EGG AND LARVAL DEVELOPMENT OF THE ATLANTIC THREAD HERRING, *OPISTHONEMA OGLINUM*[1,2]

WILLIAM J. RICHARDS,[3] ROBERT VICTOR MILLER,[4] AND EDWARD D. HOUDE[5]

ABSTRACT

The egg and larval development of Atlantic thread herring, *Opisthonema oglinum*, is described, based on wild-caught eggs and laboratory-reared larvae. This description includes morphological details of the egg and osteological development, changes in body shape and pigmentation, and significant features of transformation of the larval development stages. The egg is 1.10 to 1.28 mm in diameter with a single oil globule. Ossification commences in the larvae when they attain 10 mm in standard length and all bones have at least begun to ossify by 20 mm. During transformation (15 to 25 mm), the larvae assume juvenile characteristics; particularly evident during this period is the anterior movement of the dorsal and anal fins from their posterior larval positions to their medial adult positions.

The Atlantic thread herring, *Opisthonema oglinum* (Lesueur), is a clupeid fish commonly found in the subtropical and tropical waters of the western Atlantic Ocean, but the eggs and larvae of this species have not been described previously. In 1968, Atlantic thread herring were reared from eggs in the Tropical Atlantic Biological Laboratory, Miami, Fla. (now the Southeast Fisheries Center), and a complete developmental series was obtained (Richards and Palko, 1969). This paper describes the egg and morphological development of the reared larvae. We used a dynamic approach, similar to that of Moser and Ahlstrom (1970), to describe the sequential development of characters, instead of a static approach in which a few selected sizes of larvae are described in detail. Larvae reared under laboratory conditions provide unusually good specimens for studies of this kind.

The major purpose of describing eggs and larvae is to provide information so that they may be identified in field collections. Identification is very difficult among the clupeids because all of the larvae are very similar in appearance. This group is further complicated by the many species that occur. In the western North Atlantic 15 genera, representing about 36 species, are found. Three genera are distinctive since they are found in fresh water, or at least spawn and develop in fresh to brackish water. Five other genera are distinctive because of their long anal fin, and one poorly known genus because of its very few vertebrae. However, approximately 17 species remain represented by seven genera, which are very similar in appearance. These genera are *Clupea* (one species), *Etrumeus* (one species), *Jenkinsia* (three species), *Brevoortia* (four species), *Opisthonema* (two species), *Harengula* (three species), and *Sardinella* (three species). Some species within these genera are imperfectly known (Berry, 1964). At our laboratories, three other species have now been reared besides *O. oglinum*—*Sardinella anchovia, Brevoortia smithi, and Harengula jaguana*—and descriptions of these are in preparation. Except for *Sardinella*, it appears now that *O. oglinum* can be separated from all of the other genera on the basis of meristic characters. *Brevoortia* is similar in most meristic characters, but its anal fin is found nearly below the posterior end of the dorsal fin, unlike *Opisthonema*. The eggs are very similar to one another, but size and spawning times are helpful in separating the species. Much detailed work is needed to work out these identification problems, not only for the eggs and larvae but for the adults as well. A recent paper gives useful information on these identification problems (Houde and Fore, 1973).

[1]Contribution No. 236, Southeast Fisheries Center, National Marine Fisheries Service, NOAA, Miami, FL 33149.
[2]Contribution No. 1790, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149.
[3]Southeast Fisheries Center, National Marine Fisheries Service, NOAA, Miami, FL 33149.
[4]Southeast Fisheries Center, National Marine Fisheries Service, NOAA, Miami, FL 33149; present address: National Marine Fisheries Service, NOAA, Washington, DC 20235.
[5]Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149.

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MATERIALS AND METHODS

Eggs that were used for descriptive purposes were collected in 1971 and 1972 during ichthyoplankton surveys in the eastern Gulf of Mexico. Twenty-three eggs in varying stages of development were examined and measured. Eggs from the laboratory rearing experiment were lost and consequently could not be described.

We selected only the best specimens for this study by eliminating fish with pronounced body curvature and those in poor condition. We used 53 of the 197 available specimens. Forty-two of these specimens were measured with an ocular micrometer of a dissecting microscope to provide data on body proportions. Seventeen of the specimens were cleared and stained to provide meristic data and osteological data. Specimens shown in the illustrations were among those cleared and stained for verification of the fin-ray counts. Staining procedures followed those of Taylor (1967).

During development, *O. oglinum* undergoes some pronounced changes in structure. These changes are difficult to adequately define, particularly the metamorphic stages. We have followed the definitions used by Moser and Ahlstrom (1970), and we have also taken into account Ahlstrom's (1968) comments on the subject. Our yolk-sac larvae were lost, so our description commences with the larval period. The period between the larval period and juvenile period is termed the transitional stage, following Moser and Ahlstrom (1970). At the beginning of the transitional period (about 15 mm standard length), the animals commence metamorphosis into juveniles.

Our methods of counting and measuring closely follow Moser and Ahlstrom, but for convenience are defined as follows:

Body length—In early stage larvae and in those undergoing notochord flexion, the body length is the distance from the tip of the snout to the tip of the notochord. After the hypural complex is developed the standard length measurement is used, i.e., the distance from the tip of the snout to the posterior margin of the hypural elements. While the notochord is undergoing flexion and the hypural elements are developing, this estimated standard length measurement is denoted in the tables.

Eye diameter—Maximum width of the pigmented eye measured on the horizontal axis.

Snout length—Distance from the tip of the snout to the anterior edge of the orbit.

Head length—Distance from the tip of the snout to the posterior edge of the opercle.

Length of dorsal and anal fin bases—Distance from the origin of the first ray to the point where the posterior part of the last ray contacts the body.

Snout to origin of dorsal fin—Identical to the predorsal length defined by Hubbs and Lagler (1958).

Snout to origin of pelvic fin—Distance from the tip of the snout to the pelvic fin base.

Snout to origin of anal fin—Distance from the tip of the snout to the origin of the anal fin (in small larvae, before the anal fin develops, this measurement is defined as the distance from the tip of the snout to the end of the gut; it can be used as gut length for all larvae and small juveniles).

Origin of dorsal fin to base of caudal rays—Distance from origin of the dorsal fin to the end of the hypural plate.

Body depth—Vertical depth of the body measured at the origin of the pelvic fins (in larvae that have not developed pelvic fins, the midpoint of the body is used).

Origin of anal fin to base of caudal rays—Distance from origin of the anal fin to the end of the hypural plate.

Origin of pelvic fin to base of caudal rays—Distance from origin of the pelvic fin to the end of the hypural plate.

