

Accepted Genera	Genera in Synonymy
Colossoma	Waiteina Reganina Melloina
Piaractus	
Mylossoma	Starksina
Mylesinus	
Utiaritichthys	
Myleus	Tometes Myloplus Orthomyloplus Paramyloplus
Acnodon	
Metynnis	Myleocollops Sealeina
Catoprion	
Pygopristis	
Serrasalmus	Pygocentrus Gastropristis Rooseveltiella Pristobrycon

ACKNOWLEDGMENTS

This project was initiated in 1948 with a gift of characin specimens from the Agassiz Thayer Expedition collection, graciously given me by the Museum of Comparative Zoology through the courtesy of Mrs. Myvanwy M. Dick. Since then the bulk of the work has been done in the Division of Fishes of Chicago Natural History Museum, in which the newly acquired Carnegie collections have been utilized. There I had the benefit of constant help and exchange of ideas with the curator, Mr. Loren P. Woods. Messrs. W. I. Follett and Stanley H. Weitzman of the California Academy of Sciences were also most generous with specimens and suggestions. Mr. Weitzman

TABLE II.—CHRONOLOGICAL LISTING OF SERRASALMID GENERA

	Genus	Type Species
1.	*Serrasalmus* Lacépède (1803)	*Salmo rhombeus* L.
2.	*Myletes* Cuvier (1815)	*Salmo niloticus* L.
3.	*Catoprion* M. & T. (1844)	*Serrasalmo mento* Cuvier
4.	*Myleus* M. & T. (1844)	*Myleus setiger* Müller
5.	*Pygopristis* M. & T. (1844)	*Serrasalmo denticulatus* Cuvier
6.	*Pygocentrus* M. & T. (1844)	*Serrasalmo piraya* Cuvier
7.	*Mylesinus* C. & V. (1849)	*Mylesinus schomburgki* Val.
8.	*Tometes* C. & V. (1849)	*Tometes trilobatus* Val.
9.	*Metynnis* Cope (1878)	*Metynnis luna* Cope
10.	*Myloplus* Gill (1895)	*Myletes asterias* M. & T.
11.	*Colossoma* Eigenmann (1903)	*Myletes oculus* Cope
12.	*Piaractus* Eigenmann (1903)	*Myletes brachypomus* Cuvier
13.	*Mylossoma* Eigenmann (1903)	*Myletes albiscopus* Cope
14.	*Orthomyleus* Eigenmann (1903)	*Myletes ellipticus* Gthr.
15.	*Acnodon* Eigenmann (1903)	*Myleus oligocanthus* M. & T.
16.	*Myleocollops* Eigenmann (1903)	*Metynnis goeldii* Eigenmann
17.	*Waiteina* Fowler (1907)	*Myletes nigripinnis* Cope
18.	*Reganina* Fowler (1907)	*Myletes bidens* Agassiz (in Spix, 1829)
19.	*Sealeina* Fowler (1907)	*Myletes lippincottianus* Cope
20.	*Starksina* Fowler (1907)	*Myletes harniarius* Cope
21.	*Gastropristis* Eigenmann (1915)	*Serrasalmo ternetzi* Steindachner
22.	*Rooseveltiella* Eigenmann (1915)	*Serrasalmo nattereri* Kner
23.	*Pristobrycon* Eigenmann (1915)	*Serrasalmo calmoni* Steindachner
24.	*Paramyloplus* Norman (1929)	*Paramyloplus ternetzi* Norman
25.	*Utiaritichthys* Mirando Ribeiro (1937)	*Utiaritichthys sennae-bragi* Mirando Ribeiro
26.	*Melloina* Aramal Campos (1946)	*Melloina tambaqui* Aramal Campos

lent the X-ray films of CAS 20221 (*Mylesinus schomburgki*) and 20222 (*Utiaritichthys sennae-bragi*), which would have been unavailable otherwise except as figured by Gosline. To each of these individuals and institutions I am indeed most grateful.

THE SWIM BLADDER OF THE SERRASALMINAE

The swim bladder of serrasalmid fishes (fig. 111) is a two-chambered, physostomous, gas-filled sac. It is to be classified in Tracy's type 2, characteristic of the cypriniform ostariophysine fishes.

The anterior chamber is generally oval in shape, whereas the posterior chamber is conical, with its apex to the rear. The anterior chamber is about a quarter to a half of the length of the posterior chamber except in the genera *Serrasalmus* and *Piaractus*, where the anterior chamber is as much as one and one-half times the length of the posterior chamber. As a whole, the swim bladder is about a fourth to a fifth of the standard length of the individual fish.

