LARVAL DEVELOPMENT OF *ENGYOPHRYS SENTA* (BOTHIDAE), WITH COMMENTS ON INTERMUSCULAR BONES IN FLATFISHES

Dannie A. Hensley

ABSTRACT

Development of *Engyophrys senta* is described from larvae collected in the Gulf of Mexico. Larvae are characterized by a deep, highly compressed body; an elongate second dorsal ray in small larvae; four (three in small larvae) spines in the otic region; and spinous serrations on the cleithra, urohyal, and basipterygia. As metamorphosis is approached, optic papillae develop, spines (otic, urohyal, basipterygial, and cleithral) become reduced in size, and larval teeth are lost, replacement teeth forming on the right dentary and premaxillary. Metamorphosis apparently occurs at about 20 mm SL.

Five series of intermuscular bones are present in juvenile and adult *E. senta*. Four of these series are composed of highly branched (brush-like) bones. There are reasons for interpreting the presence of these bones as a derived character. Some authors have shown, on the basis of presence or absence of intermuscular bones, that there are two groups of species within the Bothidae; these two groups generally agree with the Bothinae (bones present) and Paralichthyinae (bones absent) of the most widely accepted classification. This is true among the western North Atlantic species except in regard to *Engyophrys, Trichopsetta*, and *Monolene*, which have intermuscular bones and have been placed in the Paralichthyinae by previous workers. Other adult and larval characters also support the possibility that these three genera are more closely related to the Bothinae than the Paralichthyinae. These observations suggest that the subfamilial groupings within the Bothidae should be reexamined and subjected to a more rigorous analysis than previous workers have given them.

The bothid genus *Engyophrys* includes two known species, *E. sanctilaurentii* Jordan and Bollman in the eastern tropical Pacific and *E. senta* Ginsburg in the western Atlantic from the Bahamas, throughout the Gulf of Mexico, to Brazil. A third nominal species, *E. ciliaris* Roux, has been shown to be a synonym of *E. senta* by Staiger (1973). *E. senta* is distinguishable from other western Atlantic bothids by the following combination of characters: (1) narrow-based pelvic fins, the left inserted on the midventral line slightly anterior to the tips of the cleithra and the origin of the right pelvic fin; (2) no lateral line on the right side; (3) the lateral line of the left side highly arched over the pectoral fin; (4) rudimentary gill rakers; (5) a small mouth with teeth almost entirely (or entirely) confined to the right sides of the jaws; and (6) a narrow interorbital ridge with 2–5 retrorse spines (Ginsburg,

1933; Norman, 1934; Gutherz, 1967; Staiger, 1973). In addition, Anderson and Lindner (1941) have discussed two sexually dimorphic characters; presence of optic papillae and coloration of the blind side. An optic papilla is present on both eyes, that of the lower eye usually longer, in immature specimens of both sexes. However, mature males nearly or completely lose these. Mature males develop 3–7 dark, diffuse, curved bars on the anterior part of the body on the right side; these are entirely absent in all females and immature males.

Adults of *E. senta* are relatively uncommon and typically occur at depths of 40–90 m, occasionally as shallow as 32 m and as deep as 180 m. Virtually nothing is known of the life history of this species. Spawning, at least in the northern Gulf of Mexico, apparently occurs in spring (Anderson and Lindner, 1941).

Ahlstrom (1971) identified and gave several important characteristics of *E. sanctilaurentii* larvae. Gutherz (1970) has intimated that he identified *E. senta* larvae and discussed the pelvic fin placement and caudal fin formula for this species. This paper describes the larval stages of *E. senta*.

MATERIALS AND METHODS

All larvae examined in this study were collected in the Gulf of Mexico by the R/V HERNAN CORTEZ in March 1968 and from June to October 1969, using a 1-m plankton net. Details of the cruises are given by Presley (1971). These cruises yielded 85 larvae identifiable as *E. senta*, 76 (3.1–19.9-mm standard length) of which were sufficiently free from damage and distortion so that counts and measurements could be made. After counts and measurements were made on all larvae in this series, 18 (4.6–19.9-mm standard length) were cleared and stained according to the method of Taylor (1967). In order to determine the ranges of variation in juvenile and adult character states, 45 juveniles and adults from Gulf of Mexico localities were examined. Two juveniles (38.7 and 45.7-mm standard length) from this series were cleared and stained.

I have followed Moser and Ahlstrom (1970) in defining the larval period as the period between hatching and attainment of juvenile characters. Transition from larva to juvenile is termed the metamorphic stage. Although metamorphosis in flatfishes involves a very complex series of changes, the most obvious is migration of the right eye in sinistral species. Therefore, metamorphic larvae are defined as those in which migration of the right eye was detectable at a gross level.

Measurements of larvae were made with an ocular micrometer. Measurements of juveniles and adults were made with dial calipers. All measurements were recorded to the nearest 0.1 mm. Lengths of larvae given in the text refer to standard length. Measurements taken from larvae, juveniles, and adults are defined as follows:

STANDARD LENGTH (SL): Two methods were employed for standard length measurements. Prior to notochord flexion, SL measurements were taken from the tip of the snout to the indentation in the dorsal finfold above the area where notochord flexion takes place. In specimens in which notochord flexion had taken place, SL measurements were taken from the tip of the snout to the bases of the middle caudal rays.

HEAD LENGTH (HL). Tip of snout to posterior edge of cleithrum on a horizontal line.

EYE DIAMETER (ED). Horizontal distance across the left eye.

PREANUS LENGTH (PAL). Horizontal distance from tip of snout to a vertical through anus.

BODY DEPTH (BD). Vertical distance from anus to base of dorsal fin rays.