DESCRIPTION OF THE EGGS

Twenty-three eggs ranged from 1.10 to 1.28 mm in diameter (mean = 1.19 mm). The chorion is thin and fragile, unsculptured, and unpigmented. A single oil globule is present, ranging from 0.12 to 0.16 mm in diameter (mean = 0.15 mm). As in most clupeid eggs, the perivitelline space is wide, and the yolk mass is vaguely segmented. For 10 embryos at the blastodisc stage the yolk diameter averaged 59% of the egg diameter, while for 13 advanced embryos the yolk diameter averaged only 53% of the egg diameter. A paired dorsolateral series of tiny melanophores is present on embryos that are about to hatch (Figure 1). *Opisthonema* eggs

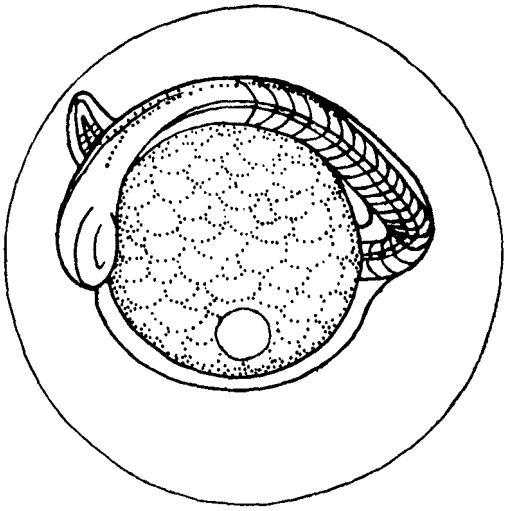

FIGURE 1.—*Opisthonema oglinum* egg.

are similar to those of most other clupeids (e.g., Reintjes, 1962; Simpson and Gonzalez, 1967) but differ markedly in total egg diameter and oil globule diameter from *Harengula* spp., with which they may cooccur. Houde, Richards, and Saksena (1974) reported that the diameter of *Harengula jaguana* eggs was never less than 1.50 mm, and that the oil globule diameter never exceeded 0.10 mm.

MORPHOLOGY OF LARVAE

Meristic values were obtained and these are shown in Table 1. To describe the change in shape and to note changes in various structures, 13 measurements were made. These are shown in Table 2. The larvae are also illustrated for several selected sizes (Figures 2 to 8). *Opisthonema oglinum* larvae, prior to the start of the transition to juveniles, are very slender larvae with a well-developed finfold and long gut. Prior to notochord flexion gut length averages about 86% of the body length. During notochord flexion this increases to 91% because body length is slightly reduced. The abruptness of this flexing is evidenced in the measurement of origin of anal fin to base of caudal rays in Table 2. After notochord flexion this distance is smaller due to the upturning of the notochord. Following flexion (10 mm SL) the gut averages 92% of standard length up until transformation commences at 15 mm SL. At that time there is a gradual shortening of the gut until it becomes about 75% of the standard length as a juvenile. The large finfold decreases at about the time of notochord flexion and is almost lost by the time the anal fin is well differentiated at 13 mm SL, except for a remnant beneath the foregut (Figures 2 to 4).

The first fin to form is the pectoral fin but, as described later under the osteology section, it is not the ossified pectoral fin of the juvenile. The caudal fin, dorsal fin, and anal fin all develop within the finfold itself, and their development is discussed in the osteology section. The pelvic fin is the last fin to be discernible as a small fleshy protuberance at 14 mm SL.

At first, the gut is a straight simple tube. At 5 mm SL it can be differentiated into a foregut and hindgut. The hindgut becomes ridged or banded with tissue, which is quite evident in Figure 4 of a 13.7-mm SL specimen. This ridging is still evident through much of the transitional period (Figure 5).

The most striking feature of development is the anterior migration of the dorsal fin during transformation. The fin nearly has its full complement of rays before this commences and like the shortening of the gut and anterior advancement of the anal fin, it is a rapid change. It is more striking than the latter since the fin is so visible. The predorsal length averages more than 60% of the body length until about 17 mm, then it rapidly decreases to an average of 43% of body length when transformation is completed. The position of both the dorsal and anal fin in relation to the vertebrae also vividly demonstrates this movement (Table 3). The fin movement begins at 15 mm. At that size, the anal fin origin begins to move forward from its position under vertebra 38 (Table 3 and Figure 6) to its final position under vertebrae 33 to 34 at 24 mm (Table 3 and Figure 7). Similarly, the origin of the dorsal fin is transferred forward over vertebra 23 (Table 3 and Figure 6) to over vertebra 15 when larvae measure 19 and 25 mm (Table 3 and Figure 7). To about 20 mm, there are 21 predorsal myomeres and no ossified predorsal bones (free interneurals), but shortly thereafter eight predorsals become ossified.

One character which may be instrumental in separating the various genera and possibly species of clupeids is the distance between the dorsal and anal fins. For practical reasons, the best way to determine this distance is to count

TABLE 1.—Meristic characters of larval and juvenile *Opisthonema oglinum*.

SL (mm)	Caudal rays	Dorsal rays	Anal rays	Pectoral rays	Pelvic rays	Length of last dorsal ray as fraction of prior longest ray	Gillrakers			Scutes		Vertebrae
							Epibranchial	Ceratobranchial	Hypobranchial	Prepelvic	Postpelvic	
3.8-7.4	Nothing countable on 4 specimens in this size range.											
8.4	17	11	—	—	—	—	—	—	—	—	—	—
9.0	18	9	—	—	—	—	—	—	—	—	—	46
9.6	18	9	—	—	—	—	—	—	—	—	—	44
10.0	19	13	—	—	—	—	—	—	—	—	—	—
10.4	19	15	—	—	—	—	—	—	—	—	—	45
10.5	19	—	9+	—	—	—	—	—	—	—	—	—
10.7	19	13	—	—	—	—	—	—	—	—	—	46
12.1	18	15	—	—	—	—	—	—	—	—	—	—
12.5	—	16	7±	—	—	—	—	10	—	—	—	45
13.5	19	17	12	—	—	—	—	—	—	—	—	—
13.7	19	17	16	—	—	0.5X	—	—	—	—	—	—
14.2	19	16	14	—	—	—	—	—	—	—	—	—
14.3	19	14	—	—	—	—	—	8	—	—	—	—
14.3	19	17	10	—	—	—	—	—	—	—	—	46
curved	19	16	16	—	4	—	—	10	—	—	—	—
15.5	19	20	19	—	—	—	—	—	—	—	—	—
15.6	19	20	14	—	5	—	3	13	2	—	—	45
16.2	19	19	19	—	6	0.5X	—	—	—	—	—	—
16.9	19	17	17	—	4	—	—	—	—	—	—	46
17.1	19	19	19	—	5	—	—	10	—	—	—	45
17.2	19	18	18	5	5	—	—	—	—	—	—	45
17.4	19	18	19	—	6	—	—	—	—	—	—	—
17.7	19	19	19	—	6	0.5X	—	—	—	—	—	—
17.7	19	18	16	—	4	—	—	—	—	—	—	—
18.4	19	19	19	—	5	—	3	13	—	—	—	46
19.3	19	19	17	9	6	0.5X	6	12	6	—	—	—
19.7	19	20	21	15	8	0.6X	6	13	4	—	—	45
20.3	19	21	19	13	8	0.7X	8	12	8	8	0	—
21.1	19	20	21	14	8	0.6X	10	17	10	11	2	46
23.4	19	20	22	16	8	0.7X	10	15	9	7	0	—
23.8	19	20	21	15	6	0.7X	11	16	10	12	9	—
24.4	19	20	21	14	8	—	11	16	7	14	2	45
24.8	19	22	23	16	8	0.8X	12	16	11	18	13	—
25.3	19	18	21	16	8	0.7X	10	15	12	13	5	—
25.9	19	20	20	15	8	0.7X	13	16	11	17	13	46
26.2	19	20	21	16	8	0.5X	13	16	13	18	15	46
27.0	—	21	24	16	8	1.3X	16	20	16	18	15	46
27.1	—	20	23	16	—	1.0X	14	18	16	17	14	46
27.1	—	20	23	15	—	1.0X	15	19	15	18	15	46
27.3	—	20	23	16	—	1.1X	15	18	14	18	15	46
28.2	—	20	21	17	—	—	15	18	14	18	15	46
30.0	—	22	22	16	8	1.1X	15	18	14	19	14	—
30.8	19	21	21	17	8	1.2X	18	18	16	17	14	45
34.9	19	22	23	17	8	1.8X	20	22	20	18	16	46
46.8	—	21	21	15	8	2.0X	31	25	32	16	16	—
54.0	19	20	25	16	8	2.5X	34	27	32	18	16	47

the number of myomeres between the end of the dorsal fin to the origin of the anal fin. In *O. oglinum* larvae less than 16 mm, we counted 8, 9, or 10 myomeres between the two fins. Transforming larvae and small juveniles (17 to 25 mm) had from 5 to 7 myomeres between the fins. We were unable to count these numbers with accuracy in specimens longer than 26 mm.

