

Early Osteological Development of White Perch and Striped Bass with Emphasis on Identification of Their Larvae

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Abstract

A cartilage and bone staining technique was employed to study the developmental osteology of the striped bass (*Morone saxatilis*) and white perch (*Morone americana*). Special attention was given to those osteological characters that appeared to be unique to the larvae of each species. Larval striped bass and white perch exhibited diagnostic differences in the position and shape of the median ethmoid, predorsal bones, dorsal- and anal-fin pterygiophores, vertebral column, and caudal skeleton. These differences were discernible at the earliest appearance of these elements as cartilage, and allow identification of striped bass and white perch larvae above a length of about 7.5 mm.

Osteological development of teleostean fishes has received little attention from ichthyologists. Osteological studies have been concerned primarily with adults and juveniles. Those studies dealing with the osteology of larvae generally have involved nonteleostean fishes (Aumonier 1941) or have been concerned with histology investigations (Edgeworth 1923; Haines 1937). It is only in recent years that interest in the study of larval osteology has begun to develop (Weisel 1967; Potthoff and Richards 1970; Richards et al. 1974; Potthoff 1974, 1975, 1978; Houde and Potthoff 1976; Hensley 1977; Mook 1977; Leiby 1979, in press). Our purpose is to describe the osteological development of two closely related species and to apply this information to identification of their larvae.

The value of osteological characters in the study of the interrelationships of fishes has long been accepted. Recent research on osteology of larvae has resulted in part from the realization that an understanding of the development of bony elements not only can provide additional characters useful for identification purposes, but may also affect our interpretation of osteological characters in the adult. Ontogenetic transformations, losses, and fusions of bony

elements provide valuable keys to the origin and possible homologies of various bones.

Besides helping to answer questions of relationships, osteology provides another suite of characters which can be used in identifying fish larvae. However, preparation of skeletons of larval and small juvenile fishes has not been possible until recently. Whole skeleton preparations of small specimens have been accomplished by Taylor's (1967) clearing and staining technique, which only allows for staining of calcium phosphate and, therefore, is ineffective when the skeleton is still primarily cartilaginous. A recently developed technique allows for the staining of cartilage and bone in whole cleared specimens (Dingerkus and Uhler 1977), and has been modified and used successfully on larval fishes (Fritzsche and Johnson 1979). It is now possible to study the osteology of fishes from the first formation of bones as cartilage (preossification).

We have applied this staining technique in a study of the osteological development of striped bass, *Morone saxatilis* (Walbaum), and the white perch, *M. americana* (Gmelin). These two species are widely distributed along the Atlantic coast of the United States and are sympatric throughout most of their ranges. Both species spawn in the early spring and the re-

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sultant larvae are very difficult to distinguish. The similar external appearance of these larvae is most striking in the size range from 5 to 15 mm standard length. Characters involving the yolk sac can be used to separate these species at smaller sizes and adult meristic and morphometric characters can be used for larger individuals. We began our study of the osteological development of these fishes with the goal of identifying characters that could be used to separate these two species within the problem size range. Fritzsche and Johnson (1979) discussed the staining technique and how it could be used to rapidly sort ichthyoplankton samples with appropriate osteological characters. *Morone saxatilis* and *M. americana* were chosen for this study because they are both important commercial and recreational species and no traditional external morphological character was known for separating their larvae.

Methods

Laboratory-reared series of each species were used for the descriptions. *Morone saxatilis* yolk-sac larvae were obtained from the Brookneal Fish Hatchery on the Staunton River, Virginia. *Morone americana* eggs were stripped and fertilized from adult fish collected from the Patuxent River near Lower Marlboro, Maryland. Rearing was done at the Chesapeake Biological Laboratory, Solomons, Maryland, according to standard procedures developed by Bonn et al. (1976). Wild-caught specimens were used as a control to identify developmental abnormalities in laboratory-reared specimens.

Larval and juvenile *M. saxatilis* and *M. americana* were cleared and stained for both bone and cartilage by the method of Dingerkus and Uhler (1977) as modified by Fritzsche and Johnson (1979). Several hundred larvae were examined during the course of this study, but not all of these were utilized for the osteological descriptions. Series of approximately 80 laboratory-reared specimens of each species covering a size range of 5 to 50 mm standard length were examined to determine the sequence of osteological development and the size at ossification of each element. Although complete descriptions are given, the primary emphasis is on diagnostic differences.

Lengths are given as notochord length (NL) for the preflexion individuals and as standard length (SL) for flexion and postflexion specimens. Notochord length was measured from

the most anterior part of the head to the posterior tip of the notochord. Standard length was measured to the posterior edge of the hypural elements. The formula given for predorsal bone configuration follows the format given by Ahlstrom et al. (1976). In this formula, each 0 represents a predorsal, each slant a neural spine, and the numerals indicate the number of spines borne by each pterygiophore. All drawings and photographs were made with a Wild M5A stereomicroscope equipped with a camera lucida and an MPS 10 Microphoto System.

Osteology

Neurocranium

Smallest specimens (about 4.6 mm) showed no evidence of ossification, however, the trabecula communis, parachordal cartilages, and partially developed synotic tectum were present. By 6.0–7.2 mm, larvae were beginning to show chondrification of the lateral wall of the otic capsule and the orbital cartilages had reached anteriorly to a point midway over the orbits. Median ethmoid first appeared at 7.7–8.7 mm and was simply a small dorsal flange on the trabecula communis (Fig. 1). At 8.4 mm, specimens had a complete cartilaginous sheet covering the otic region, the orbital and paranasal cartilages were complete, the epiphyseal tectum was present, and the taenia medialis was beginning to chondrify in the region of the epiphyseal tectum. At 9.0 mm, the ethmoid was still triangular but was beginning to fill in on each side between it and the orbits. By 10.4 mm, the ethmoid had a flattened dorsal surface. A complete cartilaginous otic capsule and taenia medialis were present at 12 mm, and the parasphenoid was ossified as well as portions of the exoccipitals, basioccipital, and the portion of the frontal bones just above the orbits. By 12.7 mm, some ossification was evident along the ventroposterior portion of the supraoccipital and in the otic region. By 13.4 mm, the region of ossification above the orbits had increased slightly in size. The ventral portion of the neurocranium was completely ossified by 14 mm and the frontals were weakly ossified. The prevomer and basisphenoid were ossified by 20 mm. The former bore about 14 teeth in a V-shaped patch in *M. americana*. By 22 mm the neurocranium was completely ossified except for some cartilage remaining in the epiotics, pterotics, and opisthotics and the ethmoid. The

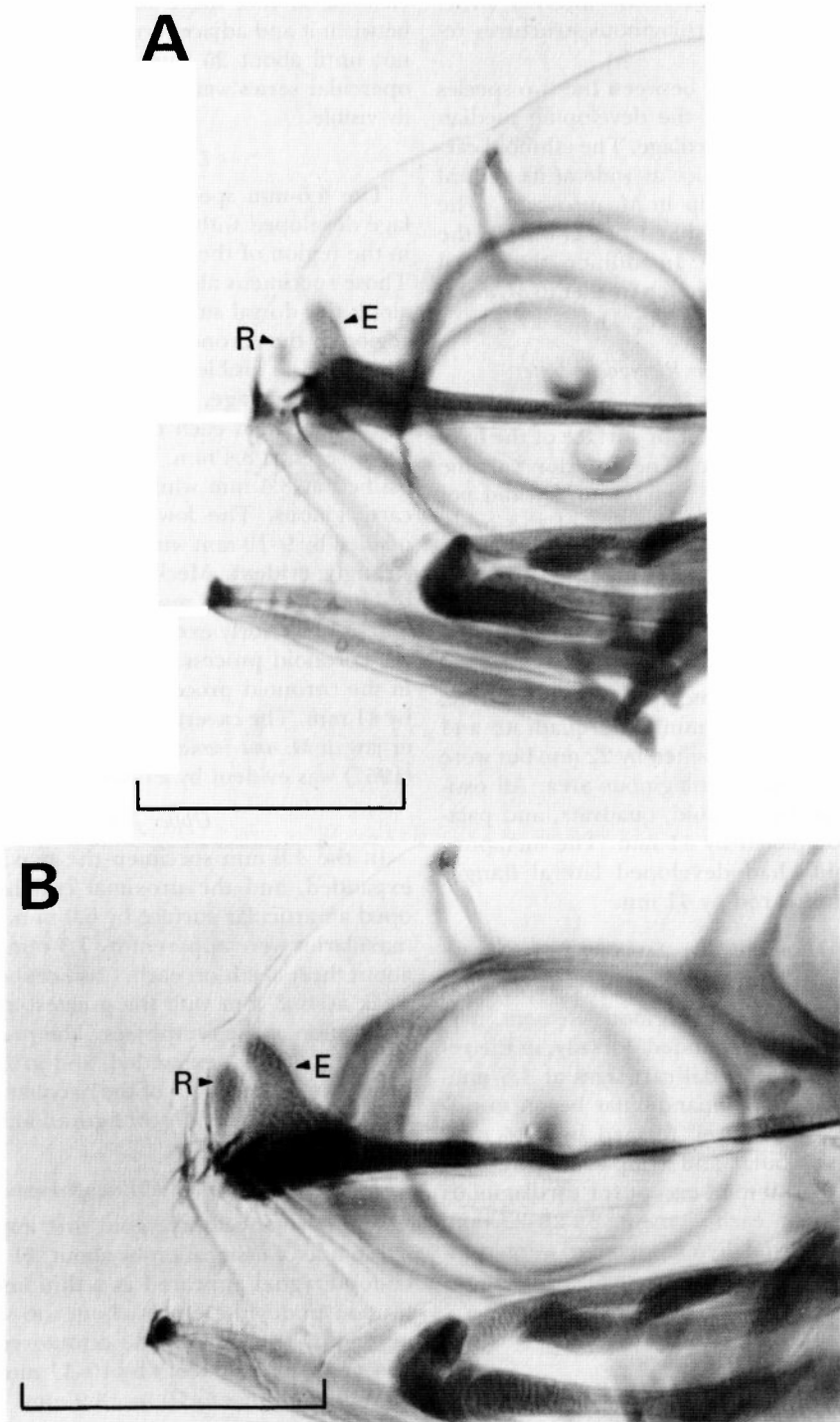


FIGURE 1.—Head region of cleared and stained *Morone* larvae. (A) *M. americana*, 7.9 mm. (B) *M. saxatilis*, 9.0 mm. R = rostral cartilage; E = rthmoid. Horizontal bar represents 0.5 mm.