UPPER JAW LENGTH (UJL). Anterior tip of premaxillary to posterior edge of maxillary.

Ricker's (1973) predictive model was used for regression analyses of all measurements on SL and upper jaw length on head length. All variates were transformed to natural logarithms. Regression lines for larvae were calculated separately from those for juveniles and adults due to a gap in the series between the largest larva (19.9 mm) and the smallest juvenile (38.2 mm). Regression lines of larvae and juveniles and adults were compared by analysis of covariance according to procedures of Snedecor and Cochran (1967). Differences are considered to be significant at the $P \leqq .05$ level. Table 4 presents sufficient information from the regression analyses to allow computation of any of Ricker's (1973) other models and analysis of covariance should other workers wish to make interspecific comparisons.

Dorsal and anal fin ray counts were taken on all larvae where possible. All rays were counted in these fins since cleared and stained specimens showed the last two rays had separate basal support. It was possible to make vertebral counts on most larvae in

which vertebrae were developed due to the diaphanous nature of the body. Vertebral counts and caudal fin formulae for juveniles and adults were taken from radiographs made with a Softex Type "E" x-ray unit using Polaroid type 55 P/N film. Precaudal vertebrae lack hemal spines, the first caudal vertebra is the most anterior vertebra bearing a hemal spine. The terminal half-centrum was included in vertebral counts. Gutherz (1970) discussed the use of caudal fin formulae in the identification of larval bothids. He enumerated the number of caudal rays supported by each caudal element in a dorsal to ventral direction (posterior to anterior before notochord flexion). In order to be more consistent with the practice of numbering hypural elements ventral to dorsal, I have reversed Gutherz's method of expressing the caudal fin formula. For example, most *E. senta* specimens have a caudal fin formula of 1-3-4-5-3-1. This formula indicates that one ray is supported by the hemal spine of the penultimate vertebra (second preural centrum), three by the parhypural, four by the first hypural element, five by the second hypural element, three by the hypural + epural element, and one by the neural spine of the penultimate vertebra. Caudal fin formulae of larvae could be determined with certainty only in cleared and stained specimens.

The description of developmental osteology is based mainly on cleared and stained material and radiographs. The information presented on the sequence of ossification of bony elements is intended to imply general trends only, as precision is limited by the number of cleared and stained specimens examined and variation in the length of time larvae had been in Formalin. The slightest uptake of stain was interpreted as an indication that ossification had started. A great deal of important information was obtained by viewing cleared and stained larvae under polarized light. Cartilaginous precursors of endochondral elements and developing fields of dermal elements were observed before the uptake of stain. Terminology for caudal fin osteology was synthesized from Gosline (1961a, 1961b, 1965), Nybelin (1963), Monod (1968), Amaoka (1969), and Rosen (1973); that for the osteocranium follows Harrington (1955) with additions from Amaoka (1969) for processes of the urohyal; that for the appendicular skeleton follows Futch et al. (1972); and that for the vertebral processes and intermuscular bones follows Phillips (1942) and Amaoka (1969).

All larvae examined are deposited at the Florida Department of Natural Resources Marine Research Laboratory (FSBC). Juvenile and adult specimens examined were from the U.S. National Museum of Natural History (USNM), University of Miami, Rosenstiel School of Marine and Atmospheric Science (UMML), Gulf Coast Research Laboratory Museum (GCRL), and the Florida State University Collection (FSU).

Material examined.—LARVAE. FSBC 8921; 21°42'N, 86°30'W, 18 m-surface, 4 March 1968, 1 specimen (18.9 mm SL): 8922; 29°55'N, 85°55'W, 18 m-surface, 26 June 1969, 1 (7.4): 8923; 29°32'N, 87°46'W, 19 m-surface, 29 June 1969, 2 (4.6–5.5) (1 cleared and stained): 8924; 30°05'N, 85°45'W, surface, 5 August 1969, 2 (3.3–12.8): 8925; 29°45'N, 86°07'W, 26 m-surface, 6 August 1969, 2 (5.2–11.5): 8926; 29°35'N, 86°18'W, 73 m-surface, 6 August 1969, 7 (6.5–12.8) (1 cleared and stained): 8927; 30°05'N, 86°42'W, surface, 7 August 1969, 7 (8.0–12.9) (2 cleared and stained; 1 destroyed): 8928; 29°53'N, 86°49'W, surface, 7 August 1969, 1 (15.6): 8929; 29°38'N, 86°55'W, surface, 7 August 1969, 3 (8.4–11.8) (2 cleared and stained): 8930; 29°38'N, 86°55'W, 46 m-surface, 7 August 1969, 12 (4.0–15.5) (2 cleared and stained; 1 destroyed): 8931; 29°47'N, 87°52'W, 14 m-surface, 8 August 1969, 1 (19.9) (cleared and stained): 8932; 29°32'N, 87°46'W, 19 m-surface, 8 August 1969, 2 (7.5–9.2): 8933; 29°18'N, 87°40'W, 46 m-surface, 8 August 1969, 1 (8.8): 8934; 29°17'N, 85°40'W, 29 m-surface, 10 August 1969, 1 (19.6): 8935; 28°39'N, 85°10'W, surface, 12 August 1969, 1 (10.3) (cleared and stained): 8936; 30°05'N, 86°42'W, surface, 4 September 1969, 4 (5.5–7.7) (3 cleared and stained; 1 destroyed): 8937; 30°05'N, 86°42'W, 21 m-surface, 4 September 1969, 7 (4.3–6.4) (2 cleared and stained; 1 destroyed): 8938; 29°53'N, 86°49'W, surface, 5 September 1969, 4 (6.1–8.0) (2 cleared and

