Reproductive Behavior, Embryology, and Larval Development of Four Species of Pygmy Sunfish

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by

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Introduction: Are Pygmy Sunfishes Sunfishes?

The pygmy sunfishes of the genus *Elassoma* include six described species, all of which are native to swamps and backwater areas of the southeastern United States and middle Mississippi Basin.

• *Elassoma zonatum* Jordan 1877, the banded pygmy sunfish, is the most widespread, found from North Carolina through the southeastern states into western Texas and Oklahoma and northward into southern Illinois. A *zonatum*-type specimen collected in a Rotenone survey in Tennessee may represent a new, undescribed species.

• *Elassoma evergladei* Jordan 1884, the Everglades pygmy sunfish, extends from South Carolina into Florida and westward to the Mobile drainage in southern Alabama.

• *Elassoma okefenokee* Böhlke 1956, the Okefenokee pygmy sunfish, is restricted to southern Georgia and the northern third of Florida. A population in northwest Florida appears to be a distinct, undescribed species.

• *Elassoma boehlkei* Rohde and Arndt 1987, the Carolina pygmy sunfish, is found in the Waccamaw and Santee River drainages of North and South Carolina.

• *Elassoma okatie* Rohde and Arndt 1987, the blue-barred pygmy sunfish, is endemic to three river drainages in South Carolina: Lower Edisto, New and Savannah.

• *Elassoma alabamae* Mayden 1993, the spring pygmy sunfish, was previously known from collections at only two locations in Alabama: Cave Spring, Lauderdale County, in 1937; and Pryor Spring, Limestone County, in 1941. No other specimens were seen for more than 30 years, leading most ichthyologists to conclude the species was extinct. But in 1973, David A. Etnier discovered a new population at Moss Spring, a tributary of Beaverdam Creek in Limestone County. Since then additional populations have been found within the Beaverdam Creek system. In 1984, the senior author was part of a team of local landowners and state and federal biologists who worked together to successfully introduce gravid adults from Beaverdam Creek into Pryor Spring (Mettee and Pulliam, 1986).

Since the description of *E. zonatum* in 1877, the taxonomic position of the genus *Elassoma* has been the subject of much controversy. Originally, the fish was thought to be a cichlid (Jordan, 1877), but that opinion soon changed. Hay (1881) and Jordan and Gilbert (1882) placed *E. zonatum* into its own family, the Elassomatidae, because they believed it was intermediate between the pirate perch (family Aphredoderidae) and the centrarchids. Boulenger (1895) placed *Elassoma* into the sunfish family Centrarchidae because of the similarity and kinds of vertebrae; he was also probably the first to postulate that *Elassoma* was a dwarf sunfish.

Over the years, several investigators have presented evidence they felt was sufficient to exclude *Elassoma*
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from the Centrarchidae. After examining the olfactory organs of three centrarchid species and *E. zonatum*, Eaton (1956) stated that *Elassoma* was a neotenous sunfish—that is, capable of being sexually mature as a juvenile. Branson and Moore (1962) surveyed the acousticolateralis systems of 26 centrarchid species and the three described *Elassoma* species at that time; they concluded that while elassomids were closely related to centrarchids and possibly shared a common ancestry with them, they had specialized and diverged sufficiently to be considered a separate family. Moore and Sisk (1963) stated that the eye structure of *Lepomis* and *Elassoma* were markedly different. Roberts (1964) examined the chromosome complements of 20 centrarchid species and found that while *E. zonatum* possessed the modal centrarchid number of 48 diploid chromosomes, its chromosome morphology differed significantly from that of any other centrarchid species. This led him to the conclusion that while *Elassoma* is distantly related to the sunfishes, it still differs to the extent that it should be placed in a separate family. Similar findings based on biochemical studies were presented by Avise and Smith (1977).

One aspect of the life history of *Elassoma* which has received little investigation, but which might be important in providing additional information regarding its relationships to centrarchids, is reproductive behavior. Because elassomid fishes are usually found in slow-moving waters that are less than one foot deep and choked with aquatic vegetation, observations on their reproductive behavior would be difficult; consequently, all reports on their spawning behavior have been based on aquarium experiments.

Several investigators have indicated that the spawning habits of elassomid fishes are similar to those of other centrarchids, since the male constructs a nest into which the eggs are deposited during spawning. Such behavior was observed in *E. evergladei* by Axelrod and Shaw (1971), Innes (1969), and Axelrod and Schultz (1971). Contrarily, Nachstedt and Tusche (1954), Sterba (1961), Breder and Rosen (1966), and Branson (1974) stated that this species was *not* a nest builder. Shortt (1956) observed that the eggs of *E. okefenokee* were deposited in "moss," but did mention a nest. After he had observed spawns of *E. zonatum* in aquaria, Poyser (1919) speculated that this species preferred to spawn over a nest, but if bottom conditions were unfavorable, it would alternately spawn on algae or aquatic vegetation. In a paper on the life history and ecology of *E. zonatum* at Mound, Louisiana, Barney and Anson (1920) noted that the eggs of this species were always found scattered about in the aquatic vegetation. It is obvious from this summary that the reproductive behavior of *Elassoma* is incompletely known and in need of additional research before it can be compared to that of the Centrarchidae.

This article is an adaptation of the senior author's Ph.D. dissertation (Mettee, 1974), which documented the reproductive behavior of the four *Elassoma* species known at the time—*zonatum*, *okefenokee*, *evergladei*, and the then undescribed *alabamae*—with the intent of comparing it with that of the family Centrarchidae. Composite descriptions of the embryology of elassomid fishes were also presented, as well as information on growth rates and fin development.