In life the larvae are very transparent and gradually become opaque during transformation because of an increase in pigmentation and a compacting of the visceral cavity. Other than the gross features of the gut mentioned above, the development of the visceral organs was not considered in the present study, but we assume that abrupt changes take place. The swim bladder first appears during transformation. Before transformation, a cavity develops above the anterior end of the hindgut (just posterior to the pelvic fins) in larvae as small as 10 mm, but a definite swim bladder is not apparent until the larvae are 15 mm long. In living larvae the swim bladder is well defined.

OSTEOLOGICAL DEVELOPMENT

Larvae of *O. oglinum* undergo no ossification of any parts before they measure about 10.0 mm SL (all body lengths will be given in standard length unless otherwise indicated). In the youngest cleared and stained larva examined (4.1 mm TL, total length), the cranial bulb was outlined, as were the lower jaw, hyoid apparatus, and dorsal and caudal fin lobes (Figure 2). All these

TABLE 2.—Measurements of larvae and juveniles of *Opisthonema oglinum*. Specimens between dashed lines are undergoing notochord flexion.

Body length	Eye diameter	Snout length	Head length	Length of dorsal fin base	Length of anal fin base	Snout to origin of dorsal fin (predorsal)	Snout to origin of pelvic fin	Snout to origin of anal fin	Origin of dorsal fin to base of caudal rays	Body depth	Origin of anal fin to base of caudal rays	Origin of pelvic fin to base of caudal rays
3.6	0.20	0.10	0.60	—	—	—	—	3.1	—	0.20	0.50	—
4.1	0.18	0.10	0.53	—	—	—	1.9	3.4	—	0.25	0.63	2.0
4.6	0.20	0.10	0.60	—	—	—	2.0	3.9	—	0.20	0.63	2.5
5.2	0.23	0.13	0.73	—	—	—	2.4	4.4	—	0.33	0.63	2.7
7.3	0.25	0.18	0.90	0.35	—	4.8	3.2	6.5	2.2	0.50	0.75	4.1
7.4	0.25	0.18	1.0	0.38	—	5.0	3.3	6.6	2.3	0.60	0.78	4.1
9.1	0.35	0.28	1.1	0.75	—	5.9	4.0	8.1	3.4	0.95	0.95	5.0
9.7	0.35	0.30	1.2	0.85	—	6.5	4.2	8.8	3.3	0.85	0.95	5.4
10.0	0.35	0.27	1.2	0.94	—	6.8	4.4	9.2	3.4	0.95	0.95	5.6
10.1	0.43	0.38	1.5	1.3	—	6.4	4.4	9.4	3.9	1.0	0.63	5.6
10.4	0.38	0.35	1.7	1.5	0.25	6.3	4.6	9.6	3.9	1.1	0.83	5.8
10.7	0.40	0.40	1.7	1.3	0.35	6.7	4.7	9.7	3.9	1.0	1.0	6.0
12.1	0.45	—	—	—	—	7.9	5.2	11.1	—	—	1.0	6.9
12.8	0.50	0.48	2.0	1.7	0.45	8.1	5.8	11.6	4.9	1.1	1.2	7.2
12.9	0.53	0.48	2.1	1.9	0.75	8.2	5.9	11.4	5.2	1.3	1.6	7.2
13.7	0.55	0.73	2.8	1.9	0.63	8.9	6.2	12.4	5.0	1.6	1.4	7.6
14.0	—	—	—	—	—	9.0	6.3	12.6	5.3	—	—	8.0
14.0	0.58	0.63	2.6	2.1	0.60	8.8	5.8	12.9	5.5	1.7	1.4	8.5
15.0	0.63	0.68	2.7	2.1	0.95	9.0	6.7	13.2	6.0	1.6	1.8	8.4
15.8	0.63	0.78	3.0	2.2	0.88	10.0	7.1	13.8	6.3	1.7	1.9	8.8
16.2	0.63	0.60	3.0	2.4	1.0	9.7	7.0	13.9	6.5	1.7	2.1	8.9
16.8	0.80	0.68	3.2	2.6	1.1	10.2	7.7	14.9	6.9	1.9	2.2	9.1
17.1	0.65	0.73	3.1	2.6	1.0	10.0	7.4	15.3	6.9	1.9	2.1	9.5
17.7	0.70	0.75	3.3	2.7	1.2	10.7	8.5	15.3	7.1	2.0	2.4	9.2
17.7	0.80	0.85	—	—	—	10.4	8.1	15.4	—	—	2.3	9.6
18.4	0.83	0.76	3.5	2.9	1.3	10.9	8.8	16.1	7.8	2.5	2.3	9.6
19.3	1.1	—	—	—	—	10.9	9.3	16.3	—	—	3.0	10.0
19.7	1.1	0.85	3.9	3.1	1.8	10.5	9.0	16.6	9.2	2.6	3.1	10.7
20.3	1.2	1.1	4.9	3.5	2.1	10.0	9.8	16.8	10.0	3.3	3.5	10.5
23.4	1.4	1.5	6.0	4.0	3.4	10.7	11.5	18.0	13.1	4.6	5.4	11.9
23.8	1.7	1.6	6.1	4.0	3.7	10.7	12.1	18.1	13.0	4.7	5.7	11.7
24.4	1.5	1.6	6.4	3.7	3.6	12.0	11.9	18.6	12.5	4.4	5.8	12.5
24.8	1.7	1.9	6.7	4.4	4.5	11.0	13.0	18.7	14.0	5.5	6.1	11.8
25.3	1.7	1.7	6.6	4.5	4.2	11.5	12.7	18.9	14.0	4.8	6.4	12.6
26.2	1.5	1.8	6.6	4.0	3.9	12.0	12.6	19.7	14.2	4.8	6.5	13.6
27.0	1.9	1.6	6.4	4.3	4.3	12.3	13.5	19.7	14.7	5.7	7.3	13.5
27.1	1.8	1.9	7.3	4.4	4.4	11.6	14.2	20.2	15.5	5.8	6.9	12.9
27.1	1.9	1.7	6.7	4.0	4.0	11.4	13.3	20.3	15.8	4.5	6.8	13.8
27.3	1.6	1.8	6.8	4.1	4.3	11.8	14.0	19.9	15.5	5.0	7.0	13.3
28.2	1.9	1.9	7.3	4.3	4.2	12.5	14.3	20.7	16.7	5.0	7.0	13.9
30.0	2.3	2.4	8.5	5.0	5.0	13.0	15.5	22.8	16.8	8.3	8.2	14.5
30.8	2.2	2.4	8.0	5.0	5.0	13.4	15.7	22.9	17.3	7.7	7.9	15.1

structures were clear, however, indicating no ossification. The first structures to ossify were the dentaries and maxillaries when specimens measured about 10.0 mm (bone nomenclature follows Mead and Bradbury, 1963). Almost simultaneously, the very thin cleithral ring (cleithrum, supra-cleithrum, and postcleithrum) and the hypurals began to ossify very slightly. At sizes between 12 and 13 mm, the skull bones began to ossify, as did the vertebral rings. As size increased, various other parts of the fish began to ossify—the caudal fin rays, parts of the branchial apparatus (ceratobranchials, hypobranchials, epibranchials), and the dorsal and anal fin rays; skull bones ossified further (Figure 3). At about 20 to 22 mm, essentially all bony structures of the larvae had at least begun to ossify, and some were well developed.