Table 1. Meristic counts of adult bothids and scophthalmids known to occur in the Gulf of Mexico

| Species | Dorsal Fin Rays | Anal Fin Rays | Vertebrae | | Source |
			Precaudal	Caudal	
Ancylopsetta dilecta (Goode and Bean)	68–79	53–60	10	25–27	Gutherz (1966, 1967)
Ancylopsetta quadrocellata Gill	67–76	54–61	10–11	25–27	Gutherz (1966, 1967)
Bothus ocellatus (Agassiz)	79–91	58–68	10	25–27	Jutare (1962); Gutherz (1967)
Bothus robinsi Topp and Hoff	78–90	59–68	10	26–28	Jutare (1962); Gutherz (1967)
Chascanopsetta lugubris Alcock	111–122	76–85	16–17	38–39	Norman (1934); Deubler and Rathjen (1958); Gutherz (1967) Amaoka (1971)
Citharichthys abbotti Dawson	72–81	52–60	9–10	21–23	Dawson (1969)
Citharichthys arctifrons Goode	75–87	58–71	10–11	26–28	Gutherz (1967); Richardson and Joseph (1973)
Citharichthys cornutus (Günther)	74–84	59–67	9–10	25–26	Gutherz (1967); Topp and Hoff (1972); Miller and Jorgenson (1973)
Citharichthys dinoceros Goode and Bean	90–95	70–76	10–11	26–29	Gutherz (1967)
Citharichthys gymnorhinus Gutherz and Blackman	70–77	51–61	10	23–24	Gutherz and Blackman (1970); Topp and Hoff (1972); Miller and Jorgenson (1973)
Citharichthys macrops Dresel	79–85	56–64	10	24–25	Gutherz (1967); Topp and Hoff (1972)
Citharichthys spilopterus Günther	74–84	56–63	10	23–25	Gutherz (1967); Dawson (1969)
Cyclopsetta chittendeni Bean	82–90	63–69	10	27–28	Gutherz (1967)
Cyclopsetta fimbriata (Goode and Bean)	78–87	59–67	10	26–27	Gutherz (1967)
Engyophrys senta Ginsburg	71–85 74–83	59–69 60–67	10 10	27–28 27–29	Gutherz (1967); Staiger (1973) present study
Etropus crossotus Jordan and Gilbert	75–87	58–68	10	25–26	Gutherz (1967); Miller and Jorgenson (1973)
Etropus microstomus (Gill)	67–84	50–63	10	24–25	Gutherz (1967); Richardson and Joseph (1973)
Etropus rimosus Goode and Bean	74–83	57–63	10	24–25	Gutherz (1967)
Gastropsetta frontalis Bean	58–65	46–53	10	25–28	Gutherz (1966, 1967)
Monolene sessilicauda Goode*	92–109	76–89	10–11	35–38	Gutherz (1967); Futch (1971)
Paralichthys albigutta Jordan and Gilbert	71–85	53–63	9–10	26–28	Gutherz (1967); Woolcott et al. (1968)
Paralichthys lethostigma Jordan and Gilbert	80–95	63–74	10–11	27–28	Gutherz (1967)
Paralichthys squamilentus Jordan and Gilbert	76–85	59–65	10	27–29	Gutherz (1967)
Scophthalmus aquosus (Mitchill)	63–73	48–56	11	23–25	Moore (1947)
Syacium gunteri Ginsburg	74–85	59–68	10	23–26	Gutherz (1967)
Syacium micrurum Ranzani	83–92	64–74	10	24–25	Gutherz (1967)
Syacium papillosum (Linné)	79–94	62–75	10	25–26	Gutherz (1967); Fraser (1971) Topp and Hoff (1972)
Trichopsetta ventralis (Goode and Bean)	89–95	69–75	10	30–31	Anderson and Gutherz (1967)

* Data for *M. sessilicauda* were combined with those given for *M. antillarum* Norman, since the two may be conspecific (Gutherz, 1967).

stained): 8939; 29°47′N, 87°52′W, surface, 5 September 1969, 3 (7.7–11.7) (1 cleared and stained): 8940; 29°18′N, 87°40′W, 37 m-surface, 6 September 1969, 2 (6.8–7.2): 8941; 28°52′N, 86°01′W, 46 m-surface, 7 September 1969, 1 (5.0) (cleared and stained): 8942; 28°43′N, 84°54′W, 26 m-surface, 8 September 1969, 1 (16.5) (cleared and stained): 8943; 29°25′N, 86°30′W, 91 m-surface, 10 October 1969, 1 (3.1): 8944; 29°38′N, 86°55′W, 46 m-surface, 11 October 1969, 2 (7.2–15.3) (1 cleared and stained): 8945; 29°47′N, 87°52′W, surface, 11 October 1969, 2 (10.6–15.7): 8946; 29°47′N, 87°52′W, 15 m-surface, 11 October 1969, 2 (8.2–12.4): 8947; 29°32′N, 87°46′W, surface, 12 October 1969, 1 (8.4): 8948; 29°18′N, 87°40′W, surface, 12 October 1969, 2 (12.8–12.9) (1 cleared and stained; destroyed).