The posterior chamber is a single-walled sac, but the anterior chamber has two walls: a thin *tunica interna* which is continuous

TABLE III.—SERRASALMIDS STUDIED (74)

Genus and Species	Specimens Used[1]	Number of Specimens
Colossoma		
bidens	CAS 15670, 15701, CNHM 56824, 59337	4
mitrei	CNHM 59339	1
Piaractus		
nigripinnis	CAS 15668, CNHM 56825 (3), 56826, 62184	6
Mylossoma		
albiscopus	CNHM 56827, 56828	2
aureus	CAS —, CNHM 56905, 56907, MCZ 19092 (2)	5
duriventris	CAS 15678, 20215	2
Acnodon		
normani	CAS — (juv.)	1
Catoprion		
mento	CAS —, CNHM 53273, 56910	3
Metynnis		
hypsauchen	CNHM 53543, 56917 (2)	3
lippincottianus	CAS 20229	1
luna	CAS 15610	1
maculatus	CNHM 52745, 52748	2
Mylesinus		
schomburgki	SU 55344	1
	(CAS 20221, x-ray film)	(1)
Myleus		
asterias	CNHM —	1
ellipticus	CNHM 59294	1
micans	CNHM 56927	1
pacu	CNHM 59292, 59298	2
schomburgkii	CNHM 56934 (2), 62185, 64001	4
setiger	CAS —	1
Pygopristis		
denticulatus	CNHM —, 7503, 52744, 54928	4
Serrasalmus		
brandti	CNHM 56947 (2), 56951, MCZ 19263 (2)	5
calmoni	CNHM 56982	1
elongatus	CNHM 56942	1
gymnogenys	CNHM 52747, 56984	2
humeralis	CNHM 56975	1
maculatus	CNHM 56976	1
nattereri	CNHM 57556, 57558, Shedd Aquarium (juv.)	3
notatus	CNHM 57562	1
piraya	CNHM 52723, 57552, MCZ 19266 (2)	4
rhombeus	CNHM 42860 (2), 53730, 59270	4
spilopleura	CNHM 56960	1
ternetzi	CNHM 44707, 50611	2
Utiaritichthys		
sennae-bragi	(CAS 20222, x-ray film)	(1)

[1] CAS=California Academy of Sciences
CNHM=Chicago Natural History Museum
MCZ=Museum of Comparative Zoology, Harvard University
SU=Stanford Natural History Museum

with the posterior chamber via the inter-chamber duct; and a *tunica externa* which is made up of a heavy, white, fibrous connective tissue arranged in two crossed layers. Between these two tunics is a loose connective tissue. The arrangement of the fibers of the external tunic has been postulated to prevent over-extension of the anterior chamber (see Nelson, 1961).

The two chambers are connected by an inter-chamber duct that passes between the antero-inferior border of the posterior chamber and the postero-inferior border of the anterior chamber. The extreme ventral position of the duct distinguishes the serrasalmids from the other cypriniform fishes, in which this duct ordinarily connects the central areas of the adjacent chamber surfaces.

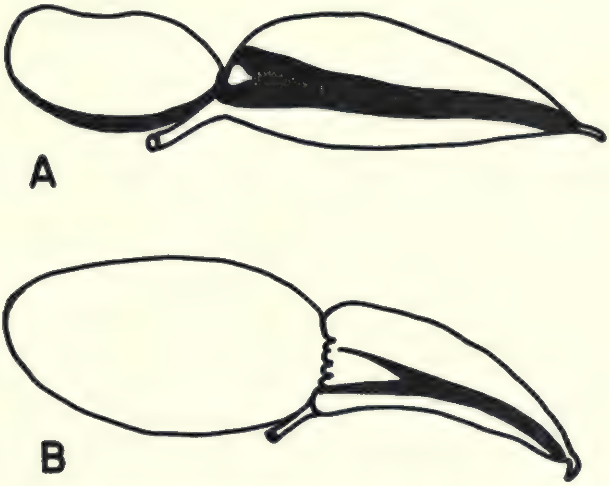

FIG. 111. Types of serrasalmid swim bladders. A, The general type, with the posterior chamber most prominent. B, The special type, with the anterior chamber most prominent; this type is to be seen in the genera *Serrasalmus* and *Piaractus*.

The swim bladder is connected to the esophagus by a relatively straight and simple pneumatic duct that arises from the antero-inferior margin of the posterior chamber immediately below the inter-chamber duct or directly from the ventral surface of that duct. The pneumatic duct enters the esophagus on its left dorsal corner, where there is an enlargement of the duct and esophagus to form a "valve-like" apparatus (see also Rowntree, 1903).

As is characteristic for ostariophysine fishes, the anterior chamber is also connected to the ear by a Weberian apparatus.

The swim bladder as a whole lies dorsally in the body cavity. The lining of the peritoneal cavity covers the ventral surface of the swim bladder and reflects laterally onto the costal and intercostal elements of the body wall below the level of the swim bladder. In this retroperitoneal space the swim bladder is surrounded by a loose connective tissue and fat. The fatty tissue becomes consolidated in the region between the two chambers and in the humeral hiatus lateral to the anterior chamber. A transverse fascial sheet extends ventrally from the Weberian apparatus covering the anterior end of the swim bladder and then turns posteriorly to extend between the ventral and lateral surfaces of the anterior chamber and the peritoneum–body-wall. Anteriorly and ventrally this transverse fascia is considerably thickened.

Various kinds of extensions are to be found on the swim bladder of serrasalmid fishes. In all genera studied there is an extension of the posterior end to varying degrees. It may be a small "nipple-like" process or a long projection that extends beyond the body cavity into the caudal region. This latter situation is particularly true of the genera *Metynnis, Mylossoma* and *Serrasalmus,* in which the posterior extension passes out of the body cavity posteriorly immediately to the right of the haemal spines of the caudal vertebrae and between these haemal spines and the caudal musculature.