Materials and Methods, with Notes on Aquarium Care

All reproductive studies were conducted in the laboratory. The fishes were contained in four 40-liter and six 20-liter all-glass aquaria. Continuous air was supplied by aquarium pumps and air stones. Water temperature was controlled within 3°C by tube-type aquarium heaters with internal thermostats. A 15.5 hour light period was maintained throughout the study using daylight supplemented with fluorescent light banks on an automatic timer. Because elassomid fishes will not readily eat dry foods, they were fed live brine shrimp (*Artemia*) nauplii either daily or every second day, depending upon their size and breeding condition.

In order to duplicate their natural environment as closely as possible, aquatic plants, principally of the genus *Ceratophyllum*, were collected with breeding stocks of elassomid fishes and used in the spawning aquaria. Specimens were transported from the field to the lab in Styrofoam boxes and then placed into a 40-liter aquarium filled with 21°C distilled water. After a period of 7-10 days, five or six mature females were transferred into each of two 20-liter aquaria with physical conditions similar to those of the holding tank. Using aquarium heaters, the water temperature in these two aquaria was gradually raised 2.5-4.5°C over a period of 10-14 days until the female abdomens began to enlarge, indicating egg production. This temperature was maintained for another 7-8 days, at which time one or two males of the same species were introduced into each tank with the females. After a

period of 2-3 days, during which the males established territories, spawning usually occurred.

Within 10 minutes after spawning, the eggs were transferred into 50 ml petri dishes and maintained under similar physical conditions. Photographs of live eggs were taken of each embryological stage, upon which the accompanying composite illustrations were drawn.

The prolarvae were maintained in the same petri dishes until they reached a total length of 8-10 mm. At this time they were transferred into a 20-liter all-glass aquarium and allowed to grow to adult size. Periodically, specimens were preserved in a 5% formalin solution for later observation. Because of the small number of eggs produced by a single spawn, and the high mortality rates of eggs and larvae, several spawns were necessary in order to complete a series from newly hatched prolarvae to adult.

Behavior

Based on my observations, the reproductive behavior of the four *Elassoma* species studied is very similar.

Breeding Coloration Prior to and during the spawning period, the males of each *Elassoma* species became very brightly colored, while the females retained their characteristic olive-to-tan color with dark brown mottling, scattered dots and/or irregular bars. Except for the bright blue, symmetrical band in the dorsal and anal fins of the latter, the color pattern of breeding males of *E. evergladei* and *E. okefenokee* was very similar. During periods of active spawning, males of both species assumed a velvety black color. Located posteriorly to the head on each were 7-9 irregularly spaced, vertical, iridescent turquoise (*E. evergladei*) or blue (*E. okefenokee*) bars, 1-2 mm wide, extending the full depth of the body. A small vertical, iridescent blue bar, approximately 3 mm long, developed immediately posterior to each eye and joined another bar similar in length and color that extended horizontally below the eye. The dorsal and anal fin membranes of both species were dusky to black with one or two rows of small translucent dots that were more noticeable in the posterior half of each fin and became obliterated anteriorly. The pelvic and caudal fins were dusky and without dots; however, the distal ends of the pelvic fin membranes of *E. okefenokee* were tipped in bright blue. The pectoral fins of both species remained clear to slightly dusky.

The color pattern of breeding males of *E. zonatum* was essentially unchanged, although the colors did intensify considerably. All of the fin membranes, except those in the pectoral fins, became much darker, and the 9-11 vertical bars on the trunk darkened to the extent that the black spot usually found ventral to the dorsal fin origin was indistinguishable. A small crescent similar in size and position to the ones described for *E. evergladei* and *E. okefenokee*, but gold in color, was present around the eye, and many small, iridescent gold and blue flecks were scattered about on the cheeks and opercula.

Breeding males of *E. alabamae* were dark brown to black, and on the trunk were located 6-8 very narrow, irregularly spaced, vertical, iridescent gold bars that extended the entire body depth. An iridescent gold structure similar to that described for *E. zonatum* was present around each eye, perhaps the most outstanding color characteristic of males of this species was a distinct, clear spot in each of the last four dorsal fin and anal fin membranes which, when viewed collectively, formed a "window" in the posterior end of each fin. This "window" is a valuable key character for this species as it was present in the dorsal and anal fins of all male individuals used in this study.

The Sidling Threat Display When one or two males were placed into an aquarium with several females of the same species, each immediately selected a territory that was approximately 125 x 125 mm, extending from the surface of the water almost to the bottom in one corner. Females usually remained at or near the bottom. Gravid females could travel through a male's territory unmolested, but if another male or non-gravid female approached, a confrontation called the Sidling Threat Display by Miller (1964) occurred. During this display, the male whose territory had been violated swam to within 30-50 mm of the intruder and expanded his fins almost to their fullest extent. The caudal and pectoral fins "beat" very rapidly and the male's color intensified, indicating his apparent "anger" at his opponent. The male next turned himself broadside or nearly so in order to present the image of a larger fish and, thereby, possibly scare the intruder into retreat. If this failed, the male, while moving closer to his adversary, would arc his body so that his head and tail were closer to the intruder; when within range he would strike at him very quickly. The strike was accomplished with such haste that it was impossible to tell if physical contact had actually occurred. No physical damage to either fish was ever observed after these skirmishes. As a result of this display, the intruder usually retreated hastily from the territory and occasionally the