JUVENILES AND ADULTS.—USNM 155706; Pelican 113-8, 27°06′N, 96°53.5′W, 55 m, 31 January 1939, 9 specimens (45.7–66.0 mm SL) (1 cleared and stained): 155703; Pelican 113-9, 27°05′N, 96°49.5′W, 64 m, 31 January 1939, 6 (38.7–63.0) (1 cleared and stained): 155704; Pelican 101-3, 28°32′N, 93°36′W, 38 m, 16 January 1939, 3 (38.2–53.1): 117040; Florida, south of Dry Tortugas, 26 June 1932, 8 (61.9–82.4): 117162; Florida, Dry Tortugas, 9 (58.0–68.2): 158295; Oregon 1086, 26°10′N, 96°54′W, 68 m, 3 June 1954, 1 (58.2). UMML 32731; Silver Bay 3860, 28°05′N, 95°40′W, 41 m, 1 August 1962, 3 (53.3–59.8): 32732; Oregon 2925, 75 nmi SSW of Galveston, Texas, 55 m, 19 August 1960, 1 (60.7). GCRL V61:260; south of Grand Isle, Louisiana, 2 (51.7–54.6): V68:3016; Gulf Researcher Sta. 5, 29°19′N, 88°14′W, 1 (71.7). FSU 21478; Tursiops Cruise 7110 Sta. 20, 29°29′N, 86°2.5′W, 2 (79.5–87.7).

LARVAL IDENTIFICATION

It was possible to place the larvae into a series utilizing general body shape (deep and highly compressed), spines on the otic region of the head, spinuous serrations on the urohyal, cleithra, and basipterygia, and an elongate second dorsal ray in small larvae. Identification of the larvae was based on the following:

One metamorphic larva was available for study. Migration of the right eye in this specimen indicated a species of Bothidae or Scophthalmidae. Sinistrality was evident also in smaller larvae in which asymmetry in certain characters had developed (e.g., placement of basipterygia).

Gutherz (1967) and Topp and Hoff (1972) list 28 species of bothid and scophthalmid flatfishes from the Gulf of Mexico. On the basis of dorsal and anal fin ray and vertebral counts, *Engyophrys senta* is distinguishable from all of these except *Paralichthys* spp., *Cyclopsetta* spp., *Ancylopsetta* spp., *Bothus* spp., and *Citharichthys arctifrons* (Table 1). Larvae in which the dorsal and anal fins had developed the full complement of fin rays, and larvae in which vertebral centra had formed had counts of these structures within the ranges found in *E. senta*.

In larvae in which pelvic fins were developed, they were found to be narrow based. The first ray of the left pelvic was inserted slightly anterior to the tip of the cleithrum, and the first ray of the right fin was at the same transverse level as the second ray of the left fin (not the condition illustrated and stated in Gutherz, 1967, p. 2, 4, Fig. AA). The left fin was inserted on the midventral line. These are states characteristic of adult *E. senta*. *Bothus* has an ocular pelvic with a long base extending onto the urohyal. In *Paralichthys* and *Ancylopsetta* both pelvic fins originate posterior to the cleithra, and neither fin base is on the midventral line. *Cyclopsetta* and *Citharichthys* have ocular pelvics originating posterior to the tips of the cleithra.

Of the juveniles and adults examined 82.5% (33) had a caudal fin formula of 1-3-4-5-3-1. Cleared and stained larvae in which the adult complement of caudal rays had formed had the caudal fin formula typical of adult *E. senta*. In the western North Atlantic this caudal fin formula is found only in *Engyophrys*, *Trichopsetta*, and *Monolene* (Gutherz, 1970).

Larvae nearing or in metamorphosis had the optic papillae characteristic of juvenile *E. senta* of both sexes.

Larvae nearing or in metamorphosis were developing teeth on the medial surfaces of the right premaxillary and dentary, approaching the condition in juvenile and adult *E. senta* where teeth are almost entirely (or
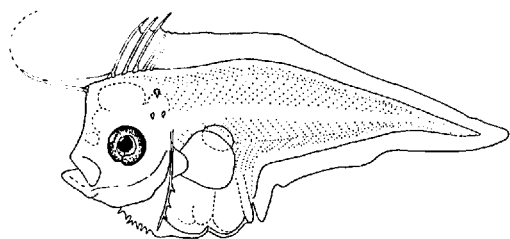
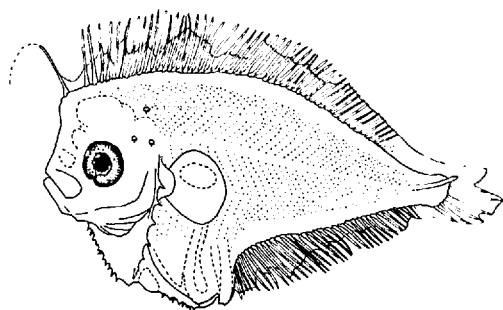Figure 1. *Engyophrys senta* larva 3.3-mm SL.

Figure 2. *Engyophrys senta* larva 4.5-mm SL.

entirely) confined to the right sides of the jaws.

Proportional measurements (expressed as percentages of SL or HL) of late stage larvae were within the ranges found in juvenile *E. senta*. Relative upper jaw length (% HL) is an important character separating *E. senta* and *Trichopsetta*. The range for this character in *E. senta* juveniles and adults is about 19–26% HL; in *Trichopsetta* species 32–43% HL (Gutherz, 1967; Anderson and Gutherz, 1967). Larvae approaching or undergoing metamorphosis had a range for this character of about 22–26% HL.

DESCRIPTION OF DEVELOPMENT

Pigmentation

The eyes of the smallest larva examined (3.1 mm) are pigmented. Two of the larvae with optic papillae have scattered melanophores on the papillae. No other pigmentation develops until during or after metamorphosis.

General morphology

Head.—In small larvae the head is deep, bordered anterodorsally by a steep frontal profile and anteroventrally by the serrated edge of the urohyal (Figs. 1–3). As development proceeds the frontal profile becomes concave due to the anterior migration of the dorsal fin (Figs. 4, 5). At or near metamorphosis, when migration of the dorsal fin is complete, the frontal area assumes the comparatively low profile of juveniles and adults (Figs. 6, 7). During metamorphosis the urohyal becomes covered by the oper-

cular elements and no longer forms the anteroventral margin of the head.