interorbital septum and some internal structures were the only cartilaginous structures remaining by 41 mm.

The only difference between the two species involved the shape of the developing median ethmoid and rostral cartilage. The ethmoid cartilage was less than twice as wide at its ventral base as at its dorsal tip in *M. americana*. The ventral base was more than twice as wide as the dorsal tip in *M. saxatilis*. In addition, the rostral cartilage was relatively much smaller in *M. nmcricana* than in *M. saxatilis* (Fig. 1).

Palatoquadrate (or Pterygoquadrate)

The palatoquadrate was present as a cartilaginous bar along the anterior surface of the hyomandibular at 4.6 mm. The anterior palatine projection was evident by 6.0 mm, but did not quite reach the anterior border of the orbit. This anterior palatine projection was almost in contact with the maxillary by about 7.5 mm and had a cartilaginous border with the ectopterygoid, quadrate, endopterygoid, and hyomandibular. The palatoquadrate bar became distinctly separated into metapterygoid, quadrate, and palatine by 13.0 mm. The quadrate and metapterygoid were ossified by 22 mm but were joined by a broad cartilaginous area. All ossification of metapterygoid, quadrate, and palatine was completed by 41 mm. The metapterygoid lamina had developed lateral flanges along the initial rod by 41 mm.

Hyomandibular-Symplectic

The hyomandibular-symplectic complex was present as a simple cartilaginous element, narrow ventrally and expanded dorsally, in the region of the parachordal cartilages at 4.6 mm. The head of the hyomandibular began to differentiate and was well formed by 13.4 mm. The hyomandibular and symplectic were ossified by 12.8–13.0 mm, except for cartilaginous areas distally on each element. By 20–23 mm, the symplectic and hyomandibular were completely ossified except for a small cartilaginous area between them.

Opercular Series

The opercle first formed as a small triangle articulating with the hyomandibular at 8.4 mm. The preopercle, subopercle, and interopercle formed by 9.0–9.1 mm, but were very weakly ossified. The opercle was still a small triangular

element so that there was considerable space between it and adjacent opercular bones. It was not until about 20 mm that all bones of the opercular series were strongly ossified and easily visible.

Lower Jaw

The 4.6-mm specimens had Meckel's cartilage developed with a dorsoanterior projection in the region of the articular coronoid process. Those specimens also showed some ossification along the dorsal surface of the dentary in the region of the coronoid process. By 5.1 mm, ossification was visible along the anterior edge of Meckel's cartilage. There were four or five teeth present in each dentary at 6.3 mm and six or seven at 8.4 mm. The dentary was weakly ossified at 8.4 mm while the articular was still cartilaginous. The lower jaw was completely ossified by 9–10 mm with Meckel's cartilage still strongly evident. Meckel's cartilage began to disintegrate by 13.9 mm. Meckel's cartilage was absent posteriorly except for a small portion in the coronoid process by 23 mm. The cartilage in the coronoid process was no longer evident by 41 mm. The cavernous condition of the lower jaw of *M. americana* as described by Woolcott (1957) was evident by 21 mm.

Upper Jaw

In the 4.6-mm specimen the maxillary had expanded, and the proximal end had developed an articular surface by 6.0 mm. The premaxillaries were apparent by 7.3 mm and bore about three teeth on each. Ossification was still weak at 10.3 mm with the greatest amount of ossification at the symphyses. The premaxillaries had flattened, expanded, and grown to approximately the length of the maxillaries, which had assumed the adult configuration, by 12–14 mm.

Ectopterygoid and Endopterygoid

The dermal ectopterygoid first appeared as a thin line of ossification by about 9.1 mm. The endopterygoid appeared as a thin line of ossification under the eye at about the same time or slightly thereafter. The ectopterygoid bore two small, pointed teeth by 10–11 mm, four by 13 mm, and nine to 10 by 13.9 mm.

Hyoid Apparatus

All hyoid bones, except the urohyal, were present as cartilage by 5.0–7.0 mm. At that size

the ceratohyal and epihyal were represented by a single cartilage. Branchiostegal rays appeared by 8.6 mm. The urohyal was weakly developed by 9.1 mm and there were already seven weakly ossified branchiostegal rays. The ceratohyal began ossifying in the region of the first three branchiostegal rays by 10 mm, while the epihyal began at 13 mm. By 11.5 mm, the center of the interhyals and the distal portion of the epihyals began to ossify; however, there still was no separation of the epihyal and ceratohyal. By about 12.3–13.9 mm, all hyoid bones were ossified, but there were still broad areas of cartilage between individual bones; the branchiostegal rays were 5 (ceratohyal) + 2 (epihyal). The glossohyal had a posterior to anterior ossification sequence. The hyoid skeleton was completely ossified by 22–23 mm, except for the distal end of the glossohyal, a zone between the epihyal and ceratohyal, and the dorsal hypohyal. The hypohyals retained a cartilaginous interior zone at 41 mm.

The glossohyal of *M. americana* bore a line of about 13 teeth on each side at 23 mm. The lateral rows of teeth on the glossohyal were better developed by 41 mm.

Branchial Skeleton

The branchial skeleton was apparent as cartilage in the smallest specimens. At 4.6 mm, there was a single long copula spanning the first three gill arches and one smaller one posterior to the first. Three pairs of small epibranchials, five pairs of ceratobranchials, four pairs of small epibranchials, and one large infrapharyngobranchial bearing two or three teeth on its toothplate, were also present in these specimens. By 7.8 mm, all remaining branchial elements were present as cartilage. Ceratobranchials and hypobranchials began to ossify by 9.1–9.8 mm and the pharyngeal tooth patches were more strongly developed. First gill rakers were apparent on the posterior three arches by 10.7 mm. Ossification of copula II between the second and third arches began by 10.4–11.6 mm and the epibranchials were also beginning to ossify. Ossification of copula I between the first and second began by 13.3 mm, leaving cartilaginous areas at the junction of the hypobranchials. All branchial elements and gill rakers were ossified by 13.3 mm, except for some cartilage present in areas of articulation between elements. The adult complement of gill

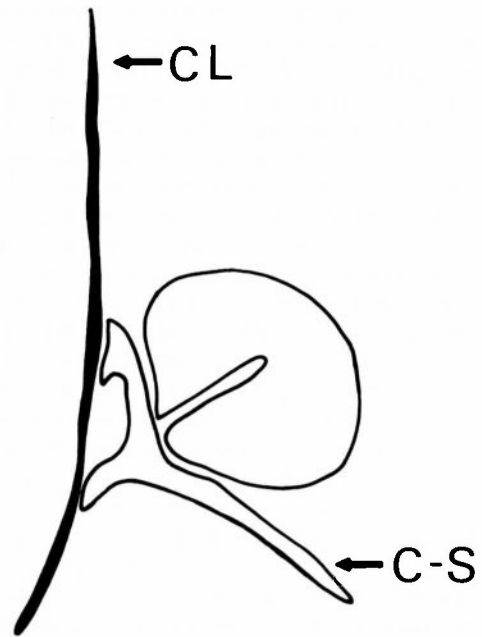


FIGURE 2.—Left pectoral girdle from a 9.0-mm *Morone saxatilis* larva. CL = cleithrum; C-S = coraco-scapular cartilage.

rakers on the first arch is 19–29 for *M. saxatilis* and 17–21 for *M. americana*.

Pectoral Girdle

By 4.6 mm, the coraco-scapular cartilage was present and the posterior process was much longer than the anterior; the cleithrum was represented by a thin line of bone. Pectoral radials first appeared as one continuous sheet of cartilage by 7.8–8.5 mm (see Fig. 2 for *M. saxatilis*). This condition remained the same except for the closer attachment of the coraco-scapular cartilage and the cleithrum until about 9.1 mm. By 9.1 mm, the four pectoral radials were visible as cartilage, the cleithra now met on the ventral midline, and supracleithra were just weakly ossified. Both supracleithra and post-temporals were ossified by 9.5–10 mm, and the postcleithra were visible as a very thin line of ossification. At 19 mm, the four pectoral radials were evident, the scapular foramen was present, and the coraco-scapular bar showed ventral extension of the anterior process along the cleithrum.