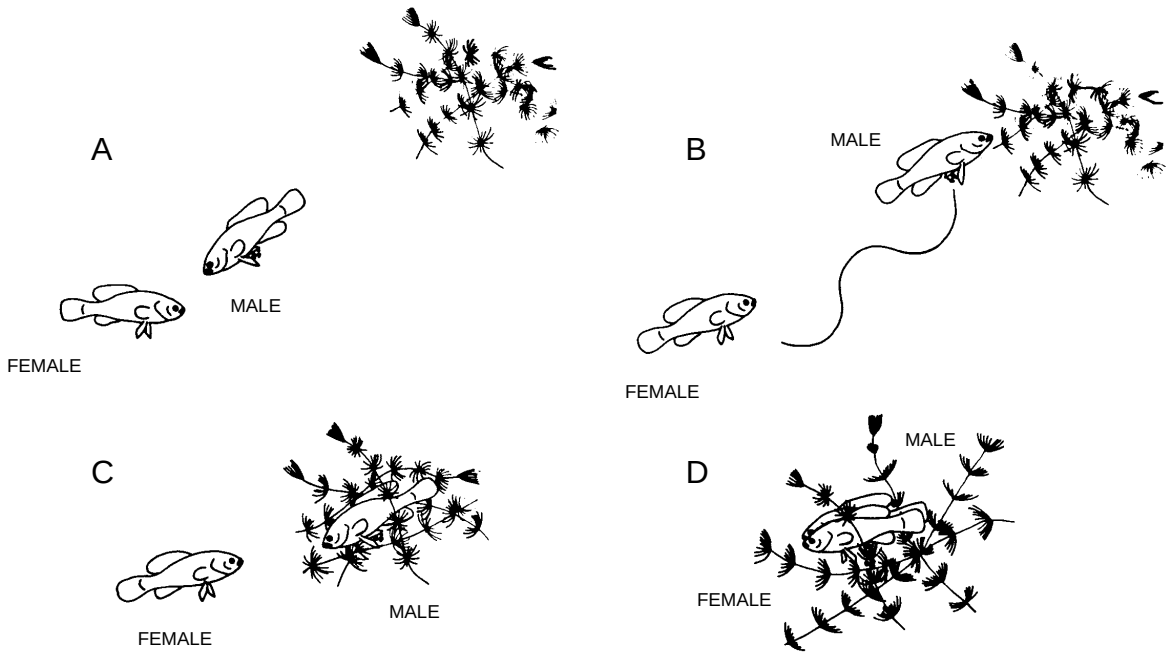

Figure 1. Stages of the reproductive behavior of elassomid fishes. A = male approaching female. B = wiggle waggle dance of male. C = female approaching the spawning site. D = the spawning act.

victorious male would chase him to the opposite end of the aquarium.

The Wiggle Waggle Display If a potential spawning partner entered a male's territory, another behavior pattern called the Wiggle Waggle Display by Miller (1964), was observed. The male would approach the female very slowly, and if she did not swim away, he would begin an erratic dance which consisted of swimming toward the potential spawning area in an up-and-down pattern, raising and lowering his dorsal and anal fins, and extending and flexing his pelvic fins alternately (Figure 1). These gestures were repeated several times by the male, always in the direction of the aquatic vegetation that he had previously selected as the potential spawning site. In his apparent "impatience" to spawn, the male would bite the female, which usually sent her in a hasty retreat. But if he was persistent, the male would eventually persuade the female to accompany him to the spawning area. Once the female entered the aquatic vegetation, the male became brightly colored, and his body began to quiver as he gently nipped the female's genital papilla and nudged her abdomen on one side and then the other. During this time the female would position herself in the aquatic vegetation once or twice, presumably to select the best position for egg deposition. The male continued his activities for 2-3 minutes after which he aligned himself on one side of the female. While both fishes remained in the upright position, the eggs and sperm were extruded.

Vegetation and Egg Deposition Most of the eggs fell into the fine-leafed *Ceratophyllum*, where they would stick in small clusters; however, it was common for one or two eggs to drop through to the bottom of the aquarium. After both participants rested briefly, the male chased the female from the spawning site, as she would cannibalize her own eggs. The entire spawning act lasted from 5-6 minutes.

Depending on the species, the male continued to guard the eggs for the next 72-100 hours. If another individual approached, it was confronted by a Sidling Threat Display and chased from the area. When the eggs were being collected for observation, it was not uncommon for the male to bite on the end of the pipette; if that failed to stall collection efforts, he would eat his own eggs. Once the eggs were removed from the spawning site, the male would renew his efforts to spawn with another female.

After witnessing several spawns of each of the four elassomid species, it became evident that the lack of aquatic vegetation as a suitable spawning medium may have been the reason why Axelrod and Shaw (1967), Innes (1969) and Axelrod and Schultz (1971) have observed these fishes spawning on the bottom rather than in aquatic vegetation. As mentioned in the Materials and Methods section, most of the vegetation collected with elassomid breeding stock was *Ceratophyllum*, a thick-

growing, fine-leafed plant. Elassomid eggs were always found attached to leaves of *Ceratophyllum*, except in cases where this plant was either not available or in a decomposing state, at which time the eggs were found on the bottom. Because of their semi-adhesive nature, the eggs would become covered with debris soon after they reached the bottom of the aquarium. In his efforts to clear away the debris, the male would clean an area that could be construed as a nest by those familiar with the bedding habits of centrarchid species. Photographs that lend support to this idea were given in Axelrod and Shaw (1967). The first sequence of photographs showed specimens of *E. evergladei* spawning in what appeared to be dying strands of *Ceratophyllum* or some closely related plant on the bottom of the aquarium, while the second photograph depicted a male *E. evergladei* guarding eggs that had been scattered about in healthy strands of aquatic vegetation that were floating away from the bottom.

Comparison and Conclusion The following aspects of the reproductive behavior of elassomid fishes contrast with the behavior patterns of centrarchid species as outlined in Breder and Rosen (1966):

1. Unlike centrarchids, elassomids did not construct nests for egg deposition.
2. When given the proper spawning medium, elassomids always spawned in aquatic vegetation above the bottom.
3. The displays of male elassomids described herein and by Miller (1964) are more complex than those previously reported for any centrarchid species.
4. Both male and female elassomid fishes remained in the upright position during the spawning act, while in most centrarchid species the female assumed an inclined position when the eggs were released.