Nasal capsules are present in the smallest larva examined (3.1 mm); tubular nostrils develop as metamorphosis is approached. The brain is distinctly trilobed by 3.1 mm. Each eye has an anteroventral optic fissure that persists throughout the larval period and closes during metamorphosis. Optic papillae, characteristic of juveniles of both sexes and at least adult females, first appear at about 15 mm. The left papilla tends to develop faster than the right (Figs. 6, 7). Migration of the right eye occurs below the previously advanced dorsal fin origin. Eye migration is evident in only one larva (19.6 mm; Fig. 7); two other large larvae (18.9 and 19.9 mm) show no evidence of eye migration. In the metamorphic larva the right eye has already passed below the dorsal fin origin but has not reached its ventral limit on the ocular side of the head. The otic region is transversely broad, bulbous, and bears three spines in small larvae (Figs. 1–3). Another otic spine develops between 6.2 and 7.7 mm, and is present in all larvae 8.0 mm and larger (Figs. 4–7). The cleithra bear spines. All spines in the head region (otic, urohyal, and cleithral) become reduced in size as metamorphosis is approached and lost during metamorphosis.

Relative head length averages 33.0% SL in the smallest larvae (3.1–3.3 mm) and shows a steady reduction to a mean of 21.3% SL in 16.5–19.9-mm larvae. In juveniles and adults head length is 20.6–26.5% SL (Tables

Table 2. Measurements (mm) of larval *Engyophrys senta*

Table 2. (Continued)

SL*	Head Length	Body Depth	Preanus Length	Eye Diameter	Upper Jaw Length
3.1(S)	1.2	2.0	2.3	0.4	0.4
3.3(S)	0.9	1.5	1.6	0.3	–
4.0(S)	1.2	2.0	1.9	0.4	–
4.3(S)	1.3	2.2	2.1	0.4	0.4
4.5(S)	1.1	2.0	1.8	0.4	–
4.5(F)	1.4	2.7	2.2	0.4	0.4
4.6(F)	1.3	2.8	2.3	0.5	0.4
4.9(PF)	1.5	2.9	2.6	0.5	0.4
5.0(PF)	1.4	3.2	2.3	0.4	0.4
5.2(S)	1.4	2.5	2.4	0.4	–
5.4(PF)	1.5	3.0	2.3	0.5	0.4
5.4(F)	1.4	2.8	2.2	0.5	0.4
5.5(PF)	1.5	3.3	2.4	0.5	0.4
5.5(PF)	1.5	3.2	2.9	0.5	0.5
5.5(F)	1.5	3.0	2.5	0.5	0.5
5.9(PF)	1.6	3.4	2.4	0.5	0.5
6.1(PF)	1.6	3.9	2.5	0.7	0.5
6.2(PF)	1.8	4.1	2.9	0.6	0.5
6.3(PF)	1.7	3.5	2.8	0.6	0.5
6.4(PF)	2.0	4.6	2.9	0.6	0.5
6.4(PF)	1.8	3.6	2.7	0.6	0.5
6.5(PF)	1.7	3.3	2.4	0.6	0.5
6.5(PF)	1.7	3.7	2.5	0.6	0.5
6.5(PF)	1.9	4.5	2.5	0.7	0.5
6.6(PF)	1.8	4.3	2.9	0.6	0.5
6.7(PF)	1.7	3.8	2.7	0.6	0.5
6.8(PF)	1.7	3.3	2.8	0.6	0.5
7.0(PF)	1.6	3.8	2.0	0.6	–
7.0(PF)	1.7	4.2	2.3	0.6	0.6
7.2(PF)	2.0	4.3	2.9	0.6	0.6
7.2(PF)	2.1	5.0	3.3	0.7	0.6
7.2(PF)	1.9	4.4	3.0	0.6	0.6
7.4(PF)	2.0	4.8	3.4	0.6	0.6
7.5(PF)	2.1	5.2	2.9	0.7	0.6
7.5(PF)	2.0	4.4	2.2	0.8	–
7.6(PF)	2.0	4.8	2.9	0.7	0.6
7.7(PF)	2.0	5.2	2.8	0.7	0.6
7.7(PF)	2.0	4.6	2.8	0.7	0.6
8.0(PF)	1.9	4.9	2.9	0.8	0.6
8.0(PF)	2.2	4.8	3.4	0.7	0.6
8.1(PF)	2.1	5.4	3.1	0.8	–
8.2(PF)	2.1	5.4	2.9	0.7	0.6
8.4(PF)	2.4	6.4	3.2	0.9	–
8.4(PF)	2.3	5.3	3.1	0.8	0.6
8.4(PF)	2.3	5.2	3.1	0.8	0.6
8.8(PF)	2.2	4.9	3.1	0.8	0.6
9.0(PF)	2.4	6.2	3.1	0.7	–
9.0(PF)	2.3	5.7	3.5	0.7	–
9.2(PF)	2.2	5.8	3.1	0.9	0.7
9.8(PF)	2.4	6.6	3.2	0.8	0.7
10.3(PF)	2.5	6.6	2.9	1.0	0.7
10.5(PF)	2.5	6.8	3.2	0.8	0.7
10.5(PF)	2.6	6.2	3.3	0.9	0.7