A crenulated anterior margin of the posterior chamber is to be seen in the genera *Piaractus, Mylossoma* and *Serrasalmus.* Here a series of small antero-marginal projections extends anteriorly from the margin of the posterior chamber where it surrounds the posterior end of the anterior chamber. Internally these projections are separated by small ridges of the internal surface of the posterior chamber. In *Piaractus* this anterior edge is merely scalloped, while in some of the *Serrasalmus* species these antero-marginal projections of the posterior chamber may become quite complex.

In the genus *Mylossoma* anterior extensions of the swim bladder are also to be found (fig. 112). From the mid-ventral aspect of the front end of the anterior chamber arises a single tube, which almost immediately bifurcates into two dendritic extensions proceeding into the "head kidneys" on either side of the posterior skull. The dendrition of *M. albiscopus* is rather simple as compared with that of *M. aureus.* However, the smaller (thus younger) specimens of *M. aureus* have a simpler degree of dendrition than do the larger (older) ones. In all cases, the lumen of this anterior extension is continuous with the lumen of the anterior chamber. It has three walls:

the internal and external tunics continued from the anterior chamber plus a modification of the thickened anterior transverse fascial sheet.

The posterior chamber of the serrasalmid swim bladder in general has a lateral longitudinal band of intrinsic muscle fibers. In *Serrasalmus* two such longitudinal bands are on each side, dorso-lateral and ventro-lateral (this condition in the catostomid swim bladder represents the more generalized condition; see Nelson, 1961). In most genera this longitudinal band is single but with varying degrees of doubling at the anterior end so as to form a Y-shaped figure. The amount of the band which is double varies from species to species; only in *Serrasalmus* is it double throughout its entire length.

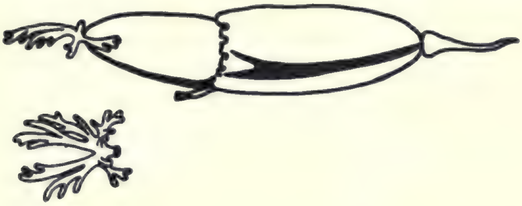

FIG. 112. Swim bladder of *Mylossoma aureus*. Note the long posterior extension which passes into the tail between the haemal spines and the caudal musculature on the right side. (The posterior extension of the species *M. albiscopus* is small and does not reach beyond the body cavity as in *M. aureus* and *M. duriventris*.) The dendritic anterior extension is figured in both dorsal and lateral aspects. It is complex as shown in *M. aureus* and *M. duriventris* but is simple in *M. albiscopus* (and young of *M. aureus*).

A slight mid-ventral longitudinal band of intrinsic muscle fibers may be seen in the anterior chamber of some species.

In three genera, *Pygopristis*, *Catoprion* and *Serrasalmus*, an extrinsic musculature has been acquired by the anterior chamber. In each of these three genera this muscle appears to be derived from the internal intercostal musculature and in each case is associated with the sixth pleural rib (the second "normal" rib, since the first four have become incorporated into the Weberian apparatus). In each case the spinal nerve of the intercostal space between pleural ribs 5 and 6 sends branches to the extrinsic muscle of the anterior chamber.

In the genus *Pygopristis* (fig. 113) the extrinsic muscle is a ribbon-like band originating from the proximal anterior surface of the sixth pleural rib and extending downward, curving slightly forward to insert partially upon the fifth pleural rib at about the junction of its upper and middle thirds. The thickened transverse fascia passes along the ventral surface of the anterior chamber.

In the genus *Catoprion* (fig. 114) the extrinsic muscle of the anterior chamber is biventered. It originates from the anterior surface of the proximal end of the sixth pleural rib. The upper belly of this muscle passes downward and slightly forward. At about the middle of the lateral surface of the anterior chamber it joins the lower belly in a broad inscription-like junction. The lower belly passes anteroventrally to almost the mid-ventral aspect of the anterior chamber where it inserts into the thickened fascia along the ventral surface of the anterior chamber. The spinal nerve gives off separate branches to each belly of this muscle.

FIG. 113. Swim bladder in the genus *Pygopristis*. The sixth pleural rib and the extrinsic muscle of the anterior chamber are included.

In the genus *Serrasalmus* (fig. 115) the extrinsic muscle of the anterior chamber is strongly developed. It originates from a specialized elongated plate developed on the medial surface of the proximal end

FIG. 114. Swim bladder in the genus *Catoprion*. The sixth pleural rib and the extrinsic muscle of the anterior chamber are included. Note that the muscle is biventered.

of the sixth pleural rib and passes ventrally to insert about half-way down the lateral surface of the chamber into the thickened transverse fascia surrounding the chamber. The body of this muscle is quite broad and thick so that it overlaps the sixth pleural rib and fills the humeral hiatus between the fifth, sixth, and seventh pleural ribs.

An occasional specimen of *Metynnis* has been observed to exhibit a thin band of muscle which originates on the anterior surface of the sixth pleural rib and extends slightly forward and ventrally to insert into the outer surface of the membrane which forms the innermost layer of the lateral body wall. It is very suggestive of the condition seen in *Pygopristis*.