A later study by Walsh and Burr (1984) confirms that *E. zonatum*, like other pygmy sunfishes, deposits its eggs in aquatic vegetation rather than in cleared nests.

According to Mayr (1969), behavioral taxonomic characters are often superior to morphological characters in the study of two closely related groups. From this study, it is evident that the behavior of elassomid and centrarchid fishes is not similar. Based on the morphological, chromosomal, biochemical and behavioral differences, as given in Eaton (1956), Branson and Moore (1962), Roberts (1964), Avise and Smith (1977), and this study, it is our opinion that the elassomid fishes have specialized to an extent to justify their being placed into a separate family, the Elassomatidae.

Embryology

The embryological stages illustrated in Figure 2 are based on the observation of eggs collected from 17 spawns of *E. okefenokee*, 10 spawns of *E. evergladei*, six spawns of *E. alabamae*, and 24 spawns of *E. zonatum*. Because there is variability in developmental rates within groups of eggs from the same spawn, observations were made on a time schedule, and developmental stages were assigned based on the stage demonstrated by the majority of eggs at that time. The time period from fertilization to hatching is given in Table 1. A comparison of fecundity rates (number of eggs fertilized) and percent survival of eggs is found in Table 2. Egg diameters immediately after spawning and at hatching time are given in Table 3.

During the hatching process, movements inside the egg became more frequent and violent until eventually, by using the tail as a lever, the larva ruptured the chorion, freeing the posterior end of its body. After a short rest the larva would shake itself free.

Description of the Prolarvae and Postlarvae

Prior to metamorphosis, elassomid larvae cannot be distinguished from each other; therefore, descriptions included herein pertain to pygmy sunfish larvae in general unless otherwise specified.

Newly hatched larvae (Figure 2-U) were tadpole-like in shape, except for a large ventro-lateral bulge caused by the enlarged yolk sak. No mouth was visible. The eyes were without pigment. A small pectoral fin bud which consisted of a fan-shaped membrane without fin ray primordia was present on either side of the larvae posterior to the eye and dorsal to the yolk sac. No pelvic fin buds were present. The major areas of the brain were distinguishable. The heart beat rate remained at 100-115 beats

Figure 2. Composite illustrations of the embryology of elassomid fishes. A = unfertilized egg. B, C = fertilized egg within 10 minutes after fertilization. D = one-celled embryo. E = two-celled embryo. F = four-celled embryo. G = eight-celled embryo. H = 16-celled embryo. I = 32- to 64-celled embryo. J = early high blastula. K = late high blastula. L = early gastrula. M = late gastrula. N = neurula, end view. O = neurula, lateral view. P = early larval stage. Q = 12-14 somite stage. R = 16-18 somite stage. S = 20-24 somite stage; brain and eyes prominent; heart is pumping colorless blood. T = prehatch larva; morphological development of larva appeared complete; all areas of brain visible; blood cells light pink in color. U = newly hatched larva.

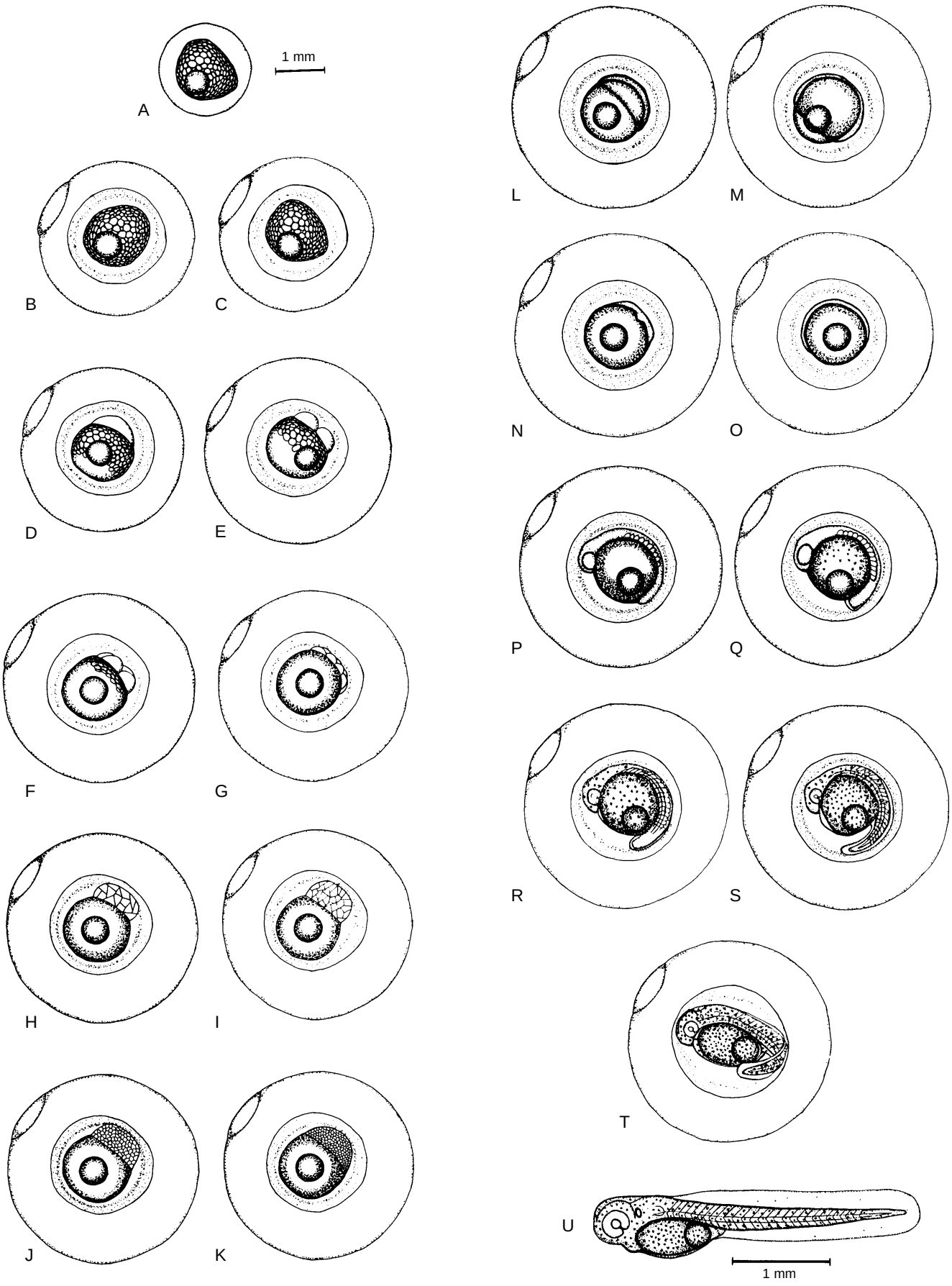
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Table 1. Developmental rates for four species of *Elassoma*.