The pectoral radials were all separate by 10.8 mm, except for the ventral two. At a size of

12.3–13.9 mm, the posttemporal, postcleithrum, and cleithrum were well ossified, the coraco-scapular was still cartilaginous, and the pectoral radials were distinct and separate. By 14.3–16.2 mm, the scapula and coracoid were beginning to ossify with cartilage remaining around the scapular foramen and between the two elements. By 21 mm, the pectoral girdle was ossified. The only cartilage remaining was a band between the scapula and coracoid and at the distal tips of the developing radials. The posttemporal was completely developed by 45 mm. Pectoral fin rays first appeared by 10.1–11.7 mm when the dorsalmost nine or ten rays were present. Development proceeded from dorsal to ventral as actinotrichia were replaced by lepidotrichia. The adult complement of 15 or 16 rays was present by 13–20 mm. By 22–23 mm, the scapula was ossified except for cartilage along its proximal edge ventrally, and along the anterior, dorsal, and ventral articulating surfaces. By 43 mm, the scapula still retained some cartilage along the anterior border of the scapular foramen and the coracoid retained cartilage at the points of articulation with the cleithrum and scapula.

Pelvic Girdle

The basipterygia were first seen as a pair of cartilages at 8.4–10.0 mm. At 9.5 mm, they were larger with a broadened posterior surface and actinotrichia were visible in the pelvic blade. By 10.0–12.4 mm, the anterior process of each basipterygium was visibly elongate and coming close to the cleithrum. Six fin rays were evident in each pelvic fin by 12.4 mm. A distinct spinous ray was present by 13.8–14.0 mm and some ossification of the soft rays was evident. By 16 mm, the pelvic fins had attained the adult configuration (one spine and five soft rays).

Vertebral Column

The usual vertebral number in *M. americana* is 25. Of the specimens examined, about half had 12 abdominal + 13 caudal vertebrae and the remainder had 11 + 14. The first caudal vertebra was taken to be that which had a fully developed haemal spine with no indication of a distal bifurcation and was recognizable by 12 mm. *Morone saxatilis* also has 25 vertebrae. All specimens examined had 11 + 14. Both species have nine or 10 pairs of pleural ribs beginning

on the third vertebra and seven or eight pairs of epipleurals beginning on the first vertebra.

Specimens as large as 4.0–7.9 mm showed no trace of neural or haemal arch development or notochord segmentation. Neural arches developed from anterior to posterior. Development of haemal arches proceeded anteriorly and posteriorly from the midregion of the body. Cartilaginous neural and haemal arches were evident by 6.8–8.0 mm. Between 7.0 and 9.0 mm, development of neural and haemal arches proceeded rapidly. Posteriorly, the 23rd vertebra was the last to form neural and haemal arches. Those of the 24th formed earlier as a part of the caudal complex. At this stage, most of the arches had met in the midline and were beginning to form spines. By 8.0–9.6 mm, ossification of the anteriormost neural and haemal arches was evident (the centers of ossification being along their midlength). At this stage most arches had met in the midline to form neural and haemal spines that ossified independently from the arches. Parapophyses were evident as far forward as the sixth vertebra in some specimens. By 9.0–16.0 mm, neural and haemal arch ossification was complete on all but the last three or four vertebrae. The anteriormost two and posteriormost several arches still had some cartilage just posterior to their bases. By 9.9–11.8 mm, the neural spines were beginning to ossify. Prior to its ossification, each neural spine gave the impression of a separate rod of cartilage impaled on a flagellumlike extension of each neural or haemal arch. This is identical to the situation described by Potthoff (1975) for blackfin tuna *Thunnus atlanticus*. As with the neural arches, ossification proceeded from anterior to posterior. By 11.2–12.6 mm, the first three neural spines were completely ossified, but all haemal spines were cartilaginous. Haemal arch ossification was evident as far posteriorly as the fourth preural centrum (22nd vertebra). By 8.0–9.1 mm, segmentation and ossification of the notochord proceeded posteriorly; however, there was no evidence of an ossification process like that described by Potthoff (1975) for *Thunnus atlanticus* wherein ossification of each centrum began at the base of each neural and haemal arch and proceeded to the center of the centrum. Here, at the onset of stain uptake, the entire centrum stained evenly. By 10.0–10.7 mm, all centra showed some staining (the 24th being the last to ossify).

By 9.6–10.7 mm, ossified parapophyses were evident as far forward as the fourth vertebra, but only those on the 10th and 11th were well developed. Anterior to the 9th vertebra, parapophyses did not form in cartilage, but were ossified at their initial appearance. By 11.2–14.0 mm, four to seven pairs of pleural ribs were beginning to develop beginning on the third vertebra. By 17.3–18.0 mm, the full complement of nine or 10 ossified pleural ribs was present, but epipleural development was completed much later, between 24 and 30 mm. Unlike the pleurals, epipleurals were ossified at their initial appearance. Ossification of neural and haemal arches and spines and pleural ribs was completed between 18 and 25 mm. As in most percid fishes the first neural arch is autogenous and retains some cartilage between its base and its respective centrum.

Development of the vertebral column of *M. saxatilis* differed from that of *M. americanus* only in that most elements appeared and ossified at a slightly larger size.

Caudal Skeleton

The adult caudal complex of both species is that of a primitive percid. There are $9 + 8$ principal rays and $10-11 + 9-11$ procurrent rays in *M. americana*. A procurrent spur is present (Johnson 1975). The caudal complex of *M. saxatilis* is identical to that of *M. americana* with the exception that there are usually one or two more procurrent caudal rays in the dorsal and ventral series. A urostyle is present and the second and third preural centra are involved in support of the caudal fin rays. Haemal spines of the second and third preural centra are autogenous, and the neural arch of the second is reduced. Other supporting elements consist of one autogenous parhypural (with well-developed parhypurapophysis), five autogenous hypurals, two paired uroneurals, and three epurals. Radial cartilages are as follows: one each anterior to the tip of the neural and haemal spines of the third preural centrum; one or two between the distal ends of the second and third preural haemal spines; one at the distal tip of the second preural haemal spine; and one at the distal tip of the fifth hypural.

Caudal development was similar to that described for sea bream *Archosargus rhomboidalis* by Houde and Potthoff (1976). At 6.9–7.4 mm, the parhypural and the first three hypurals

were present as cartilaginous nodules lying below the unflexed notochord. Between 7.0 and 8.0 mm, the notochord began to flex, and flexion was complete in most by 8.0 mm. By 8.0–8.4 mm, the second preural haemal spine and the fourth hypural were present in cartilage and a few principal caudal rays were beginning to form. Formation of caudal fin rays proceeded from the midline dorsally and ventrally. Although the parhypural and the first and second hypurals formed as separate cartilaginous buds, they rapidly fused at their proximal bases to form a continuous block of cartilage lying along the ventral side of the urostyle (as illustrated, but not described, by Potthoff 1975). Connection of these three elements is only temporary. They eventually form three separate ossifications. A similar temporary fusion was observed in some specimens between the third and fourth hypurals. By 8.0–9.1 mm the fifth hypural was evident in most specimens and all three epurals were present as cartilaginous buds. One group of reared *M. americana*, spawned from a single male and female, developed an anomalous condition in the caudal skeleton wherein there were 4–7 epurals (Fig. 3). No other reared or wild specimens were observed with more than three epurals and we know of no other percid with more than three. The caudal development of these specimens otherwise appeared normal. Unfortunately the parents were discarded, and thus it was not possible to identify this anomaly as either genetically or environmentally induced. Twelve to fifteen principal caudal rays were evident and beginning to stain at 8.0–9.1 mm. By 8.6–10.7 mm, the full complement of $9 + 8$ principal caudal rays was present. By 8.9–10.7 mm, all hypurals were well developed and beginning to ossify at their centers. Hypurals ossified from a single center, whereas the parhypural had two centers of ossification apparently corresponding to the haemal arches and spines of the preceding vertebrae. By 10.6–12.6 mm, preural haemal spines, parhypural, and hypurals all showed considerable ossification, and the parhypurapophysis was developing. The parhypurapophysis was ossified at its initial appearance. Radial cartilages were evident at this size: one between the third and fourth hypurals; one at the tip of the second hypural, extending to the tip of the parhypural; and one at the tip of the fifth hypural. The first (ante-