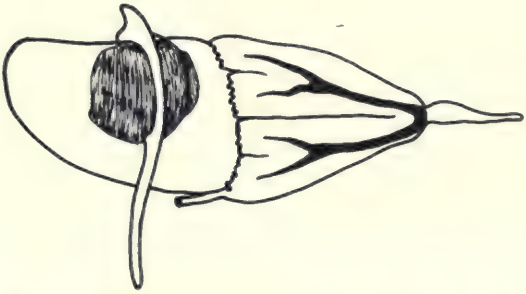

FIG. 115. Swim bladder in the genus *Serrasalmus*. The sixth pleural rib and the extrinsic muscle of the anterior chamber are included. Note that the origin of the muscle in this genus is from a special basal plate of the rib rather than the proximal edge as in *Pygopristis* and *Catoprion*. Also note the greatly enlarged mass of the muscle.

THE LATERAL BODY-WALL MUSCULATURE AND HUMERAL HIATUS

As in vertebrates in general, the serrasalmids have a lateral body wall made up of two oblique sheet-like layers of musculature. This musculature is situated between the pleural ribs as a thin inner layer of internal intercostal fibers and a thick outer layer of external intercostal fibers. The internal fibers characteristically slope downward anteriorly while the external slope downward posteriorly. Toward the ventral margin of the body both layers of fibers tend to become aligned horizontally, paralleling the ventral margin. The internal intercostal fibers begin in the intercostal space just ventrad of the angles of the ribs and extend downward to the ventral margin. The external intercostal fibers completely fill the intercostal space from the horizontal myoseptum above to the ventral margin. The indi-

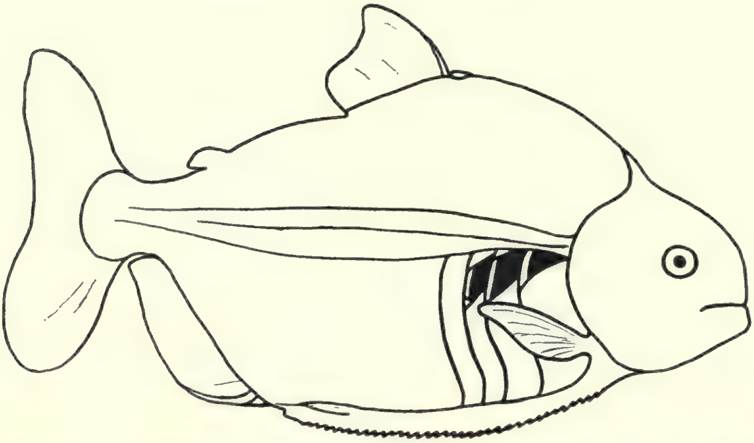

FIG. 116. Lateral view of *Serrasalmus rhombeus*. The skin has been removed to demonstrate the location and extent of the humeral hiatus. In this genus the fifth and sixth pleural ribs are exposed in the humeral hiatus area.

vidual fibers of the internal layer extend from one rib to the next. The individual fibers of the external layer extend from one rib to the next on the lateral portions of the ribs, and more laterally from one myocomma of the myomeres to the next. Anteriorly, both layers extend to the pectoral girdle and the external layer also extends to the postero-lateral aspect of the skull. The fascial myocommata of the serrasalmids extend laterally and posteriorly from the lateral margins of the pleural ribs to the deep fascia surrounding the body under the skin, and thus the body musculature is separated into a linear series of segmental muscles. The internal layer may be much reduced, or even absent, in some species.

In *Serrasalmus* the area immediately behind the pectoral girdle above the pectoral fin has a hiatus in the muscular wall of the body (figs. 116 and 117). Because of its location it is termed the humeral hiatus. Specifically this hiatus begins anteriorly, where the external fibers arise from the postero-lateral skull. It gradually widens so that an elongated triangular figure is formed in the body wall, one edge of which is the horizontal myoseptum. In some specimens the sixth rib and in others the seventh forms the posterior edge with the fibers of the external intercostal muscle forming the ventral edge. Thus the proximal portion of the fifth rib is exposed and sometimes also that of the sixth.

The initial portion of the lateral-line nerve passes along the dorsal boundary of the humeral hiatus. Opposite the fifth rib it gives off a primary branch which passes ventrally and then posteriorly to the ventral margin of the caudal region.

In the genera *Acnodon, Metynnis, Pygopristis* and *Catoprion* a humeral hiatus, essentially as described for *Serrasalmus,* is to be found. In the genera *Myleus* and *Mylesinus* a slit-like hiatus is present. In the genera *Colossoma, Piaractus* and *Mylossoma* no hiatus is present, although there is usually a depression in the musculature of this region. In *Myleus* and *Mylesinus* the slit hiatus is also surrounded by a depression. The lateral-line nerve and its primary branch have the same relationship to the depression as to the hiatus.