Developmental Stages	Species, Incubation Temperatures and Times							
	E. okefenokee (23°C)		*E. evergladei* (25.5°C)		*E. alabamae* (23.5°C)		*E. zonatum* (21°C)	
	Hours	Minutes	Hours	Minutes	Hours	Minutes	Hours	Minutes
One-celled embryo		30		20		30		45
Two-celled embryo		50		40		50	1	20
Four-celled embryo	1	30	1		1	30	2	
Eight-celled embryo	2		1	45	2	10	2	55
16-celled embryo	2	45	2	30	3		4	
32- to 64-celled embryo	4		3	15	4	30	7	
Early high blastula	7		4		8		9	15
Late high blastula	10		8		9	15	11	30
Early gastrula	12		10		12		13	
Late gastrula	15		14		13		16	
Neurula	17		15		14		19	
Early larval stage	27		25		22		29	
12-24 somite stage	30		28		27		35	
16-18 somite stage	38		35		32		43	
20-24 somite stage	50		45		40		53	
Prehatch larva	70		60		52		72	
Beginning to hatch	82		65		72		110	

per minute for *E. okefenokee*, 145-150 for *E. evergladei*, 140-144 for *E. alabamae* and 134-136 for *E. zonatum*, and the blood pathway around the yolk sac and through the vessels of the body was visible. When viewed from the dorsal side, four pairs of gill arches and the rhythmic movements of the gill covers were observed.

Several morphological and behavioral changes were observed after the transition from prolarval to postlarval stages. The standard lengths at which these changes occurred are given for each species in Table 4. Because of its cumbersome yolk sac and lack of functional fins, the prolarvae spent most of their time lying on their sides on the bottom. Periodically, they would swim in short rapid spurts. Eyesight was apparently very poor since the larvae would often collide with each other or frequently swim headlong into the side of the petri dish. As the yolk sac was absorbed, the larvae, by "beating" their pectoral fins buds very rapidly, would balance themselves in an upright position for short periods of time. This behavior became more frequent until by the fifth day after hatching; they remained in the upright position most of the time. In the first two or three days after hatching, eye color of the larvae began to darken; by day four or five it was completely black. Eyesight and other sensory perception were apparently much improved at this time; when brine shrimp nauplii were introduced into the petri dishes, the larvae had no difficulty in catching and eating them. Species color development did not begin until after metamorphosis and at standard lengths of over 9.0 mm.

Food and Larval Mortality As stated in Lagler, Bardach and Miller (1962), food is a primary concern to the prolarvae. Due to the lack of a suitable food source, the greatest mortalities occur during the first few days after hatching. Mortality rates for elassomid larvae varied between 45-55% for the first week after hatching. Using

Table 2. Comparison of fecundity range and percent survival of eggs for the four species of *Elassoma* .

Species	Fecundity Range	Percent Egg Survival
E. okefenokee	20 to 25	45 to 50
E. evergladei	25 to 30	50 to 55
E. alabamae	60 to 65	35 to 40
E. zonatum	20 to 68	55 to 60

Table 3. Egg diameters of four species of *Elassoma* immediately after spawning and at hatching time.

Species	Egg Diameters in Millimeters	
	After Spawn	At Hatching Time
E. okefenokee	1.5 to 1.7	2.0 to 2.1
E. evergladei	1.4 to 1.2	2.1 to 2.2
E. alabamae	2.2 to 2.3	3.0 to 3.2
E. zonatum	2.6 to 2.7	3.7 to 3.8

the larvae of four marine species, Farris (1959) demonstrated that prolarvae undergo three distinct growth periods after hatching. Initially, there was a period of rapid growth followed by a period of slower growth. The third and most critical stage followed the absorption of the yolk materials, when the larvae had to metabolize themselves until they could actively feed. This was when the largest mortalities occurred. Fortunately, a number of the larvae of each elassomid species lived through the "critical phase" between yolk absorption and active feeding, but those that survived grew smaller. Larval shrinkage was observed on day 4, and recovery occurred on days 7-10.

Temperature and Larval Growth The time period necessary for newly hatched prolarvae to grow to adult size (approximately 16 mm standard length) was 160 days for *E. okefenokee*, 90 days for *E. evergladei*, 325 days for *E. alabamae*, and 100 days for *E. zonatum*.