SL*	Head Length	Body Depth	Preanus Length	Eye Diameter	Upper Jaw Length
10.6(PF)	2.6	7.4	3.1	0.9	0.7
10.8(PF)	2.5	7.2	3.0	0.9	0.7
11.5(PF)	2.8	7.5	3.6	0.8	–
11.7(PF)	2.9	7.8	2.8	0.9	0.7
11.8(PF)	2.7	7.3	3.3	1.0	0.7
11.8(PF)	2.8	7.8	3.3	1.0	0.8
12.1(PF)	2.8	7.7	2.7	1.0	–
12.2(PF)	2.9	7.8	3.5	1.0	0.7
12.3(PF)	3.0	7.7	3.5	0.9	0.7
12.4(PF)	2.9	7.9	2.8	1.0	0.8
12.8(PF)	2.9	7.9	3.8	1.0	0.7
12.8(PF)	3.0	7.9	3.9	0.9	–
12.8(PF)	2.8	7.5	3.4	0.9	0.8
12.9(PF)	2.9	8.3	3.5	1.0	0.8
12.9(PF)	3.0	7.8	4.2	1.0	0.8
15.3(PF)	3.5	8.4	3.8	1.2	0.9
15.5(PF)	3.2	9.0	4.2	1.1	0.9
15.6(PF)	3.4	8.7	3.9	1.2	0.9
15.7(PF)	3.6	9.1	4.0	1.1	0.9
16.5(PF)	3.2	9.2	3.2	1.3	0.9
18.9(PF)	4.1	9.8	4.2	1.3	0.9
19.6(PF)	4.3	8.2	4.0	1.3	1.1
19.9(PF)	4.4	11.4	5.0	1.4	1.1

* S = notochord straight, F = notochord undergoing flexion, PF = notochord flexed.

2, 3). Relative eye diameter also shows a regular decrease with development, with the earliest stages (3.1–4.9 mm) having a mean of about 10% SL and larvae at or near metamorphosis (16.5–19.9 mm) with a mean of 7.1% SL. Eye diameter of juveniles and adults is 6.6–8.4% SL (Tables 2, 3). Table 3 shows relative upper jaw length expressed as a percentage of head length and SL. This measurement is usually expressed as a percentage of head length. Larvae tend to show a decrease in relative upper jaw length (% HL), although much variation is present. Larvae 3.1–7.7 mm have upper jaw lengths averaging about 30% HL. Middle and late larval stages show a more regular decrease in this ratio, with larvae at or near metamorphosis (16.5–19.9 mm) having a mean value of 25.2% HL. Juveniles and adults have upper jaw lengths of 18.9–25.6% HL (Tables 2, 3). Calculated regression lines of head length and eye diameter on SL and upper jaw length on head length were com-

Table 3. Proportional measurements of larval, juvenile, and adult *Engyophrys senta* by size class

Larvae Size Class (SL)	Head Length (%SL)			Body Depth (%SL)			Preanus Length (%SL)		
	$\overline{X}$	Range	N	$\overline{X}$	Range	N	$\overline{X}$	Range	N
3.0–3.9 mm	33.0	27.3–38.7	2	54.9	45.4–64.5	2	61.3	48.5–74.2	2
4.0	29.1	24.4–31.1	6	54.3	44.4–60.9	6	48.0	40.0–50.0	6
5.0	27.2	25.9–28.0	8	56.2	48.1–64.0	8	44.7	40.7–52.7	8
6.0	27.3	25.0–31.2	11	60.1	48.5–69.2	11	41.7	36.9–46.8	11
7.0	26.4	22.9–29.2	11	62.5	54.3–69.4	11	37.6	28.6–45.9	11
8.0	26.4	23.7–28.6	8	63.8	55.7–76.2	8	37.4	35.2–42.5	8
9.0	25.2	23.9–26.7	4	65.6	63.0–68.9	4	34.9	32.7–38.9	4
10.0	24.1	23.1–24.8	5	64.9	59.0–69.8	5	29.4	27.8–31.4	5
11.0	23.9	22.9–24.8	4	65.0	61.9–66.7	4	27.8	23.9–31.3	4
12.0	23.2	21.9–24.4	9	62.3	58.6–64.3	9	27.6	22.3–32.6	9
15.0	22.0	20.6–22.9	4	56.7	54.9–58.1	4	25.6	24.8–27.1	4
16.0	–	19.4	1	–	55.8	1	–	19.4	1
18.0	–	21.7	1	–	51.9	1	–	22.2	1
19.0	–	22.1	1	–	57.3	1	–	25.1	1
19.6*	–	21.9	1	–	41.8	1	–	20.4	1
Juveniles and Adults Size Class (SL)									
35.0–39.9 mm	–	22.0	1	–	41.4	1	–	23.3	1
45.0	–	24.0	1	–	42.7	1	–	31.6	1
50.0	23.3	22.2–24.0	4	39.0	37.0–41.3	4	23.6	21.4–24.8	4
55.0	22.2	20.6–23.7	6	38.8	35.8–41.1	6	22.4	20.2–23.9	6
60.0	22.2	21.1–23.4	8	40.0	37.0–42.7	7	22.5	20.5–25.4	8
65.0	22.0	21.7–22.3	4	38.5	34.8–41.6	4	21.2	19.1–23.6	4
70.0	24.4	22.4–26.5	2	45.0	40.7–49.4	2	21.4	20.9–21.9	2
75.0	20.9	20.6–21.3	2	37.9	37.2–38.7	2	–	20.1	1
80.0	–	20.9	1	–	39.3	1	–	21.4	1
85.0	–	21.2	1	–	38.5	1	–	22.2	1