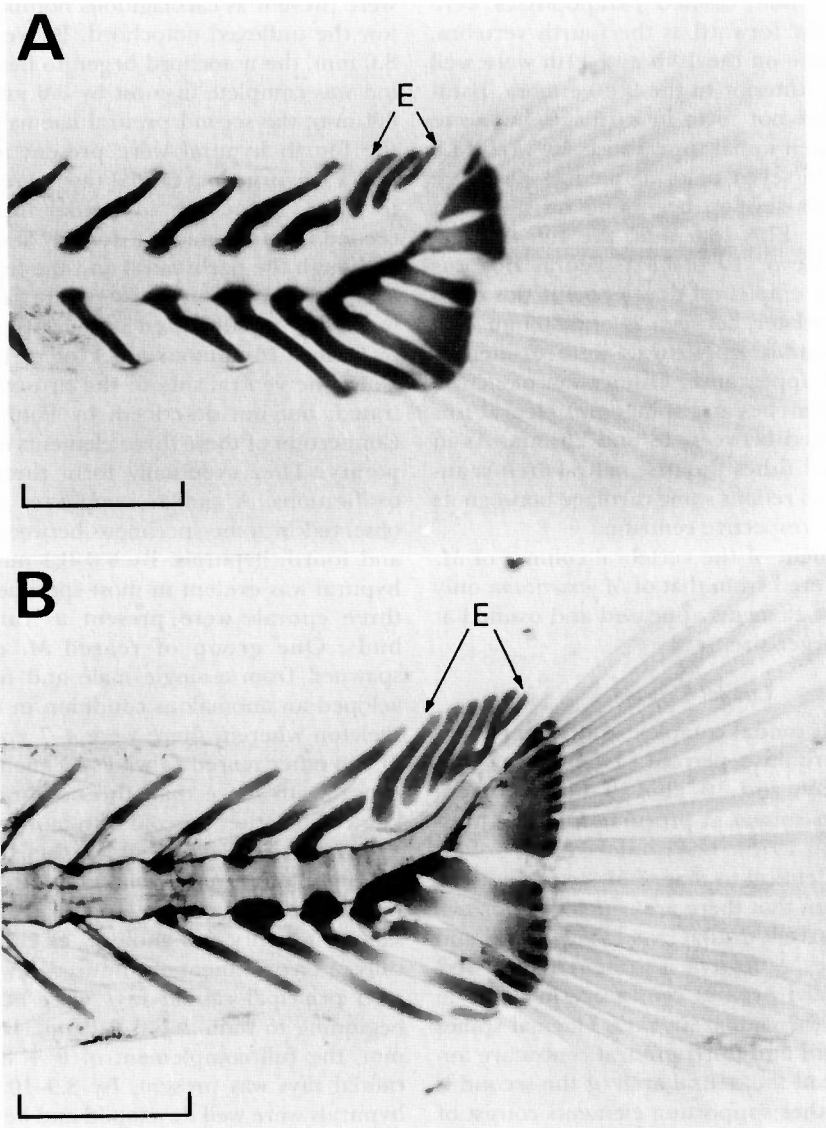


FIGURE 3.—Caudal skeleton of cleared and stained *Morone* larvae. (A) *M. saxatilis*, 8.6 mm, showing normal condition. (B) *M. americana*, 10.5 mm, showing abnormal number of epurals, E. Horizontal bar represents 0.5 mm.

riormost) uroneural pair was evident, and was ossified at its initial appearance. Principal caudal rays were well ossified. By 11.2–12.6 mm, the second uroneural pair was visible as a small sliver of bone on either side of the urostylar tip. Five to seven ventral procurrent rays were present, the posteriormost was beginning to develop a spur and the ray preceding it was shortened at its base. Most specimens had three to six dorsal procurrent rays; the posteriormost

was still separated from the first principal ray by the tip of the notochord. By 14.8–16.0 mm, ossification of the preural neural and haemal spines and parhypural was nearly complete; however, the first two hypurals were still connected at their bases by a continuous block of cartilage (this was retained to at least 30 mm). Epurals were beginning to ossify and there were 5–13 + 8–11 procurrent rays visible. By as early as 17.3 mm, ossification of the hypurals,

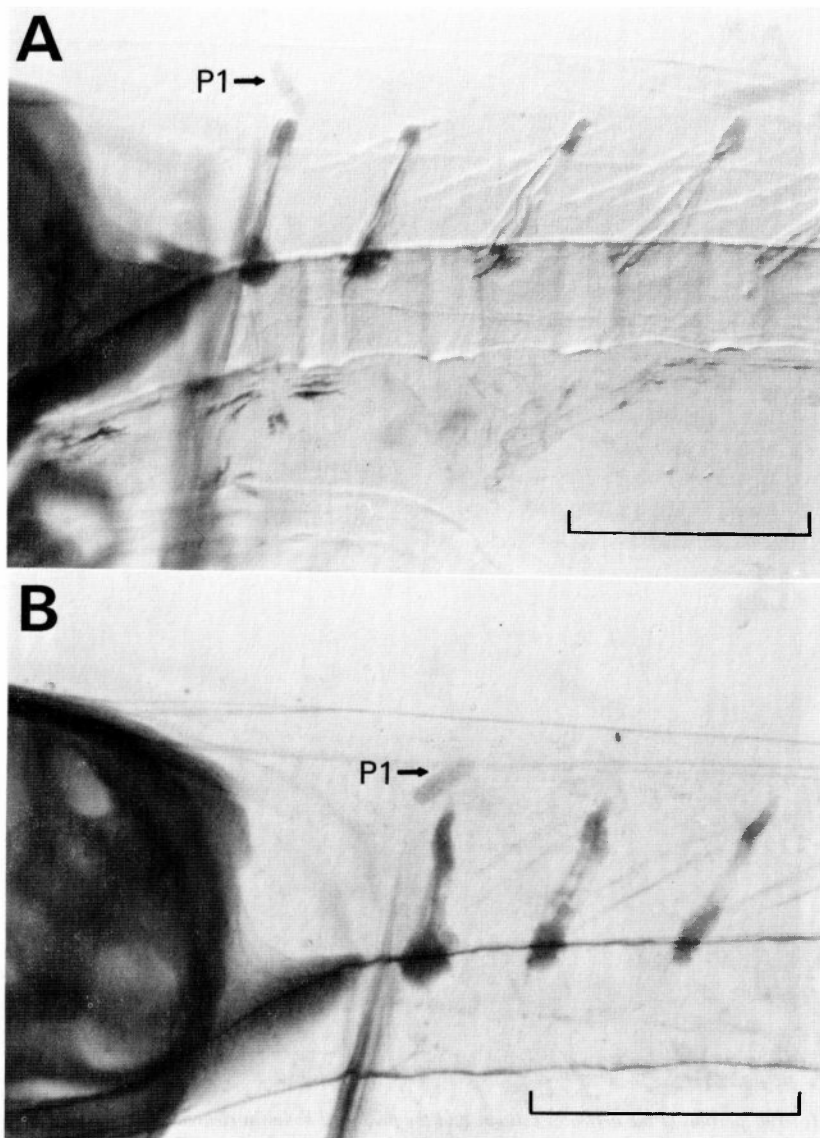


FIGURE 4.—Anterior portion of the vertebral column of cleared and stained *Morone* larvae. (A) *M. americana*, 9.5 mm. (R) *M. saxatilis*, 9.4 mm. PI = first predorsal bone. Horizontal bar represents 0.5 mm.

parhypural, and second and third haemal spines was complete. A radial cartilage had developed anterior to third preural and haemal spines and most specimens had two between the second and third preural haemal spines. By 16.2–20 mm, the full complement of procurrent rays was present in most specimens and all but the anterior two or three were ossified. By 21–28 mm, all bony elements, with the exception of the epurals, were completely ossified

and the radial cartilages showed the characteristic shape and relative size of the adults. Epural ossification was completed between 28–32 mm at which time the cartilaginous connection between the bases of the parhypural and hypurals one and two was lost.

The only notable difference between the two species was the appearance and ossification of most elements at a slightly larger size in *M. saxatilis*. However, about half the reared 14.8–

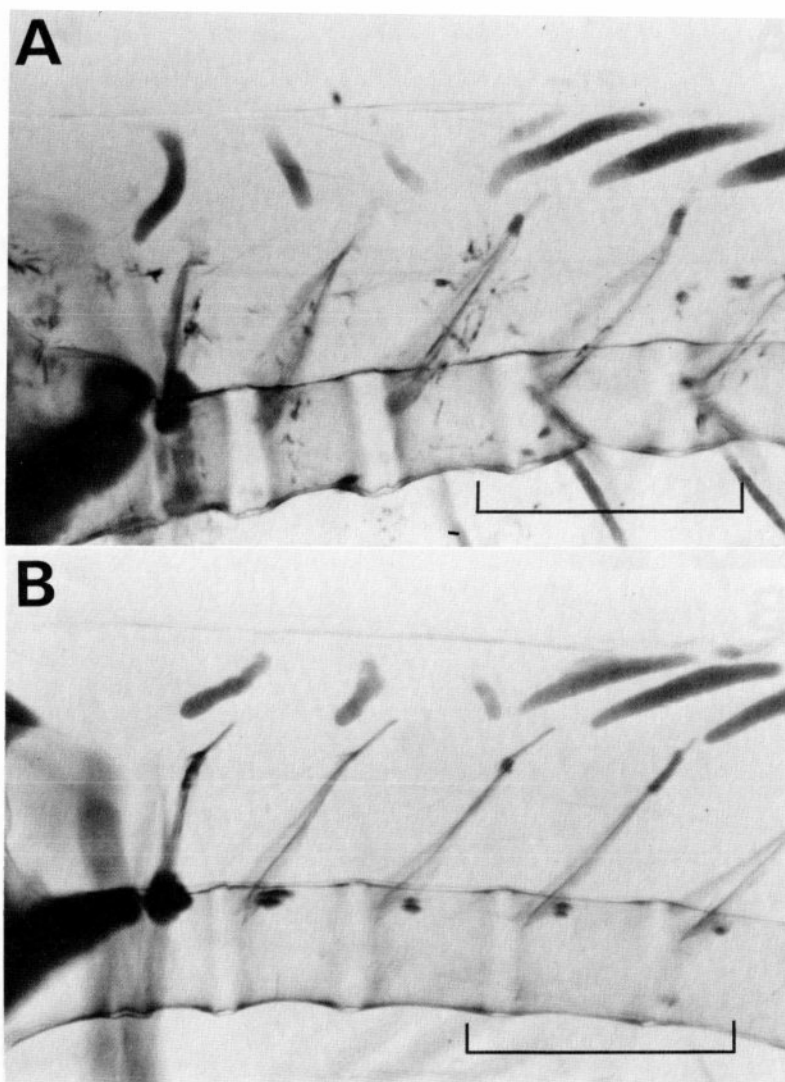


FIGURE 5.—Anterior portion of the vertebral column and the predorsal honey in cleared and stained *Morone* larvae. (A) *M. americana*, 10.6 mm. (B) *M. saxatilis*, 10.4 mm. Horizontal bar represents 0.5 mm.