In his discussion on larval metabolism and growth, Blaxter (1969) indicated that ambient temperature was one of the most important influences on the rate of development. During this study, individuals of *E. okefenokee* and *E. zonatum* that were maintained at lower temperatures (23°C and 21°C, respectively) metamorphised at an older and longer standard length than did specimens of *E. evergladei*. The growth pattern for individuals of *E. alabamae* differed from the other elassomid species. Even though they were maintained at a lower temperature (23.5°C), the larva of this species grew faster than those of *E. evergladei* (25.5°C). Once they had lived through the "critical phase" between the time of yolk absorption and active feeding, growth in *E. alabamae* larvae was rapid for approximately 40 days, after which it slowed significantly for 270 days.

Fin Development

Pen drawings of the sequence of fin development in elassomid fishes are given in Figure 3. The standard lengths at which various fin primordia were first observed are listed in Table 5.

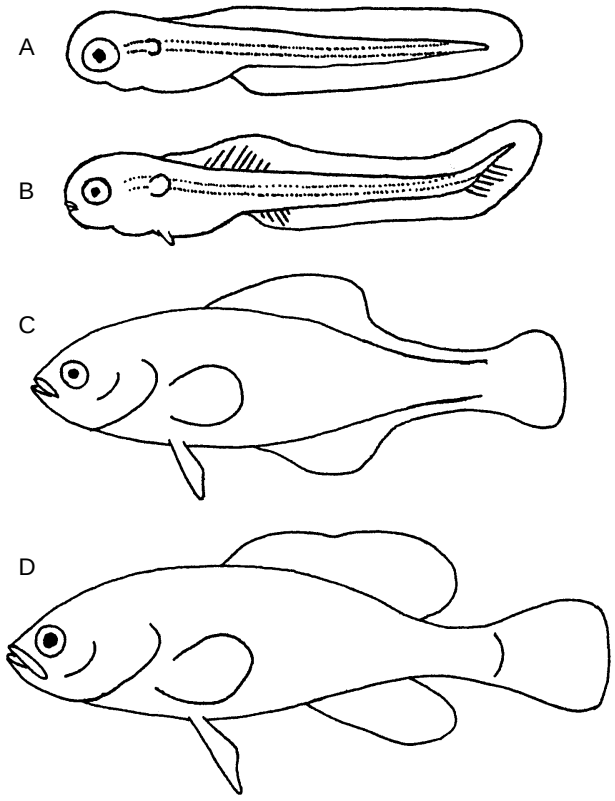


Figure 3. Stages of fin development. A = newly hatched prolarva. B = postlarva with fin fold primordia. C = late postlarva with fin fold remnants. D = young adult.

All larvae hatched with a pair of pectoral fin buds and a continuous fin fold, neither of which contained fin rays. No pelvic fins were present. At approximately 3.8-5.0 mm, depending on the species, the posterior end of the notochord and associated fin fold turned dorsally, temporarily forming a heterocercal tail. Shortly thereafter, caudal fin primordia were observed developing out from the posterior edge of the notochord. Several caudal fin primordia were present before the first dorsal and anal fin primordia were seen. The fin fold remained intact until most of the dorsal and anal fin primordia were present, at which time it began to decrease in depth until the

Table 4. Standard lengths (mm) at which *Elassoma* change from prolarvae to postlarvae and postlarvae to juveniles.

Species	Prolarvae to Postlarvae	Postlarvae to Juvenile
E. okefenokee	3.2 to 3.4	8.0 to 9.0
E. evergladei	3.4 to 3.5	6.4 to 7.0
E. alabamae	3.4 to 3.5	5.3 to 5.7
E. zonatum	3.5 to 3.7	8.0 to 8.5

Table 5. Standard lengths (mm) at which fin primordia were first observed in four species of *Elassoma.*

Species	Caudal Fin	Dorsal and Anal Fin	Pelvic Fins
E. okefenokee	4.9	5.9	5.5
E. evergladei	4.4	4.6	5.5
E. alabamae	4.3	5.0	5.3
E. zonatum	4.9	5.7	5.5

sections joining the dorsal and anal fins to the caudal fin disappeared. Ray formation proceeded from the ventral to the dorsal margins in the pectoral and caudal fins, and posterior to anterior in the dorsal and anal fins. By the time that the anterior spines were developing in the dorsal and anal fins, the soft rays of those fins were beginning to branch. Although it was extremely difficult to observe them because of their small size, soft rays appeared to develop before the single spine in each pelvic fin.

Fin development was complete at standard lengths of 8.0-9.0 mm for *E. okefenokee*, 6.4-7.0 for *E. evergladei*, 5.3-5.7 for *E. alabamae*, and 8.0-8.5 for *E. zonatum*.

Squamation

The fishes of all four elassomid species studied here are covered with cycloid scales except for *E. okefenokee* and *E. alabamae*, which do not have scales on the tops of their heads. Small scales were first observed on late prolarvae of each species; by the time metamorphosis had occurred, scales covered the entire body.

Epilogue: The Changing Face of Elassomid Systematics

Since the completion of the senior author's initial study on elassomids, several additional studies have come forth indicating an even more distant relationship between pygmy sunfishes and centrarchids, and perhaps no relationship at all. Humphries and Lauder (1985) found no evidence to support the notion that elassomids are a sister group of centrarchids. Johnson (1984, 1993) presented evidence that elassomid affinities lie outside the Percoidei, the large perciform suborder that includes such familiar fishes as groupers, perches and darters, butterflyfishes, marine angelfishes, and sunfishes. Johnson and Patterson (1993) expounded on this belief, finding that elassomids share some derived features with synbranchids (swamp eels), mugilomorphs (mullets), gasterosteiformes (sticklebacks, seahorses, etc.), mastacembelids (spiny eels), and atherinomorphs (rainbowfishes, killifishes, etc.). They even proposed a name for this new group—Smegmamorpha—an acronym using the initials (S-M-E-G-M-A) of the six taxa which comprise the group. In addition, the name derives from the Greek and Latin *smegma*, meaning cleansing or cleansing agent. In this usage, the name refers to the authors' "expectation that grouping these taxa will have the effect of cleaning up or tidying the systematics of higher teleosts . . .".