Vertebral development

No ossification took place before 10 mm, but cartilaginous structures were visible. At the time of notochord flexion, seven hypural elements were formed (four superior and three inferior elements including the parhypural). In specimens measuring 10.5 mm, the hypurals were weakly ossified but the seven elements were distinct. The first vertebral centra to ossify was the first preural centrum and the ventral portion of the centra of the first and second ural centra. This differs somewhat from the development noted in

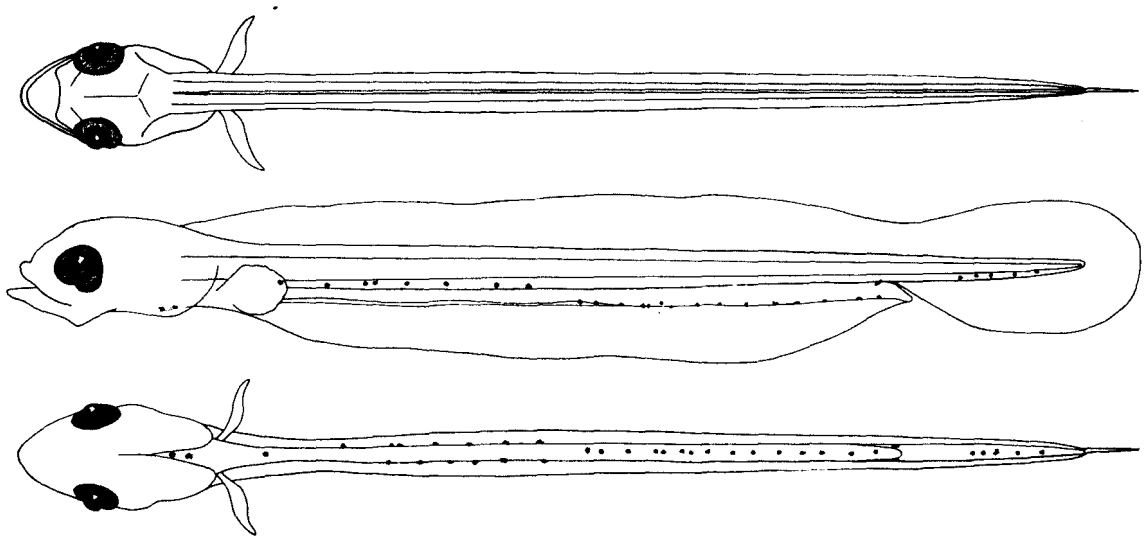

FIGURE 2.—*Opisthonema oglinum* larva 4.0 mm total length.

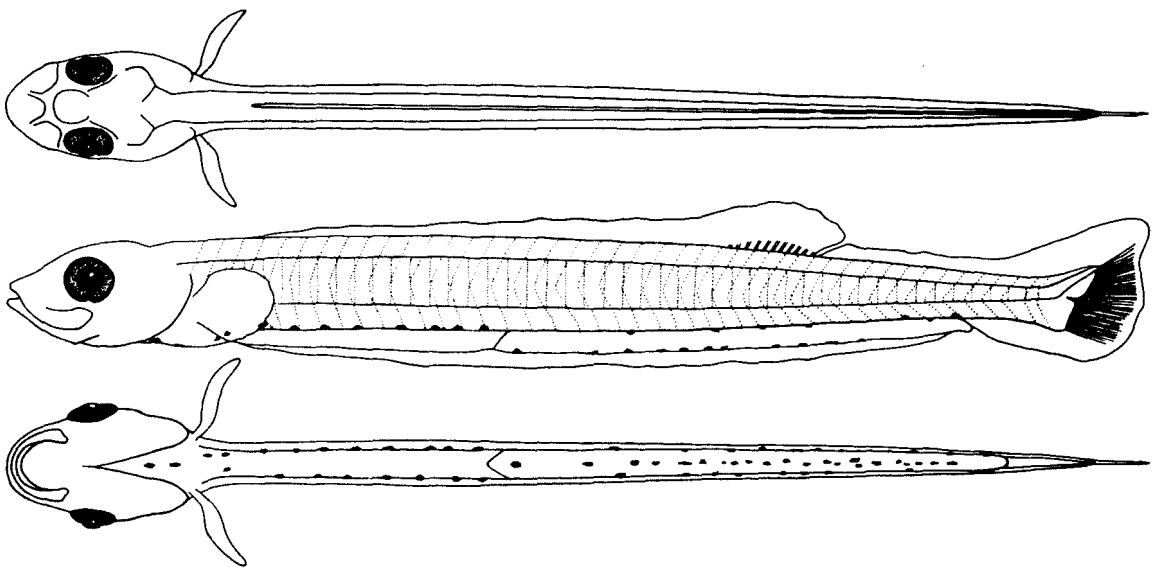

FIGURE 3.—*Opisthonema oglinum* larva 10.7 mm standard length.

H. jaguana by Houde et al. (1974). They noted that the second ural vertebra ossified first. Epural development displayed some variation (two instead of the normal three in some specimens), as was also noted in *Harengula* by Houde et al. (1974). Hollister (1936) noted this variation in *Harengula* but not in *Opisthonema*. Other than these differences, caudal development was essentially the same for *Opisthonema* and *Harengula*. For a more complete account, consult Houde et al. (1974).

At 10.5 mm, ossification also started on vertebrae 12 through 40. This ossification starts on the dorsal and ventral surfaces of the centra, thus making it quite easy to count vertebrae. The degree of ossification of these vertebrae indicates that the middle ones were most ossified, with ossification proceeding anteriorly and posteriorly. By 12.5 mm, dorsal and ventral ossification of the centra is complete on vertebrae 2 through 41, while only the ventral centrum surface has ossified on the first vertebra and the

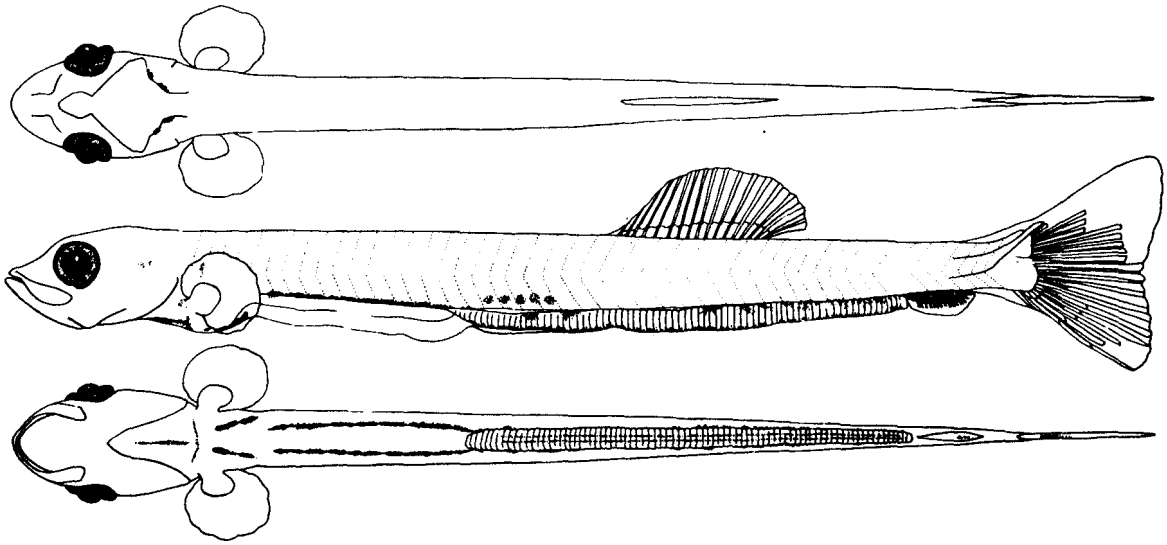

FIGURE 4.—*Opisthonema oglinum* larva 13.7 mm standard length.