16.0-mm specimens of *M. saxatilis* had a radial cartilage between the third preural neural spine and the first epural. This cartilage also occurred in some wild specimens but was never observed in *M. americana*. An apparently anomalous condition was seen in a few 17.3-mm reared specimens (very rare in wild specimens) of *M. americana* in which the neural arches of both the second and third preural centra were shortened. This did not appear to be the result of duplication of the second preural centrum

because all these specimens still had only 25 total vertebrae. In these specimens the neural spine of the fourth preural vertebra was elongated and extended posteriorly to support the dorsal procurent rays. In this case, a radial cartilage developed anterior to the fourth rather than the third preural neural spine.

Predorsals

The position and shape of the predorsal bones showed diagnostic differences between

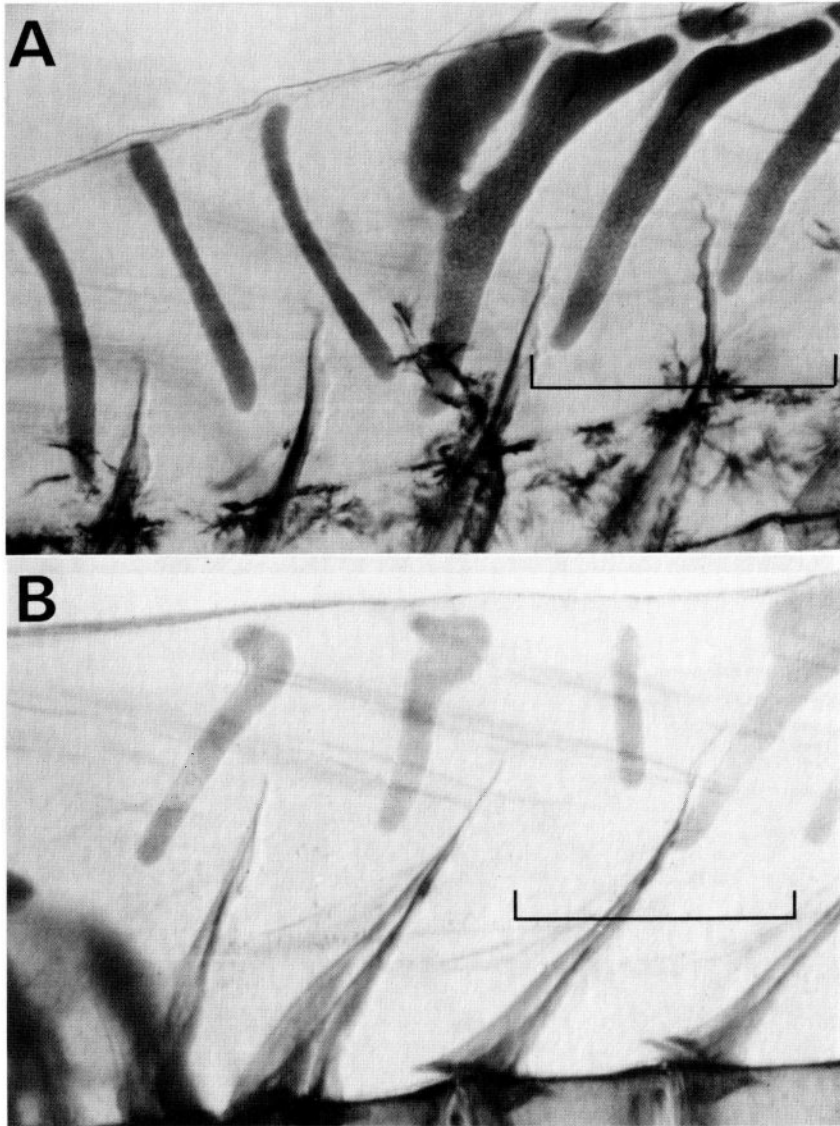


FIGURE 6.—Relationship of predorsal bones to the vertebral column in cleared and stained *Morone* larvae. (A) *M. americana*, 13.4 mm. (B) *M. saxatilis*, 14.7 mm. Horizontal bar represents 0.5 mm.

the two species. Because of this, each species will be described separately.

White Perch

As in most lower percoids, there are three predorsal bones. The predorsals and anterior-most dorsal pterygiophores are arranged in a consistent pattern in relation to the anterior neural spines: 0/0/0 + 2/11. The first predorsal is either parallel or tilted slightly forward with

respect to the neural spine axis (Fig. 4A). It typically has a slightly forward curve (convex posteriorly) and has an expanded dorsal tip. The second predorsal is typically tilted slightly forward with respect to the first two neural spine axes. It may be either straight or curved slightly forward. Axes of the first two predorsals are parallel dorsally; however, their ventral portions usually diverge notably (Fig. 5A). The third predorsal usually tilts forward over the

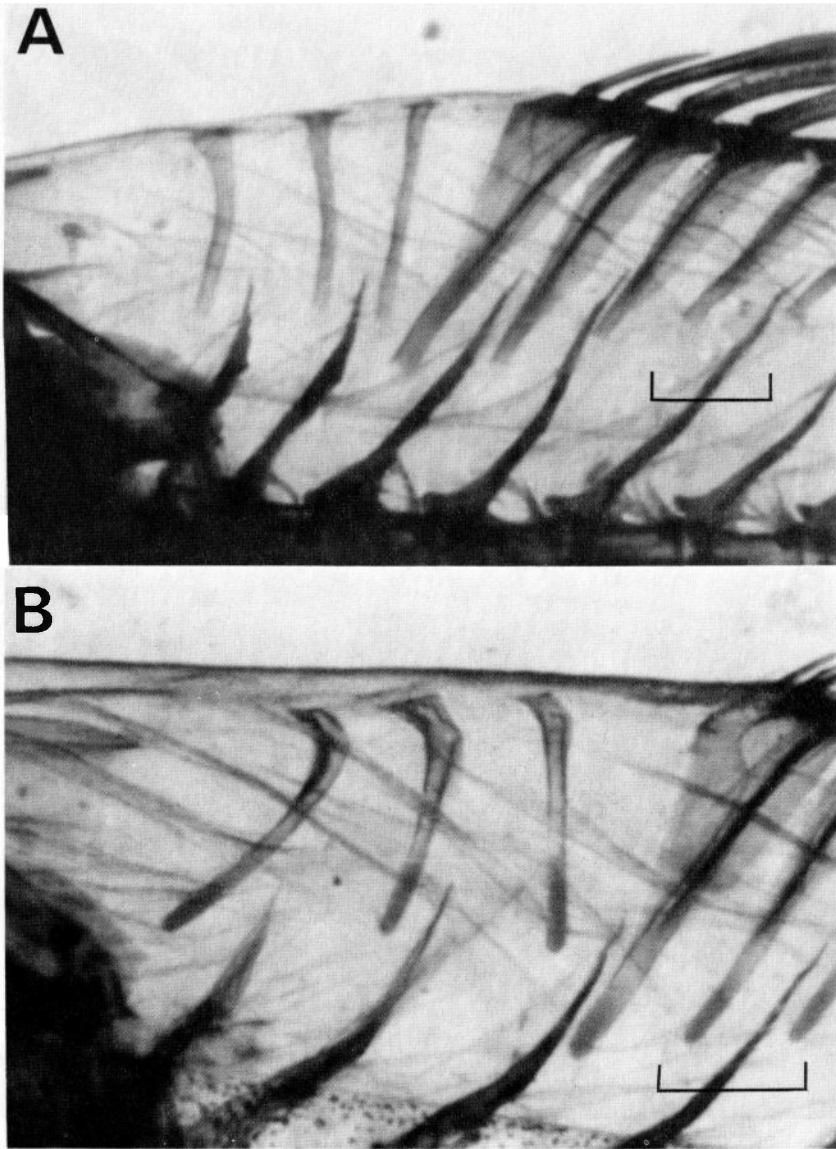


FIGURE 7.—Relationship of predorsal bones to the vertebral column in cleared and stained *Morone* juveniles (A) *M. americana*, 17.6 mm. (B) *M. saxatilis*, 25.1 mm. Horizontal bar represents 0.5 mm

tip of the second neural spine. It may be either straight or curved forward or backward. Axes of the posterior two predorsals converge ventrally, thus the distance between the ventral tips of the first and second predorsals is usually considerably greater (often two times) than that between the second and third predorsals. The first dorsal pterygiophore lies between the second and third neural spines, closer to the third

than the second (Figs. 5–7). It is tilted strongly backward and its ventral tip converges with that of the third predorsal at an angle of less than 45° . Departures from the basic configuration described above were rare in the reared and wild specimens examined and always involved obviously misshapen predorsal bones indicative of anomalous conditions.