More recently, Johnson and Springer (1997) presented evidence that in every aspect an elassomid's skeleton is trying to be like a stickleback's. A formal rationale for placing elassomids into Gasterosteiformes is being prepared (G. D. Johnson, pers. comm. with CS).

Until their relationships are more clearly and definitively resolved, most ichthyologists retain pygmy sunfishes in the order Perciformes, within their own suborder (Elassomoidea) and family (Elassomatidae) (Nelson, 1994; Helfman et al., 1997). Please note, however, that many publications, including the popular *How to Know the Freshwater Fishes* (Eddy and Underhill, 1978) and the American Fisheries Society list of common and scientific names (Robins et al., 1991), still place pygmy sunfishes among the centrarchids. This will no doubt change in future editions.

Literature Cited

Avise, J. C. and M. H. Smith. 1977. Gene frequency comparisons between sunfish (Centrarchidae) populations at various stages of evolutionary divergence. Syst. Zool. 26:319-335.

Axelrod, H. R. and L. P. Schultz. 1971. Handbook of tropical aquarium fishes. T.F.H. Publications, Inc., Jersey City. 718 p.

---------- and S. R. Shaw. 1967. Breeding aquarium fishes. Book I. T.F.H. Publications, Inc., Hong Kong. 480 p.

Barney, R. L. and B. J. Anson. 1920. Life history and ecology of pygmy sunfish, *Elassoma zonatum*. Ecology. 1:241-256.

Blaxter, J. H. S. 1969. Development: eggs and larvae, p. 178-252. *In* W. S. Hoar and D. J. Randall (Eds.). Fish Physiology. Vol. 3. Academic Press, New York.

Böhlke, J. E. 1956. A new pygmy sunfish from southern Georgia. Notulae Naturae. 294. 11 p.

Boulenger, G. A. 1895. A catalogue of fishes of the British Museum. 2nd ed. Order of Trustees, London. Vol. 1. 349 p.

Branson, B. A. 1974. Pygmy sunfish for community aquaria. Tropical Fish Hobbyist. XXII. 17-22.

---------- and G. A. Moore. 1962. The lateralis components of the acoustico-lateralis system in the sunfish family Centrarchidae. Copeia 1932:1-108.

Breder, C. M. and D. E. Rosen. 1966. Modes of repro-

duction in fishes. Amer. Mus. Nat. Hist. Press, Garden City. 941 p.

Eaton, T. H. 1956. Notes on the olfactory organs in Centrarchidae. Copeia 1956:196-199.

Eddy, S. and J. C. Underhill. 1978. How to know the freshwater fishes. 3rd ed. Wm. C. Brown Co., Dubuque. 215 p.

Farris, D. A. 1959. A change in the early growth rates of four larval marine species. Limnol. Oceanog. 4:29-36.

Hay, O. P. 1880. On a collection of fishes from eastern Mississippi. Proc. U.S. Nat. Mus. 3:488-515.

Helfman, G. S., B. B. Collette and D. E. Facey. 1997. The diversity of fishes. Blackwell Science, Malden, Mass. 528 p.

Humphries, J. M. and G. V. Lauder. 1985. Sunfish phylogeny, outgroups, and percomorph systematics. 65th Ann. Meet. Amer. Soc. Ichthyol. and Herp., p. 78-79 (abstract).

Innes, W. T. 1969. Exotic aquarium fishes. T.F.H. Publications, Inc., Jersey City. 448 p.

Johnson, G. D. 1984. Percoidei: development and relationships. *In* H. G. Moser et al. (Eds.). Ontogeny and systematics of fishes. Spec. Publ. No. 1, Amer. Soc. Ichthyol. and Herp.: 464-498.

----------. 1993. Percomorph phylogeny: progress and problems. Bull. Mar. Sci. 52:3-28.

---------- and C. Patterson. 1993. Percomorph phylogeny: a survey of acanthomorphs and a new proposal. Bull. Mar. Sci. 52:554-626.

---------- and V. Springer. 1997. *Elassoma*: another look. 77th Ann. Meet. Amer. Soc. Ichthyol. and Herp., p. 176 (abstract).

Jordan, D. S. 1877. Contributions to North American ichthyology based primarily on the collections of the U.S. Museum. II. Notes on the Cottidae, Etheostomatidae, Percidae, Centrarchidae, Aphredoderidae, Dorysomatidae, and Cyprinidae, with revisions of the genera and descriptions of new or little known species. Bull. U.S. Nat. Mus. 10:1-68.

----------. 1884. List of fishes collected in Lake Jessup and Indian River, Florida, by Mr. R. E. Earll, with descriptions of two new species. Proc. U.S. Nat. Mus. 7:322-324.

---------- and C. H. Gilbert. 1883. Synopsis of the fishes of North America. Bull. U.S. Nat. Mus. 16:1-1068.

Lagler, K. E., J. E. Bardach and R. R. Miller. 1962. Ichthyology. John Wiley and Sons, New York. 545 p.

Mayden, R. L. 1993. *Elassoma alabamae*, a new species of pygmy sunfish endemic to the Tennessee River drainage of Alabama (Teleostei: Elassomatidae). Bull. Ala. Mus. Nat. Hist. 16:1-14.

Mayr, E. 1969. Principles of systematic zoology. McGraw-Hill Book Co., New York. 428 p.