Size Class (SL)	Eye Diameter (%SL)			Upper Jaw Length (%SL)			Upper Jaw Length (%HL)		
	$\overline{X}$	Range	N	$\overline{X}$	Range	N	$\overline{X}$	Range	N
3.09–3.9 mm	11.0	9.1–12.9	2	–	12.9	1	–	33.3	1
4.0	9.7	8.9–10.9	6	8.8	8.2–9.3	4	29.2	26.7–30.8	4
5.0	8.8	7.7–9.3	8	8.1	7.3–9.1	7	29.8	26.7–33.3	7
6.0	9.6	8.8–11.5	11	7.7	7.3–8.2	11	28.4	25.0–31.2	11
7.0	9.0	8.1–10.7	11	8.1	7.8–8.6	9	30.6	28.6–35.3	9
8.0	9.5	8.5–10.7	8	7.2	6.8–7.5	6	27.8	26.1–31.6	6
9.0	8.4	7.8–9.8	4	7.3	7.1–7.6	2	30.5	29.2–31.8	2
10.0	8.5	7.6–9.7	5	6.7	6.5–6.8	5	27.6	26.9–28.0	5
11.0	7.9	6.9–8.5	4	6.2	5.9–6.8	3	26.2	24.1–28.6	3
12.0	7.7	7.0–8.3	9	6.0	5.5–6.5	7	26.0	23.3–28.6	7
15.0	7.4	7.0–7.8	4	5.8	5.7–5.9	4	26.3	25.0–28.1	4
16.0	–	7.9	1	–	5.4	1	–	28.1	1
18.0	–	6.9	1	–	4.8	1	–	22.0	1

Table 3.   (Continued)

Size Class (SL)	Eye Diameter (%SL)			Upper Jaw Length (%SL)			Upper Jaw Length (%HL)		
	X̄	Range	N	X̄	Range	N	X̄	Range	N
19.0	–	7.0	1	–	5.6	1	–	25.0	1
19.6*	–	6.6	1	–	5.5	1	–	25.6	1
35.0–39.9	–	7.3	1	–	5.0	1	–	22.6	1
45.0	–	8.4	1	–	6.2	1	–	25.4	1
50.0	7.0	6.6–7.7	3	4.9	4.6–5.3	4	21.2	19.8–22.9	4
55.0	7.4	6.6–7.9	6	4.8	4.5–5.0	6	21.3	19.7–23.1	6
60.0	7.0	6.3–8.1	7	5.0	4.5–5.4	8	22.4	20.3–25.6	8
65.0	6.8	6.7–7.1	4	4.6	4.4–4.8	3	21.0	20.3–21.6	3
70.0	7.4	7.2–7.6	2	5.0	5.0	2	20.5	18.9–22.2	2
75.0	6.7	6.6–6.9	2	–	4.5	1	–	21.0	1
80.0	–	7.2	1	–	4.8	1	–	23.3	1
85.0	–	7.1	1	–	–	–	–	–	–

* Larva in metamorphosis.

pared between larvae and juveniles and adults. These lines differ significantly in elevation but not slope. Slopes for upper jaw length on SL are significantly different between the two groups (Table 4).

Abdominal region.—Larvae are highly compressed and deep bodied, with most of the great depth due to the distended abdomen (Figs. 1–6). The anteroventral area of the abdomen is bordered by spine-bearing basipterygia. Basipterygial spines are lost during metamorphosis. Relative body depth shows a mean of 54.9% SL in the earliest stages (3.1–3.3 mm), an increase to about 65% SL in 9–12-mm larvae, and a reduction to about 55% SL just prior to metamorphosis. During metamorphosis a marked reduction in depth

Table 4.   Statistics for regression analyses of transformed morphometric data for larvae, juvenile, and adult *Engyophrys senta*

X	Y	N	ln X̄	ln Ȳ	$\sum x^2$	$\sum y^2$	$\sum xy$	b	a	r	$100r^2$
Larvae											
lnSL	lnHL	76	2.11	0.75	13.1010	8.2636	10.2233	0.7803	0.4070	0.9826	96.55
lnSL	lnBD	76	2.11	1.60	13.1010	15.0591	13.6035	1.0384	0.5532	0.9685	93.80
lnSL	lnPAL	76	2.11	1.07	13.1010	3.4047	5.7438	0.4384	1.1551	0.8600	73.96
lnSL	lnED	76	2.11	-0.34	13.1010	8.6087	10.2352	0.7812	0.1378	0.9637	92.87
lnSL	lnUJL	63	2.13	-0.50	10.6234	4.3567	6.5867	0.6200	0.1618	0.9682	93.74
lnHL	lnUJL	63	0.77	-0.50	6.1881	4.3567	5.0113	0.8098	0.3253	0.9651	93.14
Juveniles and adults											
lnSL	lnHL	30	4.13	2.63	0.8388	0.7417	0.7474	0.8909	0.3507	0.9472	89.72
lnSL	lnBD	29	4.13	3.20	0.8386	0.9198	0.8155	0.9728	0.4431	0.9289	86.29
lnSL	lnPAL	29	4.12	2.63	0.7736	0.5723	0.5448	0.7041	0.7607	0.8187	67.03
lnSL	lnED	28	4.13	1.49	0.8151	0.7524	0.7137	0.8759	0.1188	0.9115	83.08
lnSL	lnUJL	27	4.10	1.08	0.6266	0.5582	0.5200	0.8297	0.9835	0.8792	77.30
lnHL	lnUJL	27	2.61	1.08	0.6061	0.5582	0.5125	0.8456	0.3253	0.8812	77.65

X = independent variable.
Y = dependent variable.
N = number of specimens examined.
X̄ = mean value of X.
Ȳ = mean value of Y.
$\sum x^2$ = sum of squares of X.

$\sum y^2$ = sum of squares of Y.
$\sum xy$ = sum of products.
b = slope.
a = Y intercept.
r = correlation coefficient.
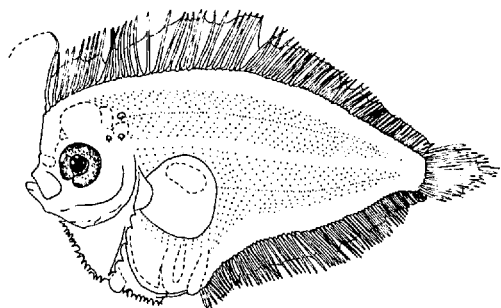$100r^2$ = percent of variation in Y attributable to variation in X.