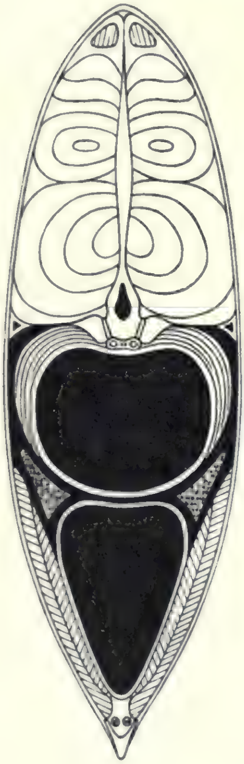

FIG. 117. Cross section of *Serrasalmus rhombeus* in the region of the humeral hiatus. The internal and external intercostal muscle layers of the body wall in this region do not extend all of the way up to the horizontal myoseptum, thus leaving the hiatus. Note that the space around the anterior chamber (with its extrinsic muscle applied to its wall) is thereby continuous to the skin.

In both conditions, depression and hiatus, the area is fat-filled; that is, a loose connective tissue filled with fat occupies this entire area and surrounds the lateral-line nerve and its primary branch.

In the condition of a hiatus this fatty tissue extends throughout the space between the anterior chamber of the swim bladder and the inner surface of the skin.

THE PROCUMBENT PREDORSAL SPINE

Eight of the eleven genera of the Serrasalminae possess the special structure known as the procumbent or predorsal spine. The genera *Colossoma, Piaractus* and *Mylossoma* do not exhibit this character. In this study, the spine has been examined in varying detail in *Catoprion, Metynnis, Myleus, Mylesinus, Pygopristis, Serrasalmus* and *Utiaritichthys* as well as its homologue in the three genera lacking it.

In the genus *Serrasalmus* (fig. 118, A) the predorsal interneurals and the dorsal pterygiophores are expanded antero-posteriorly, with median plates having lateral phalanges at right angles to the plates. The plates are embedded in the median dorsal septum of the body. The acme of this development is in the initial dorsal pterygiophore of the dorsal fin, and it diminishes to a mere spicule-like shaft for the last pterygiophore.

Although a single structural entity, the initial dorsal pterygiophore may be considered as having several functional subdivisions grouped together as A, the spine, and B, a shaft. The spine represents an enlargement of the dorsal portion of the pterygiophore and extends forward and anterior to the dorsal fin. This spine is pointed anteriorly. Posteriorly it is variously double-pointed and notched. It lies in a cutaneous "pocket" with only the upper surface at most exposed in living aquarium specimens. In fresh specimens the skin readily peels away from the latero-inferior surfaces of the spine and it is difficult in the few specimens available to know whether or not the skin is adhered to or free of the spine surfaces.

The shaft of the pterygiophore has anterior and posterior median plates plus a pair of lateral phalanges more or less at right angles to the plates. This combination greatly increases the area for attachment of the fin-ray muscles.

Dorsally the shaft is thickened—anteriorly to produce an anterior margin or area along the dorsal edge of the anterior median plate, and posteriorly to produce a knob-like projection. The anterior margin, sometimes produced into a scalloped-out area, is for the attachment of the fibers of the dorsal ligamentous portion of the dorsal median septum and of the dorsal longitudinal muscle bundles. Thus the entire predorsal margin of the body from the occipital crest of the skull to the dorsal fin is tied together, including the interneurals.

A strip of dense spongy connective tissue extends the length of this nuchal crest between the skin and the ligamentous portion of the dorsal median septum in the form of a linear pad thicker toward the dorsal fin end.

The posterior knob forms an articulation directly with the second dorsal pterygiophore by means of a syndesmosis. This is continued along the series of pterygiophores and, combined with the syndesmotic connections between the median plates of adjacent pterygiophores, forms a fairly solid mid-dorsal base for the dorsal fin. The rays of the dorsal fin have a double condylar base well suited for elevation and depression of the fin. Between the intercondylar fossae of the fin-rays and the dorsal margin of the pterygiophore group is located a series of elongated oval bodies (radialae), as bearings, which convert the fin-ray articulation into a "universal"-type joint that increases the possible movements of the fin-rays

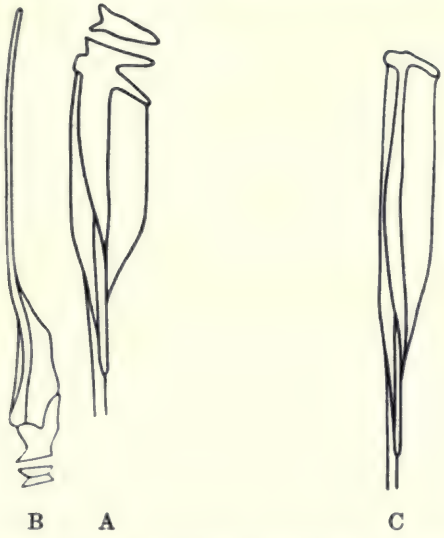

FIG. 118. A, B. Initial pterygiophores of *Serrasalmus brandti*. A, dorsal; B, anal. Note that the ventral portion of the shaft and the posterior median plate of the initial dorsal pterygiophore are closely associated with the neural spine of one of the vertebrae. The spine on the initial anal pterygiophore is unique to the genus *Serrasalmus*. C, Initial dorsal pterygiophore of *Mylossoma*. In this genus (and in the genera *Colossoma* and *Piaractus*) the initial dorsal pterygiophore lacks the procumbent predorsal spine. Note that the ventral portion of the shaft and the posterior median plate of the initial dorsal pterygiophore are closely associated with the neural spine of one of the vertebrae.

to include a lateral swing to either side, and, through a combination of the elevation-depression and the lateral swing, produces also a circumduction of the fin-rays. Rotation of the individual fin-ray along its longitudinal axis is, however, prohibited by the arrangement of the ligaments and the shape of the articulating parts.