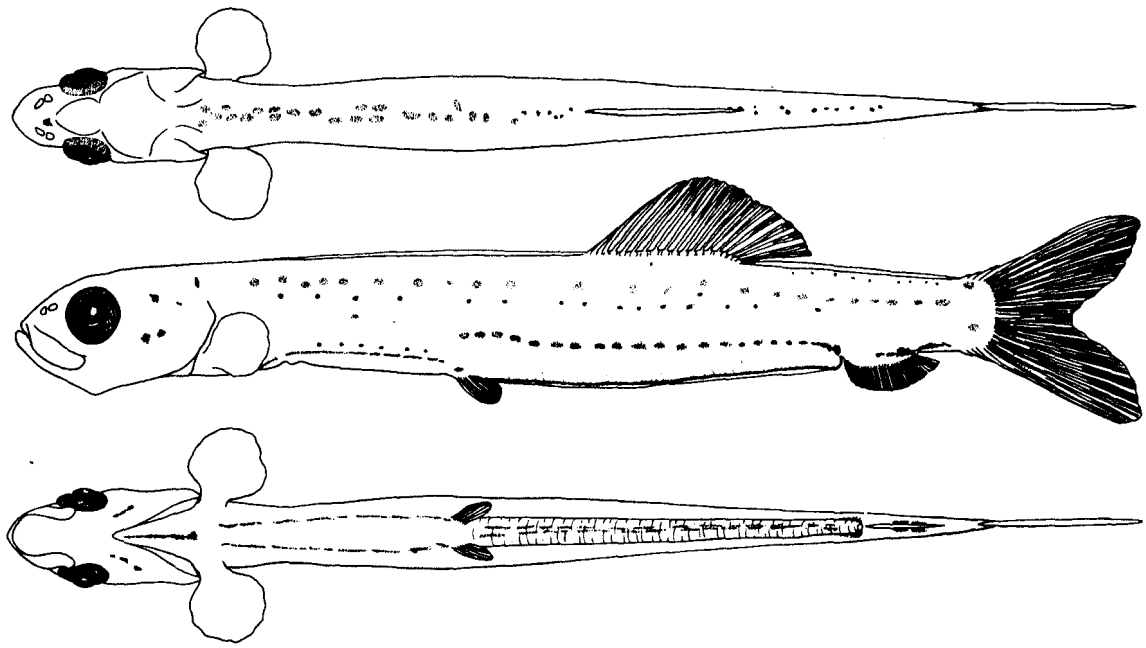

FIGURE 5.—*Opisthonema oglinum* larva 17.1 mm standard length.

three preceding the ural centra. These three centra immediately anterior to the first preural were wider ventrally and had large spaces between the vertebral segments. At 15.5 mm, all vertebral centra were partially ossified and evenly spaced with narrow spaces between. In the first preural and ural centra, the three rings of ossification had widened, but the middle ring was still wider ventrally than dorsally. (This asymmetrical shape of the ossified rings of the vertebrae associated with the caudal region obviously corresponds to flexion of the notochord. The ventral surface is longer after flexion than the dorsal surface and, consequently, to keep the

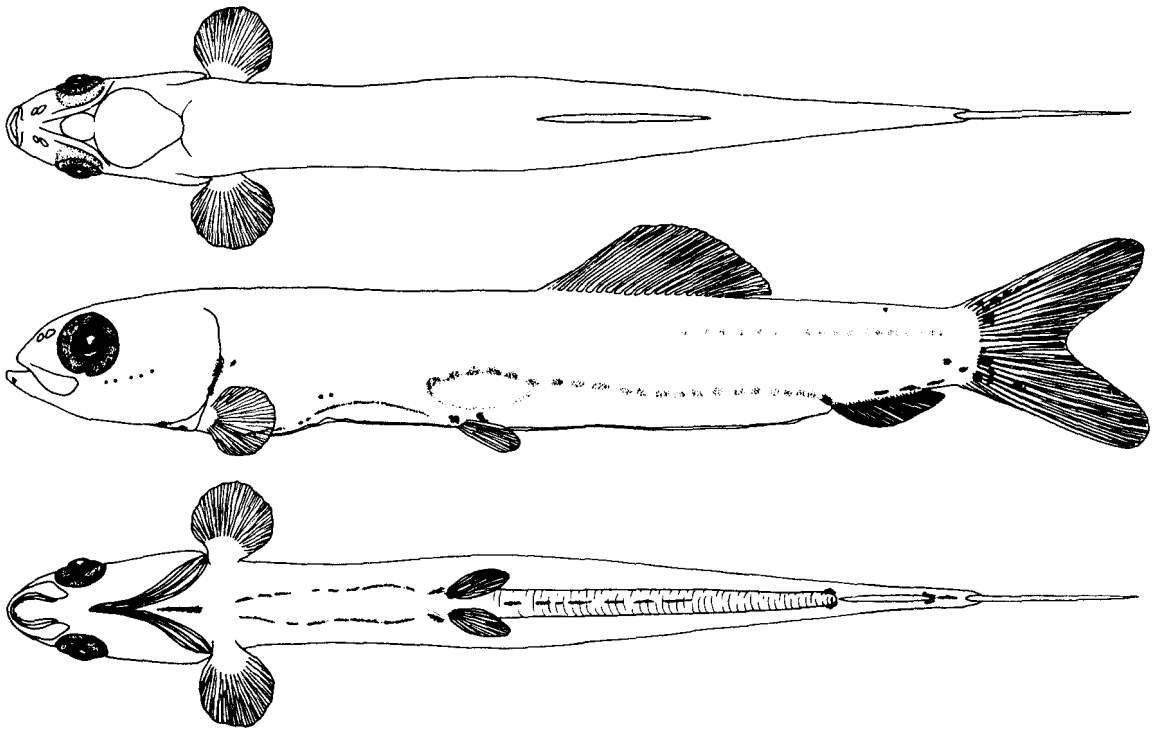

FIGURE 6.—*Opisthonema oglinum* larva 19.7 mm standard length.

spaces between ossified segments equal, the segments ossify in a wedgelike shape.) By 17.1 mm, the three rings had widened appreciably and the spaces had narrowed.

Neural and hemal spines ossify in a posterior to anterior direction. Neural spines are well formed over the last three centra, which precede the first preural well before ossification on the centra is completed. By 17.1 mm, ossification of these elements is just complete to below the dorsal fin, and by 22 mm they are all ossified.