Houde and Potthoff (1976) implied that the

predorsals of *Archosargus rhomboidalis* ossified from posterior to anterior, the third predorsal being the first to develop. In *M. americana* development proceeded in the opposite direction. The first predorsal appeared as cartilage between 7.0–8.2 mm, just after the soft-dorsal pterygiophores and well before the anterior spinous-dorsal pterygiophores developed. Typically, its orientation was vertical to the body axis, lying anterior to the tip of the first neural spine. In a few reared specimens it appeared over the tip of the first neural spine and was tilted backward; however, this configuration was never seen in wild specimens. The second predorsal was present in most specimens by 9.2 mm as a small forward tilted nubbin of cartilage between the first and second neural spines. The third predorsal appeared by 9.69.8 mm as a similar nubbin between the second and third neural spines. At this stage the first predorsal of most specimens had begun to develop the forward curvature characteristic of larger specimens, and the first dorsal pterygiophore was evident as a faint cartilaginous rod lying directly over the third neural spine. By 10.6–11.0 mm, the first predorsal was usually notably curved and the second and third predorsals were rod-shaped, lying parallel to one another and tilted forward (Fig. 5A). By 12.1–12.4 mm, the ventral tip of the first dorsal pterygiophore had extended in front of the third neural spine (Figs. 6, 7). By 14.8 mm, and earlier in some, the predorsals had developed the narrow, elongate shapes, and relative sizes and positions characteristic of the adults. The first two had begun to ossify. Ossification of the third predorsal was evident by 17 mm. All three predorsals were completely ossified, with the exception of their ventral tips, by 23 mm.

Striped Bass

There are three predorsal bones as in *M. nmericann*. We observed two patterns of interdigitation: 01010 + 2/1/ and 0101012 + 11, the difference being the location of the first dorsal pterygiophore anterior or posterior to the third neural spine. Although the first pattern was identical to that typical of *M. nmericnnn*, the overall configuration was readily distinguishable when shapes and relative angles of the bones were considered.

The first predorsal was tilted backward so that at least part of its upper portion lay pos-

terior to a vertical from the tip of the first neural spines (Figs. 4–7). Dorsally, the first predorsal bent abruptly (a more gradual curve in some) so that its tip was vertical to the body axis or tilted forward slightly. There was frequently a thin, rounded, median flange along the posterior margin of this bend or curve. The second predorsal lay anterior to the second neural spine in a vertical or slightly backward tilted orientation. It showed little or no curvature, but like the first predorsal tip was notably antero-posteriorly expanded. There was frequently a posterior flange similar to that seen on the first predorsal. Axes of the first and second predorsals were sometimes parallel, but more commonly there was a slight ventral divergence. Whereas in *M. nmericann* the ventral tip of the third predorsal was directly behind the second neural spine, in *M. saxatilis* it was back at least one-third to one-half of the distance between the second and third spines. Its orientation was either vertical to the body axis or slightly forward. Axes of the second and third predorsals were nearly parallel, but tended to diverge somewhat ventrally (Fig. 7). Thus the distance between the ventral tips of the first and second predorsals was more nearly equal to the distance between the ventral tips of the second and third than in *M. americnnn* and never approached twice that distance. In wild specimens, the first dorsal pterygiophore typically lies posterior to the third neural spine, adjacent to the second dorsal pterygiophore. The ventral tip of the third predorsal was closer to the third neural spine than to the second in these specimens. An occasional wild specimen and the majority of the reared specimens had the first dorsal pterygiophore anterior to the third neural spine, adjacent to the third predorsal, as is typical of *M. americana*. However, unlike *M. nmericnnn*, these two elements, when adjacent, usually formed an angle of 45° or greater from their ventral tips.

Sequence of predorsal development was identical to that of *M. americana*; however, configurational differences between the two species were evident at the initial appearance of the first element. The first predorsal appeared as an oblong cartilaginous nubbin by 8.7–9.1 mm (Fig. 4B). Typically it was tilted approximately 45° from the vertical to the body axis backward over the tip of the first neural spine. The second predorsal appeared in all specimens by 9.5

mm as a variously oriented cartilaginous nubbin lying just anterior to the tip of the second neural spine. At this stage the first predorsal was a well-defined rod tilted sharply backward over the first neural spine. The third predorsal was evident between the second and third neural spines by 10.4–10.7 mm (Fig. 5B). By 11.2 mm all three predorsals were rod-shaped and the adult configuration was becoming recognizable. The first was starting to curve forward dorsally, the second was vertical or tilted slightly backward, and the third was tilted strongly forward. The first dorsal pterygiophore was well developed in cartilage at this stage. In most reared specimens it was located anterior to the third neural spine, and was tilted strongly backward, forming an angle of 45° or more with the third predorsal. By 14.8–16.0 mm, all three predorsals had the narrow, elongate shape characteristic of the adults, and the anterior two had begun to ossify. The third predorsal had begun to ossify by about 17 mm and all three were completely ossified, with the exception of their ventral tips, by 25–28 mm (Fig. 7B).

Dorsal and Anal Fins and Supports

In adults of both species, the dorsal fin has 10 (rarely 11) spines and 10–12 soft rays. The anal fin has three spines and nine or 10 (rarely eight) soft rays in *M. americana*, and 10–12 soft rays in *M. saxatilis*. The dorsal fin is deeply incised. Posterior to the fourth spine, the spine lengths decrease rapidly to the penultimate spine. There is no membranous connection between the penultimate and ultimate spine in *M. saxatilis*. The ultimate spine (usually the tenth) forms the leading edge of the soft dorsal fin and is about twice as long as (*M. americana*) or several times longer than (*M. saxatilis*) the penultimate spine.

Support of the dorsal- and anal-fin rays is typical of lower percoid fishes and is essentially identical to that described for *Archosargus rhomboidalis* (Houde and Potthoff 1976). All pterygiophores in both fins have separate distal radials. Proximal and medial radials are apparently fused, with the exception of the last two or three pterygiophores in each fin. The first pterygiophore in both fins supports two supernumerary spines. The third spine of each fin (which serially corresponds to the first pterygiophore) articulates with the distal element of the first pterygiophore and with the anterodor-

sal corner of the proximal-medial element of the succeeding pterygiophore. Remaining spines and soft rays of both fins are supported in this dual articulating fashion, with the exception of the last two (counted as one) which have no secondary support. A small stay is associated with the last pterygiophore of each fin. Pterygiophores of the soft dorsal and anal fins were the first to develop. They appeared in cartilage near the future middle of these fins and were added in an anterior and posterior direction as a continuation of soft dorsal development. By 6.9–9.1 mm, 10–12 cartilaginous dorsal and anal pterygiophores were evident between neural spines 9 and 16 and haemal spines 12 and 17, respectively. A few pterygiophores near the middle had distal radials and barely discernible fin rays associated with them. By 8.6–9.6 mm, all soft dorsal-fin pterygiophores were present. Spinous dorsal-fin pterygiophores were faintly visible as far forward as the fourth neural spine. These pterygiophores were nearly horizontal to the body axis at their initial appearance. All anal pterygiophores were present and most had distals and barely discernible fin rays. By 8.9–10.7 mm, all soft dorsal- and anal-fin pterygiophores except the last had distals, and the full complement of eight spinous dorsal-fin pterygiophores was present in some (others had only seven). By 9.6–12.6 mm, all dorsal and anal soft rays were evident and beginning to ossify. The ultimate dorsal and anal spine remained transitional. By 10.6–16.0 mm, the full complement of anal spines and soft rays was evident and staining slightly; however, the third anal spine and all soft rays still had the brushlike actinotrichia tips. The first two anal spines were simple, bilaterally paired structures at their initial appearance. By 11.2–12.4 mm, all spinous dorsal-fin pterygiophores had distal elements and minute spines (some still beneath the skin). By 12.6–13.9 mm, all dorsal-fin spines were evident above the skin and were ossifying. The ultimate dorsal and anal spines were still present as soft rays and all spines and soft rays were ossified. No ossification of the dorsal-fin pterygiophores was evident, but the first anal-fin pterygiophore had begun to ossify along its midlength. By 14.8 mm, most spinous dorsal-fin pterygiophores showed some evidence of ossification. The ultimate dorsal and anal spines and all soft rays still had brushlike tips, but were well stained. By about 23 mm, all but the last