In *Serrasalmus* a somewhat similar development is to be seen in the initial pterygiophore of the anal fin (fig. 118, B). Here, however, the spine is anatomically independent of the pterygiophore, although it is bound to the ventral expanded end of its shaft by a syndesmosis. In addition, this preanal spine is double-pointed anteriorly as well as posteriorly, with a groove along its central length.

The initial dorsal pterygiophore in the genera *Colossoma, Piaractus* and *Mylossoma* (fig. 118, C) is in all respects, except for the spine, identical in form and attachments with that of the genera in which it possesses, in addition, the spine.

DISCUSSION AND CONCLUSIONS

Extrinsic muscles of the swim bladder.—Three genera of the Serrasalminae have an additional muscle, derived from outside of the swim bladder, associated with the anterior chamber of the swim bladder. In *Pygopristis* this muscle is in its simplest form. In *Serrasalmus* it is well developed in both size and attachments. In *Catoprion* it is quite different. All three forms of this muscle, however, have identical origin and relationships, indicating at least a common ancestry. Occasional slips of muscle in *Metynnis* parallel the extrinsic muscle seen in the three genera. This condition can be considered to be a preadaptive state which leads to the condition in *Pygopristis,* which in turn can be complicated into the condition existing in *Serrasalmus.* The biventered condition in *Catoprion* may have been derived independently from *Metynnis,* or possibly *Pygopristis.*

I am not in a position to explain the role played by this extrinsic muscle in the economy of the serrasalmids possessing it, since this can be done adequately only through a study of living material. However, investigators have examined similar extrinsic muscles of the swim bladders in other groups of teleost fishes. In many such groups this muscle has been acquired for the purpose of sound-production and in these cases it is termed the *musculus sonificus.* The sounds are usually produced as a result of vibrations set up in the swim bladder by the rubbing of its surface by these muscles and their central tendons (much as a boy will produce sounds by rubbing his fingers over the surface of an inflated balloon) (see also Harden Jones and Marshall, 1953).

Chranilov (1929) suggests that in the species of *Serrasalmus* that he studied this muscle controls the volume of the anterior chamber and thereby the buoyancy, and therefore he terms this muscle the *musculus compressorus.* It is a fact that in this genus the anterior chamber is the larger of the two but this is not true for either *Pygopristis* or *Catoprion,* which also possess the extrinsic muscle of the anterior chamber. Moreover, these fishes live in relatively shallow waters, where the potential changes in hydrostatic pressure are not great. Also, these fishes are said to respond quickly to vibration-producing activities, such as kicking or splashing (Myers, 1949), which would be in line with the fact that the anterior chamber is connected to the ear by the Weberian apparatus and thus has an increased vibration reception potential—a fact that would correlate with the possibility of sound-production.

A compression function for this muscle might be seen in those fishes where this function is postulated. Hagman (1921) considers that the extrinsic muscle of the anterior portion of the swim bladder in gadids acts as a compressor. He feels that the center of gravity of the gadid can be altered so that the head will go down during bottom-feeding activities. Peters (1951) has shown that the musculature of the anterior chamber in seahorses (although in this case it is intrinsic rather than extrinsic) does alter the center of gravity for postural advantages as suggested for the gadids by Hagman.

A recent experience with a live juvenile *Serrasalmus nattereri* (thanks to Mr. Walter Chute of the Shedd Aquarium) indicated that sound is produced by this species (and at least two other species located there). The sound had a repetitive buzzing character. While the specimen was held in the hand, definite contractions of the humeral area coincided with each sound period. When the swim bladder of this specimen was exposed, pressure placed upon the anterior chamber resulted in the passage of air through the pneumatic duct into the esophagus with a concomitant fluttering of the valve region and the production of sound. It would appear that the extrinsic muscle in this species does compress the swim bladder and that the esophagus-pneumatic duct valve acts as the "vocal cords" during production of sound. So far I have no evidence, either from the literature or personal communications, that these fish produce sounds under water. If they do and this is the actual sound-producing mechanism, perhaps the air has a tidal movement back and forth between the swim bladder and the esophagus.

Humeral hiatus.—As has been described, several genera of serrasalmids have an opening through the musculature of the lateral body wall in the region between the upper pectoral girdle and the pectoral limb. By means of this opening a hiatus is created in the body wall and thereby the space surrounding the anterior chamber of the swim bladder is brought into more or less direct contact with the inner surface of the skin in the humeral region.

This character is, however, by no means limited to the serrasalmids. It has been noted with almost identical morphology in several genera of gymnotids as well as in other characins (see also Rowntree, 1903). It is also present in other groups of teleosts unrelated to the characins (for example, in the zeoid *Zeus japonicus;* CNHM 57426). In the siluroid fishes this area may have a degree of skeletal margin produced from the bony covering of the lateral extensions of the swim bladder and the pectoral girdle.