Fin Development

The earliest fin development was of the caudal and dorsal fins, more-or-less as lobes, at about 4 mm TL. This early development may be due to a rearing abnormality since fin development is seldom seen in field-caught larvae less than 7 mm SL. Increasing numbers of caudal and dorsal rays were defined at lengths from 6 to 8.4 mm, but were not clear enough to count until our 8.4-mm specimen (17 caudal and 11 dorsal rays, Table 1 and Figure 3). Between 8.4 and 10.0 mm, the final two caudal rays were differentiated to complete the adult complement of 19 principal cartilaginous rays (10 superior and 9 inferior).

Rays continued to be added to the dorsal fin: 16 were present at 12.5 mm and 18 to 20 were present from 15 to 20 mm (Table 1, Figures 4 through 7). As growth proceeded, one or two more rays were added to complete the adult complement of 21 or 22 dorsal rays (Figure 8). In adult *Opisthonema*, the last ray of the dorsal fin is elongate—more than twice as long as the next longest ray. Until about larval size of 20 mm, the last ray was half as long as the longest ray, but from then on it began to elongate. From about 27 mm, the last ray grew longer than the prior longest ray (Table 1).

The anal fin formed later than the dorsal, from a thickening of the ventral finfold in the relatively short space between the anus and the caudal fin (Figure 3). At 10.5 mm, the fin rays had begun to differentiate and nine rays could be counted. Ossified rays increased rapidly to 14, 15, or 16 at about 14 mm, after which rays were added more slowly to sizes from 15 to 20 mm. Between 14 and 20 mm, counts of 17 to 20 rays

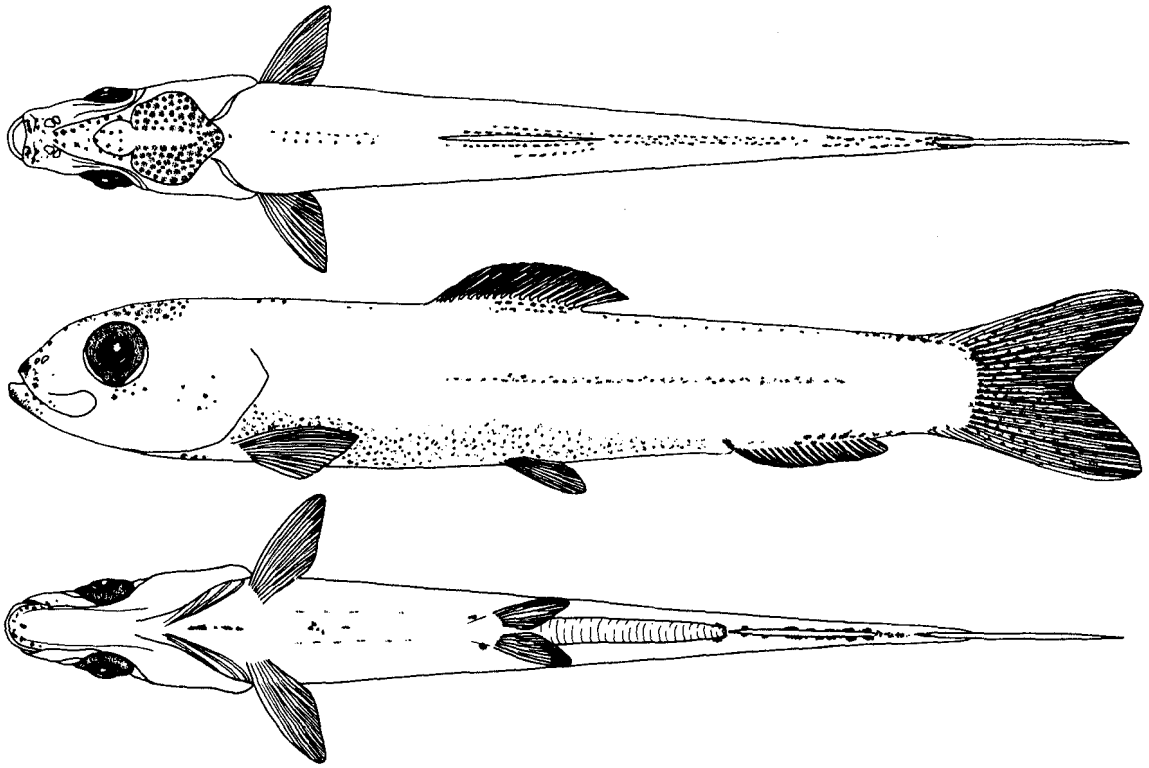

FIGURE 7.—*Opisthonema oglinum* juvenile 24.4 mm standard length.

were produced (Figure 7). Only about three or four more rays were added, from 20 mm, until the adult complement of 21 to 25 anal rays was reached at 30 mm and over (Table 1, Figure 8).

The pectoral fin appeared as a small, fan-shaped structure just behind the cleithral ring, but this structure enlarged gradually (Figures 2 to 7). [Within the fan, "ray areas" differentiated soon thereafter, but these had no apparent relation to where rays actually ossify.] Ossified rays first appeared at about 17 mm (five rays; see Table 1) and quickly increased to about 10 rays at 19 mm. The rounded fan shape of the pectoral fin changed into the pointed shape characteristic of adults between 19 and 23 mm (Figure 7). At 21 mm, specimens had about 13 or 14 rays, and the adult complement of 15 to 17 rays was reached at 23 to 25 mm. The sequence of ray ossification was in a dorsal (uppermost) to ventral (lowermost) direction.

Ossified pelvic rays appeared earlier than the pectoral rays. At about 13 mm, larvae had about four rays (Table 1), and at about 15 mm they had five or six (Figure 5). The number of rays seemed to remain static for about the next 5 mm of growth (10 specimens in the 15 to 20 mm size range), but rather suddenly two more rays appeared at about 20 mm (Table 1, Figure 7). The pelvic ray count held constant, though size increased to 50 mm, but in adults a ninth ray is added as a flattened, segmented ray closely adnate to the second (formerly most lateral) ray to produce nine total rays. In our larger (30 to 54 mm) specimens (Figure 8) the flattened first ray does not appear to be present. If it is, the ray is so tightly attached to the second ray that the two seem to be a single unit.

Cephalic Development

No ossification of any bones appeared before specimens reached about 10.0 mm. In larvae as small as 4.1 mm TL, the cranial bulb, dentaries, and hyoid bones were visible as cartilaginous elements. At about 10.0 mm, the maxillaries and dentaries were easily distinguished and began to show slight ossification (by stain uptake). The jawbones more-or-less steadily increased in