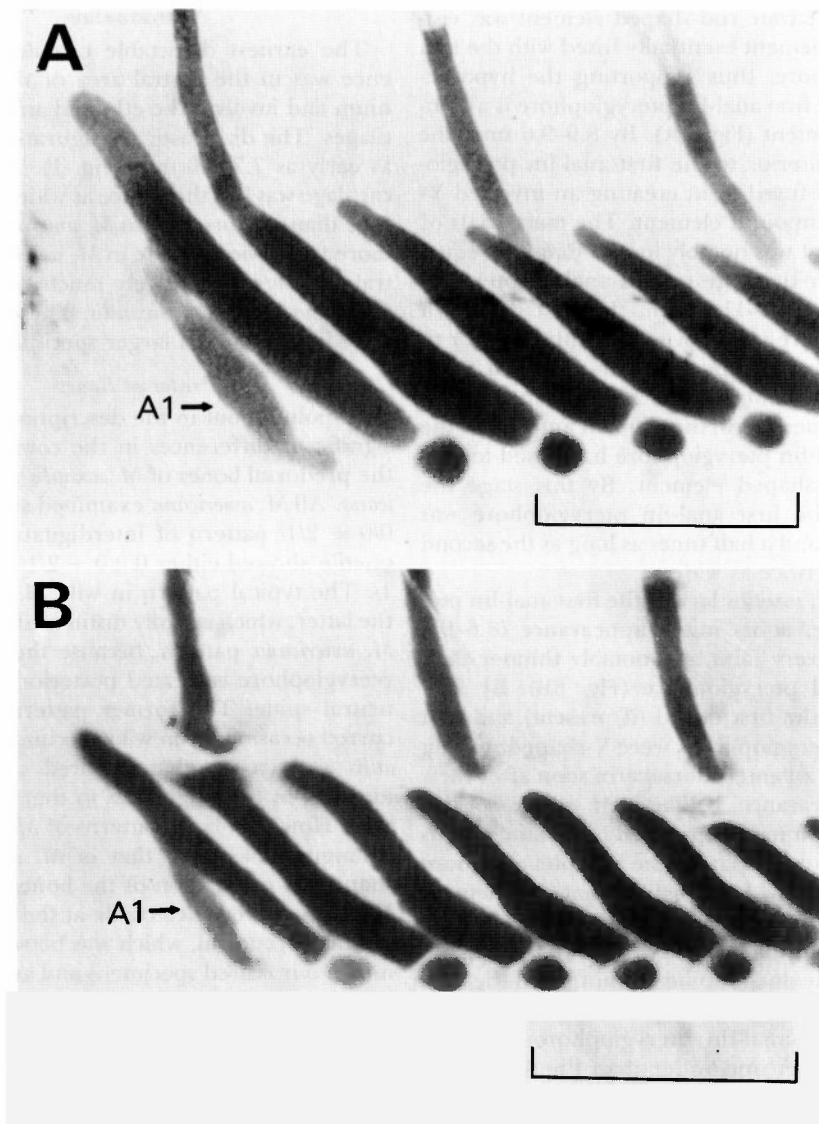


FIGURE 8.—Relationship of anal pterygiophores to the vertebral column in cleared and stained *Morone* larvae. (A) *M. americana*, 9.6 mm. (B) *M. saxatilis*, 8.6 mm. A1 = first anal pterygiophore. Horizontal bar represents 0.25 mm.

four or five dorsal-fin pterygiophores were completely ossified except at their ventral tips. Distal radials of all but the first were still cartilaginous. Segmentation was still evident at the tips of the ultimate dorsal and anal spines. By about 27 mm, the distal elements of all spinous dorsal and some soft-ray pterygiophores showed evidence of ossification. Ultimate dorsal and anal spines were completely transformed and all soft rays (except the first in each fin) had branched tips. The first anal pterygiophore was

completely ossified and the others were nearly complete. Ossification of all dorsal- and anal-fin rays and supports was complete by about 30 mm, except the medial and distal radials of the posteriormost anal pterygiophores.

The differences exhibited between the two species involved the first dorsal- and anal-fin pterygiophores. In the *M. americana* larvae, the first anal-fin pterygiophore was about equal in length and width to the second at 8.6–8.8 mm. Just anterior to the first anal-fin pterygiophore,

a small, separate rod-shaped element was visible. This element eventually fused with the first pterygiophore, thus supporting the hypothesis that the first anal-fin pterygiophore is a compound element (Fig. 8A). By 8.9–9.6 mm, the element anterior to the first anal-fin pterygiophore had fused to it, creating an inverted Y-shaped compound element. The main shaft of this element was notably longer than and equal to or wider than the second anal-fin pterygiophore. By 10.611.8 mm, the first dorsal-fin pterygiophore was above or slightly anterior to the third neural spine and there was a small separate element anterior to it. In most 12.1–12.4-mm specimens, the element anterior to the first dorsal-fin pterygiophore had fused to it to form a Y-shaped element. By this stage the shaft of the first anal-fin pterygiophore was about one and a half times as long as the second and about twice as wide.

In the *M. saxatilis* larvae, the first anal-fin pterygiophore, at its initial appearance (8.6–9.6 mm), was very faint and notably thinner than the second pterygiophore (Fig. 8B). By 9.9–10.7 mm, the first dorsal (if present) and first anal-fin pterygiophores were Y-shaped, having developed an anterodorsal arm soon after their initial appearance. Unlike in *M. americana*, this anterior arm never appeared as an autogenous element, but was part of the first pterygiophore at its inception. It is possible that this element is initially autogenous but it was not seen as such in our material. By 14.8–16.0 mm, the penultimate dorsal spine did not reach the base of the ultimate when depressed and the shaft of the first anal-fin pterygiophore was only slightly longer and wider than the second. In *M. americana*, the penultimate dorsal spine, when depressed, reached to or beyond the base of the ultimate spine.

Diagnostic Differences

Adult *M. americana* and *M. saxatilis* from the Chesapeake Bay region differ in a number of osteological features. These differences became evident at various stages of development and we feel that they may be useful in distinguishing larvae of the two species, particularly within the size range where identification with previously described external features is tenuous (Table 1).

Neurocranium

The earliest detectable osteological difference was in the rostral area of the neurocranium and involves the ethmoid and rostral cartilages. The diagnostic configuration appeared as early as 7.7–8.0 mm (Fig. 1). The ethmoid cartilage was less than twice as wide at its ventral base than its dorsal tip in *M. americana*, but was more than twice as wide in *M. saxatilis*. The rostral cartilage is relatively much smaller in *M. americana* than in *M. saxatilis*. These differences were less notable in larger specimens.

Predorsal Bones

As pointed out in the descriptions, there are significant differences in the configuration of the predorsal bones of *M. saxatilis* and *M. americana*. All *M. americana* examined showed the 0/0/0 + 2/11 pattern of interdigitation while *M. saxatilis* showed either 0/0/0 + 2/11 or 0/0/0/2 + 1/. The typical pattern in wild *M. saxatilis* was the latter, which is easily distinguished from the *M. americana* pattern, because the first dorsal pterygiophore is located posterior to the third neural spine. The former pattern, which occurred occasionally in wild specimens of *M. saxatilis* and frequently in reared specimens, is identical in interdigitation to that of *M. americana*. However, both patterns of *M. saxatilis* are distinguishable from that of *M. americana* by shape and orientation of the bones (Figs. 4–7). Differences were detectable at the inception of the first predorsal, which was between 7 and 9 mm in our reared specimens and at a somewhat larger size in the wild ones. In *M. americana* this element appeared as a vertically oriented nubbin lying anterior to the first neural spine, while in *M. saxatilis* it was tilted backward over the tip of the first neural spine.

Dorsal and Anal Pterygiophores

In *M. americana*, the anterior arm of the first dorsal and anal pterygiophores appeared initially as an autogenous element whereas in *M. saxatilis* it was part of the pterygiophore at its inception (Figs. 5, 8). This difference was only detectable at about 10–11 mm when the element first appeared, because the element remains separate for only a very short time. A more striking difference, and one that was even more pronounced in adults, was the relative size of the first anal pterygiophore. This difference was first noticeable when the anterior

TABLE 1.—*Diagnostic osteological differences for identification of early life history stages of white perch and striped bass.*

White perch	Striped bass	Standard length (mm) difference first detectable
	<i>Neurocranium</i>	
Ethmoid cartilage less than twice as wide at ventral base as at dorsal tip	Ethmoid cartilage more than twice as wide at ventral base as at dorsal tip	8
	<i>Predorsal bones</i>	
Dorsal tip of first predorsal cartilage (throughout its development) lies anterior to the vertical plane extended from the tip of the first neural spine	Dorsal tip of first predorsal cartilage lies posterior to the vertical plane extended from the tip of the first neural spine	7-9
First preclorsal cartilage with slight curvature	First predorsal cartilage strongly curved	
After all three predorsal cartilages are evident:		10-11
Second pretlorsal cartilage inclined anteriorly from its ventral tip	Second predorsal cartilage inclined posteriorly from its ventral tip	
First and second predorsal cartilages without enlarged area along the posterior margin	First and second predorsal cartilages may have an enlarged flange along the posterior margin	
Distance between ventral tips of first and second predorsals much greater (often twice as much) than that between ventral tips of second and third predorsals	Distance between ventral tips of first and second predorsals approximately equal to that between the ventral tips of second and third predorsals	
Axes of second and third pretlorsal cartilages converge ventrally	Axes of second and third predorsal cartilages are parallel or diverge ventrally	
Ventral tip of third predorsal lies just posterior to second neural spine	Ventral tip of third predorsal located at least $\frac{1}{3}$ to $\frac{1}{2}$ of the distance from the second to third neural spine	
	<i>Dorsal and anal-fin pterygiophores</i>	
Ventral tip of first dorsal-fin pterygiophore lies between second and third neural spines	Ventral tip of first dorsal-fin pterygiophore usually lies posterior to third neural spine but may lie just anterior to it	10-11
Anterior arm of first dorsal- and anal-fin pterygiophores appears initially as an autogenous element	Anterior arm of first dorsal- and anal-fin pterygiophores is part of the pterygiophore at its inception	
After all anal-fin pterygiophores are formed:		
First anal-fin pterygiophore notably longer and equal to or wider than the second	First anal-fin pterygiophore equal to or only slightly longer than and usually narrower than the second	
Dorsal tip of second anal-fin pterygiophore not expanded or bifurcate	Second anal-fin pterygiophore with expanded, occasionally bifurcate, dorsal tip	
	<i>Anal fin</i>	
Second anal-fin spine much thicker than adjacent anal elements	Second anal-fin spine slightly thicker than adjacent anal elements	about 15
	<i>Vertebrae</i>	
11 + 14 or 12 + 13	11 + 14	18-20