It is thus clear that the humeral hiatus as a character must be considered as a convergent rather than a phylogenetic character. What is the common function in all of these different fishes which has evoked this character as a response? The answer again is not readily apparent from museum specimens. It is thought, however, that this humeral hiatus may be utilized in the reception and/or transmission of sound vibrations.

As sound travels through water it is primarily a pressure pulse with relatively little amplitude. For this reason the use of an air-filled sac (swim bladder in teleost fishes, lungs in larval anurans) to act as a sound receptor is ideal. That is, an environment such as water, which is essentially non-compressible and has a greater inertia, favors the use of an enclosed body of compressible material, gas, which will oscillate (by compressions and decompressions) in harmony with the sound pressure pulses. This oscillation can then be transmitted to the membranous labyrinth either directly (as in the holocentrids, gadids, clupeoids, mormyrids, *Xenopus* larvae, etc.) or indirectly through mechanical devices (Weberian apparatus in the ostariophysine teleosts, bronchial columella of ranid larvae).

In passing through the body wall of a fish to reach the swim bladder the sound pressure pulse would have to traverse the organized tissue and muscle layers. These would tend to dampen the pressure pulse by virtue of their relative inelasticity. In the case of fishes possessing a humeral hiatus there is no substance, except the loose fatty tissue, between the skin and the receptive portion of the swim bladder (the anterior chamber; where an extrinsic muscle is present it is part of the swim bladder wall). Thus, the humeral hiatus may be considered as a specialization to enhance the reception of water-borne sound by removing the potential dampening effect of the intervening musculature. Of course this can also be true in reverse: Sounds produced by the swim bladder will be able to pass more readily out of the body undiminished, by means of humeral hiatus.

The skin over the humeral hiatus is often pigmented, or in preserved specimens tends to appear different in texture. Eigenmann (1915) used the term "pseudotympanum" for this area of skin and Böhlke has followed. In *Balistes* a similar area of skin has been termed "tympanum" by Gregory (1933). Certainly in the siluroids this skin area is directly related to the lateral surfaces of the swim bladder and appears to be active in the receiving and/or emission of sounds. Gregory's statements lead one to believe that he felt that this area was related to sound production or reception. So far I have not been able to ascertain why Eigenmann chose the term that he did for this area.

The predorsal spine.—Gosline (1951) indicates that a predorsal spine is to be found in three characin groups: Stethaprioninae, Prochilodinae and Serrasalminae. In a dissection of *Stethaprion erythrops* (MCZ 19107) an initial dorsal pterygiophore with a procumbent spine was demonstrated, as well as the lack of a spine on the initial anal pterygiophore—these conditions being similar in all respects to those in the average serrasalmid. Boeseman (1952) describes a similar situation in *Brachychalcinus,* another member of the stethaprionid group. Rendahl (1932) and Hora (1937) describe and figure a strikingly similar initial dorsal pterygiophore for *Mystacoleucus,* a deep-bodied cyprinid of Asia. I have noted a similar element on the initial dorsal pterygiophore in the skeleton of the carangid *Trachinotus paitensis* (CNHM 51376) as well as a counterpart of the *Colossoma* condition in the carp, *Cyprinus carpio.*

We may, then, postulate that this character—the procumbent predorsal spine—is to be found in many species unrelated phylogenetically but related by a common body form which presumably represents a common response to a common environmental stimulus. This form is deep-bodied, with a high or strong nuchal crest. The stress placed on the nuchal area, either as a cutwater, an anchor for the dorsal fin, or both, has resulted in the "tying together" of the occipital crest of the skull and the base of the dorsal fin. The heavy-bodied members of the genus *Serrasalmus* have in addition tied the ventral margin to the anal fin by means of a preanal spine; however, the ventral scutes already existed and presumably one of these enlarged and became the spine attached to the initial anal pterygiophore.

We may, then, consider the predorsal spine to be a convergent character and representative of the normal reaction of bone and connective tissue to stresses placed upon them. Since the stress here is more of a point attachment kind, the reaction tends to become a spine rather than a tubercle or ridge, as is the reaction to lesser or linear stresses.

The role played by the predorsal spine has been discussed (see Gosline, 1951, and Hora, 1937, for examples). The argument appears to center upon the probable use or non-use of this spine as a defensive weapon. As a result of this investigation I feel that this spine is in truth not a spine in the sense of a projection developed for offense or defense but more likely, as stated, a spine which is the reaction of connective tissue to stresses placed upon it.

Why this spine is lacking in *Colossoma, Piaractus* and *Mylossoma* can only be postulated. Perhaps these are the initial serrasalmid forms prior to the stage at which the accumulation of stresses and their responses resulted in the formation and genetic fixation of the spine.

In living forms this spine is not freely exposed as it is frequently in museum specimens. I have examined a number of specimens in which the skin and connective tissue of the median septum were still adherent to this spine. It is of some interest to note here that Eigenmann (1903) erected a new genus, *Acnodon,* because he believed that the type lacked a predorsal spine; it was apparently properly embedded in the surrounding flesh.