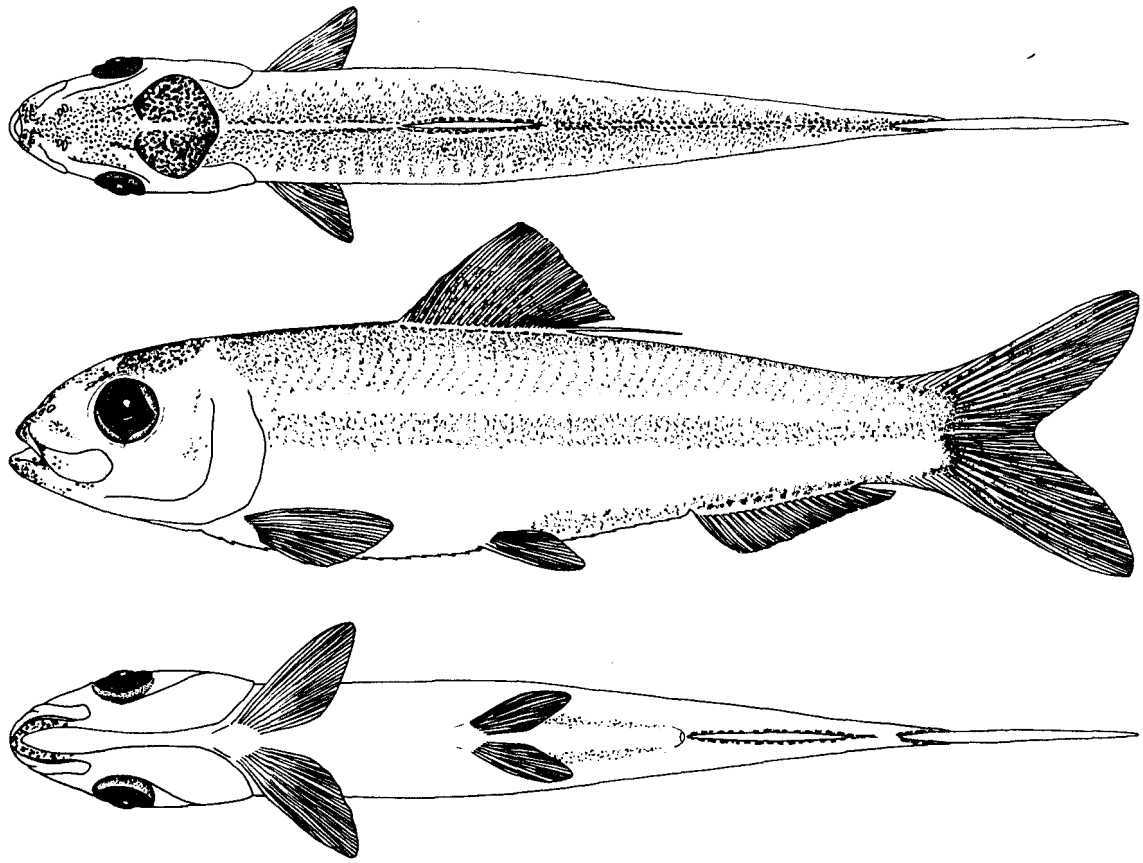

FIGURE 8.—*Opisthonema oglinum* juvenile 30.8 mm standard length.

size and became more heavily ossified; at about 14 mm, small teeth were found on the ventral edge of the maxillaries and the anterodorsal edge of the dentaries. Concommitantly, the hyoid apparatus continued to develop steadily, particularly the ceratohyals and hypohyals, which were quite distinct and slightly ossified by 14 mm. By about 17 mm, the two supramaxillaries were differentiated and partly ossified but had not obtained their characteristic adult shapes. The premaxillaries also were partly formed and ossified as two distinctly separate units close to the anterior tips of the maxillaries. By 19 mm, the articular was well developed but not fully ossified. The posterior supramaxillary was almost completely ossified but not the anterior supramaxillary. Maxillaries maintained an ossified posterior edge (the region of growth), and the teeth on the ventral edges were still prominent. The ceratohyals and urohyal were more ossified, and two small centers of heavy ossification were present in the hypohyals. One structure of interest was the presence of teeth on a few specimens on the basihyal. In a 12.0-mm specimen, two large erect teeth were noted; a 15.6-mm specimen had one such tooth, which was also present on a 17.1-mm specimen. No such teeth were evident on a 25.9-mm specimen, indicating that these teeth may be variable and limited in occurrence. Houde et al. (1974) noted the presence of these temporary teeth in *Harengula*. The branchiostegals ossified in the following sequence: fourth branchiostegal slightly ossified at 15.5 mm; fourth well ossified at 17.1 mm; fourth, third, and second ossified; first visible as cartilage; fifth and sixth not visible at 19.7 mm. By the time specimens reached 24 mm, six well-ossified branchiostegals were present, the supramaxillaries were ossified but the posterior supramaxillary had not reached a complete adult shape, all the hyals were partly ossified, the well-developed premaxillaries were ossified and

TABLE 3.—Position of dorsal and anal fins during the transformation period in larvae of *Opisthonema oglinum*.

SL (mm)	Dorsal origin over vertebra	2d dorsal pterygiophore opposite neural arch	Anal origin under vertebra	1st anal pterygiophore opposite haemal arch
15.5	25	21	38	36
17.1	23	—	37	35
17.2	22-23	20	38-39	36
18.4	23	20	38	35-36
19.7	20	17	36	34
21.1	16	12	—	—
24.4	16	11	33	30
25.9	15-16	11	33	30
26.2	16	11	33-34	30
27.0	14	9	32	29
27.1	15	11	33	30
27.1	15	10	33	30
27.3	14	10	33	30
28.2	15	10	33	30
30.8	15-16	10	33	30
34.9	15	10	34	30
54.0	15	9	34	30

joined at the anterior tip of the upper jaw, and the maxillaries appeared to be fully formed.

At about 10 mm, the cleithral ring was obvious as a thin ring of ossified bone almost encircling the head and forming a posterior line of demarkation. The three bones that actually form this ring are the supracleithrum, cleithrum, and postcleithrum, which developed fairly uniformly to about the time the pectoral fin began to develop ossified rays (about 15 to 17 mm). Thereafter, the cleithrum became the dominant element.

A cartilaginous cranial bulb was visible in our smallest larvae, but no elements were differentiated or ossified until about 12 mm. At that size, bone elements (e.g., the sphenotics, parietals, epiotics, and pterotics) were slightly outlined. Between 12 and 13 mm, the vomer and parasphenoid began to show considerable ossification, and the pterotic and prootic bullae were differentiated by ossification of the surrounding bones. The frontals began to form when specimens measured about 15 mm, and about 19 mm they were partly ossified (but not fully formed), and sensory canals were present within the bones. Canals also formed at the 19-mm size in the prootics and sphenotics, and the prootic bulla was the most obvious structure in the skull because of the heavily ossified bone around it.

The quadrate and the pterygoids had begun to form by 19 mm, and the articular had increased in size but was not yet fully ossified. At about 21 mm, the nasals began to form as thin, small plates at the anterior ends of the frontals. Formation of supraorbitals had also begun, the anterior one being moderately well developed and quite separate from the posterior one. At the 21-mm size, it also appeared that most of the head bones were at least partly formed, and ossification ranged from slight to considerable. By 25 mm, the prootic bulla was well encased in heavy bone, the sclerotics had begun to ossify along with the supraorbitals, the ethmoids had begun to form and ossify at the anterior ends of the frontals and just behind and above the premaxillaries, the vomer was quite large and well ossified, most sensory canals were partly to fully formed and encased in bone, the postorbitals had begun to form, and the pterotic bulla (which lagged far behind the prootic in development) began to grow larger. From 25 mm through the juvenile period, growth of the skull bones was restricted primarily to an increase in size and consolidation within the several multibone complexes; the dorsal and lateral frontoparietal foramina decreased in size as the bones increased, and the characteristic striae of the dorsal surface of the frontoparietals began to form; the pterotic bulla finally became larger than the prootic by about 34 mm; and the palatines began to ossify. During the 30- to 50-mm range, most of the cranial structures assumed their adult configuration, the dorsal frontoparietal foramina completely closed up, and the lateral foramina became reduced in relative size.