Mettee, M. F. 1974. A study on the reproductive behavior, embryology, and larval development of the pygmy sunfishes in the genus *Elassoma*. Ph.D. Dissertation. University of Alabama, Tuscaloosa. 130 p.

---------- and J. J. Pulliam. 1986. Reintroduction of an undescribed species of *Elassoma* into Pryor Branch, Limestone County, Alabama. Southeastern Fishes Council Proceedings 4:14-15.

Miller, H. C. 1964. The behavior of the pumpkinseed sunfish, *Lepomis gibbosus* (Linnaeus), with notes on the behavior of other species of Lepomis and the pygmy sunfish *Elassoma evergaldei*. Behavior. 22: 88-151.

Moore, G. A. and M. E. Sisk. 1963. The spectacle of *Elassoma zonatum* Jordan. Copeia 1963:346-350.

Nachstedt, J. and H. Tusche. 1954. Breeding aquarium fishes. Aquarium Stock Co., New York. 127 p.

Nelson, J. S. 1994. Fishes of the world. 3rd ed. John Wiley & Sons, New York. 600 p.

Poyser, W. A. 1919. Notes on the breeding habits of the pygmy sunfish. Aquatic Life. 4:65-69.

Roberts, F. L. 1964. A chromosome study of twenty species of Centrarchidae. J. Morph. 115:401-418.

Robins, C. R., R. M. Bailey, C. E. Bond, J. R. Brooker, E. A. Lachner, R. N. Lea, and W. B. Scott. 1991. A list of the common and scientific names of fishes from the United States and Canada. 5th ed. American Fisheries Society Special Publication 20. 183 p.

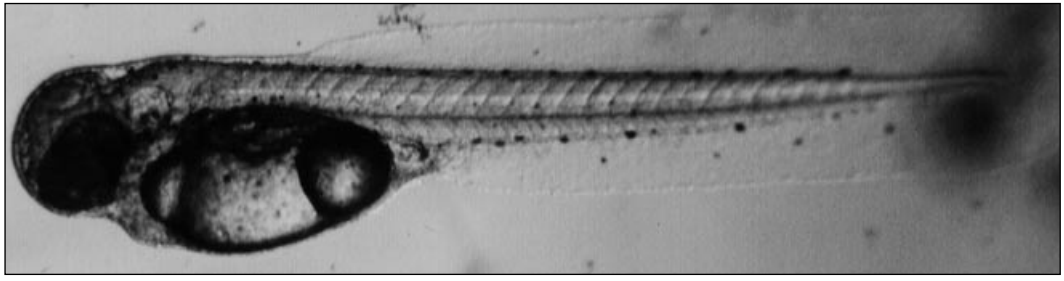
Rohde, F. C. and R. G. Arndt. 1987. Two new species of pygmy sunfishes (Elassomatidae, *Elassoma*) from the Carolinas. Proc. Acad. Nat. Sci. Phila. 139:65-85.

Shortt, L. R. 1956. A new pygmy sunfish. The Aquarium. 25:133-135.

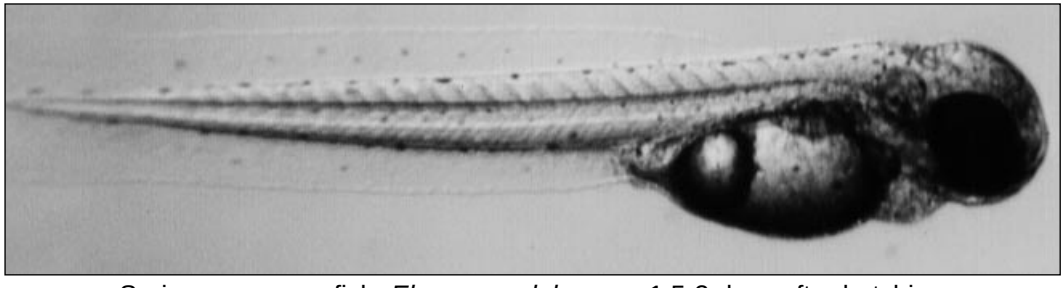
Sterba, G. 1961. Freshwater fishes of the world. Pet Library, New York. 879 p.

Walsh, S. J. and B. M. Burr. 1984. Life history of the banded pygmy sunfish, *Elassoma zonatum* Jordan (Pisces, Centrarchidae) in western Kentucky. Bull. Ala. Mus. Nat. Hist. 8:31-52.

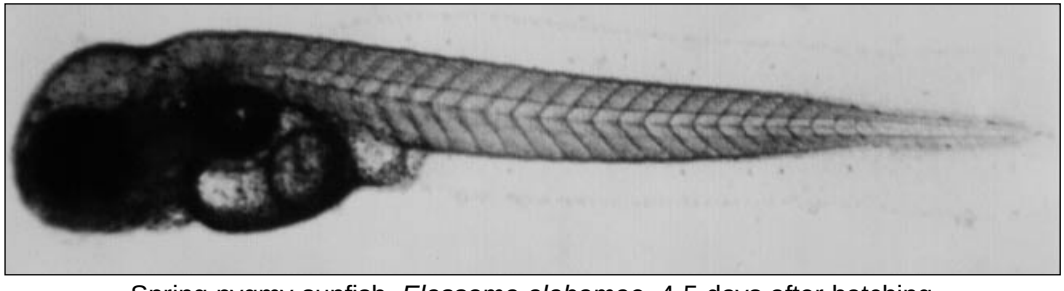
Spring pygmy sunfish larvae (Elassomaalabamae). Photographs by Maurice F. Mettee.



Spring pygmy sunfish, *Elassoma alabamae*, newly hatched.



Spring pygmy sunfish, *Elassoma alabamae*, 1.5-2 days after hatching.



Spring pygmy sunfish, *Elassoma alabamae*, 4-5 days after hatching.