There are several good reasons why this spine should be exposed only in museum specimens. One is the shrinkage which occurs during fixation and preservation of the specimens, which tends to draw the flesh and skin away from the spine. Accidents in shipping and handling will also tend to peel the skin and flesh away from the spine. Also, the present-day taxonomist is purposefully pulling the skin away from the spine to ascertain the presence or absence of this important key character!

Generic status of Pygopristis.—Gosline (1951) stated "that the species of *Serrasalmus* grade imperceptibly into *Pygopristis,* and that the distinction between the two, based on the number of tooth lobes, seems of doubtful generic rank." Although externally *Pygopristis* is very similar to *Serrasalmus* it is distinctly different internally. The swim bladder of *Pygopristis* is of the general type wherein the posterior chamber is larger than the anterior, whereas that of *Serrasalmus* is the opposite. Likewise, the longitudinal muscle band in *Pygopristis* is a single structure while that of *Serrasalmus* is double.

The condition of the extrinsic muscle of the anterior chamber of the swim bladder is another major difference between these two genera. The extrinsic muscle of the *Serrasalmus* species is well developed, with a special basal plate on the sixth pleural rib. In *Pygopristis* this muscle is simple and without any special origin. The condition seen in *Pygopristis* is morphologically, and presumably phylogenetically, antecedent to that of *Serrasalmus.*

Generic status of Piaractus.—In 1903 Eigenmann erected the genera *Piaractus* and *Colossoma,* the major apparent difference between them being the rayed adipose fin of *Piaractus.* The general tendency has been to place *Piaractus* in the synonymy of *Colossoma,* but the present study would indicate that *Piaractus* ought to retain its full generic rank. In *Colossoma* the posterior chamber of the swim bladder is the larger of the two chambers whereas in *Piaractus* the anterior chamber is very definitely the larger. Also, in *Colossoma* the longitudinal muscle band is single; in *Piaractus* it is usually double. (The relationships of *Colossoma* to *Piaractus* are quite parallel to those of *Pygopristis* to *Serrasalmus;* that is, of a general to a specialized form.)

Systematics of the subfamily (fig. 119).—The genera which make up the subfamily Serrasalminae are all inter-related, if for no other character than the ventrally located inter-chamber duct of the swim bladder. In this group this duct is situated at the infero-median aspects of the adjacent surfaces of the anterior and posterior chambers. This characteristic has not been observed in any other group of teleosts worked upon to date. In addition, the pneumatic duct frequently arises from the ventral surface of this inter-chamber duct. This characteristic has been noted elsewhere only in the gymnotids, where the two chambers of the swim bladder are widely separated.

Because of the lack of specialized features (no predorsal spine, no humeral hiatus, no extrinsic muscle to the anterior chamber of the swim bladder) *Colossoma* is believed to be the most primitive of the serrasalmid genera. *Piaractus* and *Mylossoma* are then specialized offshoots of this basic genus, each along its own line of development. *Myleus* can be considered the first of the genera

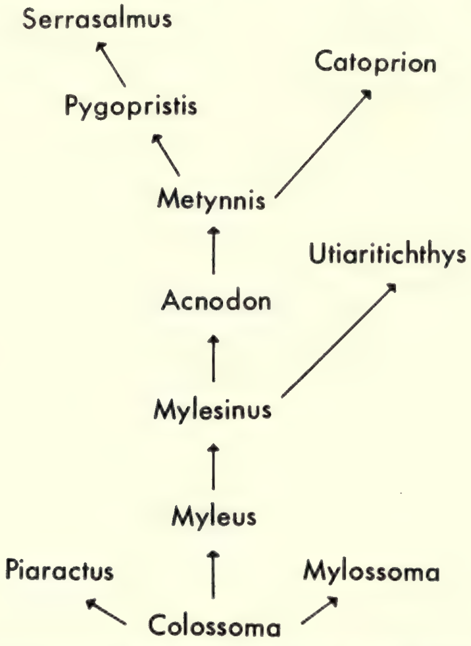

FIG. 119. Schema showing inter-relationships of the genera of the Serrasalminae, based upon internal morphology.

possessing the predorsal spine and with the beginnings of the humeral hiatus. From it *Mylesinus* would probably be the next step toward the full development of the humeral hiatus. This in turn would lead to *Acnodon* and then to *Metynnis*, which includes the incipient or preadaptive stages of the extrinsic muscle of the swim bladder. On a direct line from *Metynnis* would come *Pygopristis*, culminating in *Serrasalmus*. The special biventered extrinsic muscle of the swim bladder in *Catoprion* may be considered as a different line of development of this muscle from *Metynnis* or *Pygopristis*. Not enough is known of *Utiaritichthys* to place it properly in the "family tree."

SUMMARY

1. The subfamily Serrasalminae consists of eleven well-differentiated genera.

2. The genus *Pygopristis* is validated by internal characters in addition to the already described external ones.

3. The genus *Piaractus* is returned to its original generic rank based upon internal as well as external characters.

4. The procumbent predorsal spine is considered to be an integral part of the connective tissue mechanism to tie together the nuchal crest of the body from the occipital crest of the skull to the base of the dorsal fin.

5. The humeral hiatus is considered to be a specialization for the passage of the sound pressure pulse by the elimination of the muscular tissue which would tend to dampen this pressure pulse.

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