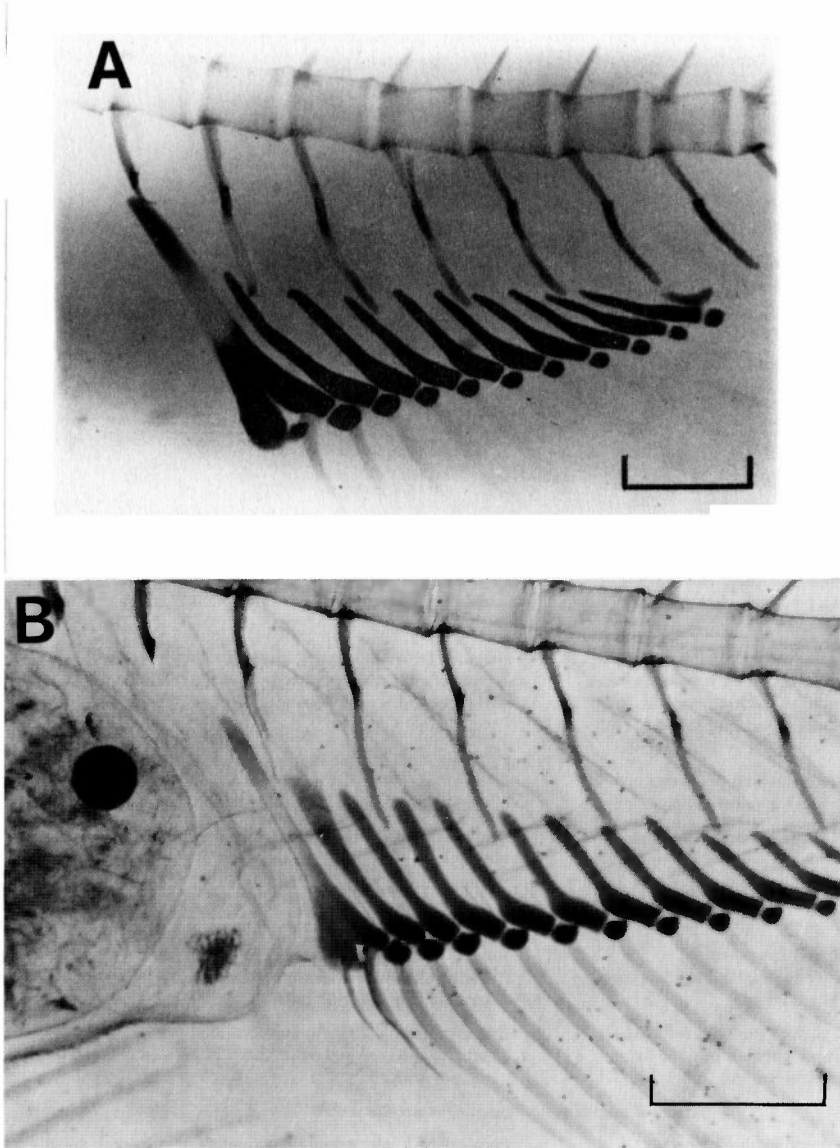


FIGURE 9.—Relationship of anal pterygiophores to the vertebral column in cleared and stained *Morone* larvae. (A) *M. americana*, 11.1 mm. (B) *M. saxatilis*, 12.4 mm. Horizontal bar represents 0.5 mm.

arm of this pterygiophore had developed (about 9 mm in *M. americana* and 10 mm in *M. saxatilis*). At this point the main shaft of the first anal pterygiophore in *M. americana* was notably longer and equal to or wider than that of the second, while in *M. saxatilis* it was equal to or only slightly longer and usually narrower than the second. In addition, the second anal pterygiophore of *M. saxatilis* usually had an expanded (sometimes bifurcated) proximal tip,

which was never seen in *M. americana* (Figs. 9, 10). These differences became more exaggerated with growth. By about 12 mm, the first anal pterygiophore in *M. americana* was about one and a half times as long and at least twice as wide as the second, whereas in *M. saxatilis*, even by 16 mm, it was only slightly longer and wider (Fig. 10). The relative massiveness of this element in *M. americana* is apparently related to its support of a longer and more massive

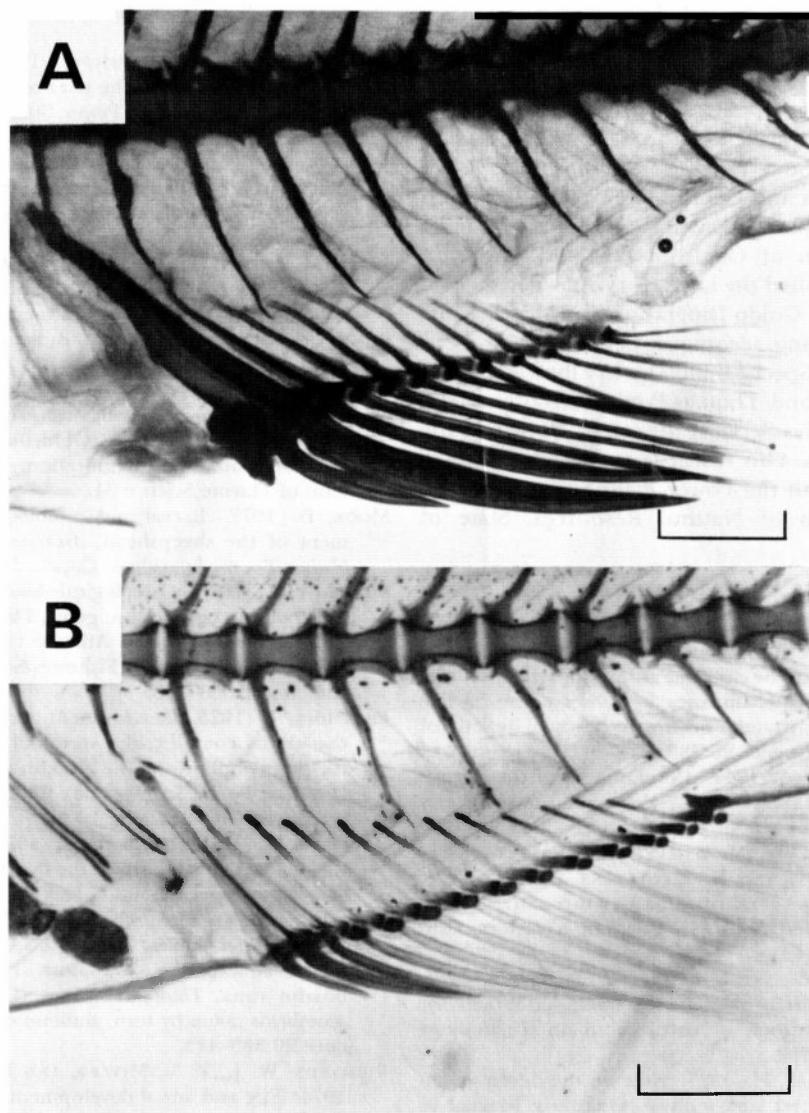


FIGURE 10.—Relatizonhrzp of anal pterygiophores to the vertebral column in cleared and stained *Morone* larvae. (A) *M. americana*, 22 mm. (B) *M. saxatilis*, 23 mm. Horizontal bar represents 1.0 mm.

second anal spine than in *M. saxatilis*. The relative size of this spine is also a useful diagnostic feature and has been described by Drewry (unpublished, University of Maryland Center for Estuarine and Environmental Studies Reference 78-81 CBL).

Vertebral Column and Caudal Skeleton

Although no consistent differences were found in these complexes certain features may be helpful. About half the *M. americana* speci-

mens which we examined had 12 + 13 vertebrae whereas all *M. saxatilis* had 11 + 14 (countable by 12-13 mm). The full complement was present by 18-20 mm in both species. We counted 10-11 + 9-11 procurrent caudal rays in *M. americana* while *M. saxatilis* had one or two more in the dorsal and ventral series. A radial cartilage was present between the third preural neural spine and the first epural in about half the reared and some wild specimens of *M. saxatilis*, but was never observed in *M. americana*.

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