The elements of the opercular complex—primarily the opercle and preopercle—began to differentiate at about 15 mm. Shortly thereafter the subopercle and interopercle began to form and by 21 mm most of the opercular series appeared to be about halfway ossified; the interopercle seemed to be the most weakly ossified. By 25 to 26 mm, the interopercle had grown to articulate with the quadrate and angular and the hyals. The other opercular bones had become quite well developed, but the posteroventral edges remained unossified, evidently to permit continuous growth.

Branchial Development

The ceratobranchials were the first elements to develop in the branchial system, becoming evident at about 10 mm. By about 12 to 13 mm, the ceratobranchials showed a slight uptake of stain, indicating that they had begun to ossify. At 14 mm, the hypobranchials had begun to differentiate, and a few unossified rakers were visible on the ceratobranchials.

The ceratobranchials, the first, second, and third epibranchials, and the hypobranchials all developed as more-or-less straight rods (although the epibranchials also developed small dorsal extensions for attachment of suspensory ligaments). The first rakers appeared on the ceratobranchials at about 12 mm (Table 1) and held almost constant between 10 to 13 rakers to about 17 mm. Two or three rakers appeared on the epibranchials and hypobranchials when larvae reached about 15 mm. The numbers of rakers on all three elements gradually increased with the numbers on the epibranchials and hypobranchials almost equal but from two to four lower than on the ceratobranchials, up to about 30 mm (Table 1). At the 30-mm size, all three bones had an equal number of rakers, but beyond that size the ceratobranchials seemed to lag behind the epibranchials and hypobranchials by five or six rakers. In adults, the hypobranchials and ceratobranchials are almost equal in numbers of rakers (30 to 45), producing lower branch counts of 60 to 90, but the epibranchial rakers almost equal the combined lower branch counts.

The fourth epibranchial (E4) was the first to develop a slight vertical extension when specimens measured about 14 mm; the shape of the fourth epibranchial at this stage is more-or-less like an inverted "T"—the crossbar (the basal shaft) is ventral and the vertical segment extends dorsally from it. On the dorsal and posterior edges a developing cartilaginous capsule (see Miller, 1969; Figure 2, for the adult configuration of the capsule) is fused to the developing E4 bone; this capsule is also joined to the epiceratobranchial "elbow." A vertical slit is present in the posterior side of the capsule, and the two raker series that will eventually grow throughout the length of the lumen of the epibranchial organ begin growing along the sides of the posterior slit. Dual fourth epibranchial raker series are present, with the lateral series growing along the ventrolateral edge of the fourth epibranchial bone, outside the epibranchial organ, and the medial fourth epibranchial series is enclosed in the organ along the anterolateral edge of the slit in the cartilaginous capsule. The single fifth epibranchial series grows along the posteromedial edge of the slit. By 15.5 mm, the vertical extension on E4 had grown much heavier and the characteristic posterior foramen had formed (see Miller, 1969; Figures 2 and 4). Three raker tubercles were present along the edges of the posterior slit (which had just begun to form). By 17 mm, the cartilaginous capsule had begun to increase in size, and by 19 mm there were four or five raker tubercles in the posterior slit. Almost no ossification had yet appeared on the fourth epibranchial, and the posterior foramen was quite large. Ossification began at about 20 mm, and by about 25 mm the posterior end of the basal shaft had expanded vertically (it resembled an axe blade), and the vertical shaft had also broadened and ossified quite heavily. At this stage there were about eight rakers along the edges of the posterior slit. When larvae measured 26 mm, the lumen of the organ had begun to form; it extended anterodorsally within the cartilaginous capsule from the bridge of the posterior slit, and 10 rakers appeared along each edge. One or two rakers were present in the developing lumen. By 30 mm, the lumen had elongated to about one-third of a full loop [the epibranchial organ in *Opisthonema* is the continuous-tube type (see Bertmar, Kapoor, and Miller, 1969; Miller, 1969) in which the lumen and included rakers extend for a full loop in adults] and there were about 15 to 20 rakers in the lumen. By 35 mm, the lumen was about a half of a full loop and

had curved anteriorly beyond the width of the vertical shaft of E4. About 30 rakers were present in each series at this stage and the epibranchial organ and E4 bone were assuming adult configuration. Estimates made on adult specimens indicate that in a full-loop, continuous-tube epibranchial organ, the definitive number of rakers in the included medial E4 and single E5 series each at least equal the total of rakers on the whole first gill arch. There are about 120 rakers in adults 100 mm or longer (Berry and Barrett, 1963). We may therefore infer that the number of rakers in the epibranchial organ increases gradually with increasing size of the fish, to about 120 or more in each series.

PIGMENTATION

Melanophores were present along the ventral midline in the smallest specimens studied (4 mm) —one or two melanophores beneath the heart just anterior to the pectoral symphysis, and a paired row along the base of the hindgut (that portion of the gut posterior to the site of the pelvic fins) continuing to the anus, and a row on the ventral midline posterior to the anus. A dorsolateral row of melanophores occurred on each side of the foregut (that portion of the gut anterior to the pelvic fin region). The eye was pigmented but no other melanophores were present (Figure 2). By 10 mm, the posterior ventral row was distributed along the posterior edge of the hypural bones, and a few internally placed melanophores appeared dorsolaterally on each side of the hindgut. The remaining melanophore pattern was basically unchanged (Figure 3). By 15 mm, the melanophores had developed into streaks of pigment along the base of the isthmus, dorsolaterally along the anterior gut, along the base of the posterior gut, and on each side of the base of the anal fin. Internal melanophores above the posterior gut had taken on a well-defined, broken-lined pattern and had begun to advance anteriorly, particularly forming a slight arch in the area of the swim bladder (Figure 4). Melanophores appeared on the cleithrum near the hindbrain, and the hypural melanophores at first clustered on the bases of the lower lobe of the caudal fin but, by 17 mm, melanophores appeared on both lobes of the caudal fin. Between 15 and 24 mm (transformation period), melanophores varied somewhat in time of appearance. In some specimens a melanophore appeared medial to the left nostril (Figure 5, dorsal view). Melanophores appeared both dorsally and ventrally on the swim bladder as it developed (Figure 6). During this period melanophores also began to appear on the dorsum, first posterior to the dorsal fin, then anteriorly. Melanophores also appeared along the lateral midline and over the hypural bones internally. The internal pigment associated with the vertebral column of these larvae is quite pronounced, particularly during transformation. A few internal melanophores over the posterior centra were first noted in a cleared and stained 12.1-mm specimen. By 15 mm, one or two melanophores or groups of melanophores were noted above each vertebra. The melanophores over the anterior vertebrae are lost or reduced by 19 mm. Some individual variation, however, is evident in both the internal and external pigmentation. The dorsal external pigmentation is noticeably reduced in the 19.7-mm specimen (Figure 6) as compared to the 17.1-mm specimen (Figure 5). The expanded state of most melanophores (a probable result of rearing under continuous illumination) makes detailed counts of melanophore patches quite difficult. Following transformation, melanophores were visible over the brain and on the jaws as well as in increasing quantities on the dorsum, lateral midline, over the gut, and in the caudal fin rays (Figure 7). By 30 mm, the dorsal pigment had increased, the foregut pigment was lost, and melanophores were seen in the dorsal fin—essentially the adult pattern (Figure 8).

In life, the larvae are transparent and the only noticeable features are the heavily pigmented eyes. The gut is usually noticeable because of the food contained in it. In larger larvae, the swim bladder is decidedly noticeable as a bubble above the gut (Figure 6). Melanophores are invisible until the specimen is examined under magnification.

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