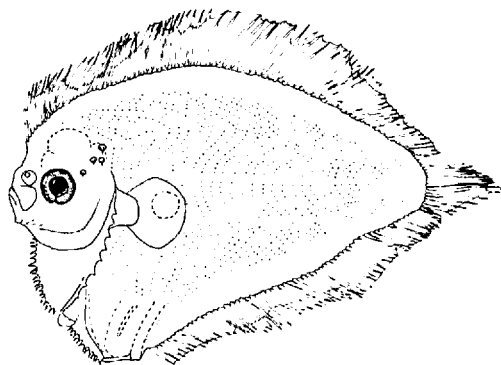Figure 3. *Engyophrys senta* larva 6.5-mm SL.

Figure 4.   *Engyophrys senta* larva 9.8-mm SL.

occurs; the metamorphic larva has a depth of 41.8% SL (Fig. 7). Body depth of juveniles and adults has a range of 34.8–49.4% SL (Tables 2, 3). Regression lines for body depth on SL could not be compared between larvae and juveniles and adults due to inequality of variances (Table 4).

In early stages the last section of the alimentary tract is vertical (Figs. 1–3). As development proceeds the anus moves anteriorly while the anterior portion of the anal fin moves below the abdominal cavity. The last section of the alimentary tract assumes an oblique anterior angle and the abdominal cavity becomes constricted (Figs. 4–6). At metamorphosis the anus is near the posterior processes of the basipterygia (Fig. 7). Anterior migration of the anus and constriction of the abdominal cavity account for the marked reduction in relative body depth. Anterior migration of the anus is reflected in relative preanus length, the smallest larvae (3.1–4.9 mm) showing a mean value of 51.4% SL and larvae at or near metamorphosis (16.5–19.9 mm) having a mean of 21.8% SL. Juveniles and adults have a range of 19.1–36.6% SL (Tables 2, 3). Slope values for preanus length regressed on SL are not significantly different between larvae and juveniles and adults. Elevations of these lines differ significantly (Table 4).

A swimbladder is present in the smallest specimen examined and throughout most of the larval series (Figs. 1–4). The presence or absence of the swimbladder in larvae over 12 mm could not be determined, however, because of the increase in thickness of the abdominal hypaxial musculature.

Caudal region.—In the earliest stages the caudal region is narrow and the ventral body margin is concave directly posterior to the anus (Figs. 1–3). With further development the anterior migration of the anus and growth of hypaxial musculature produces an increase in depth behind the anus, causing the ventral body outline to approach the smooth convex curve characteristic of juveniles and adults (Figs. 4–7).

Fin development

The fins develop the adult complement of rays in the following order: (1) caudal, (2) dorsal and anal, (3) pelvic, and (4) pectoral. Osteological development of the caudal and pelvic fins is not complete until some time during or after metamorphosis. Some fusions of caudal elements do not occur until after the adult complement of rays forms. Although the full complement of pelvic fin rays and the adult location of pelvic fin bases are developed prior to metamorphosis, a great deal of change occurs in shape and mass of basipterygia during metamorphosis. Dorsal and anal fins are apparently the only fins essentially fully developed in larvae. Pectoral fins of all larvae are of the "larval" type with a fleshy base and a distal fan-shaped membrane. Development of the rayed pectoral
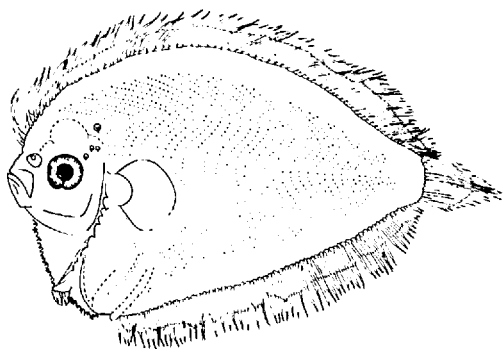
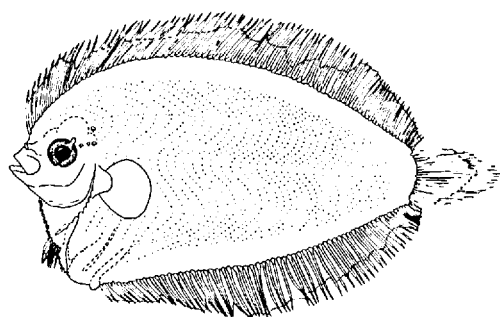Figure 5. *Engyophrys senta* larva 12.3-mm SL.

Figure 6. *Engyophrys senta* larva 18.9-mm SL.

fin and most of the girdle occurs during metamorphosis. Such "larval" pectorals, however, are probably the main locomotor elements in small larvae.

Dorsal fin.—Development of cartilaginous pterygiophores proceeds anterior to posterior. Most are present, with the exception of the last few, in the smallest specimens (4.6–7.7 mm). All pterygiophores are developed but unossified in an 8.4-mm specimen. Pterygiophores 3–9 are ossified in a 15.3-mm specimen, and all are ossified at 19.9 mm. One 16.5-mm larva has no ossified pterygiophores. The first dorsal pterygiophore is bifurcated and supports the first two dorsal rays. As metamorphosis is approached the first eight or nine pterygiophores come to rest on the cranium. Posterior to the pterygiophores supported by the cranium, one pterygiophore directly precedes the neural spine of the second precaudal vertebra. The remaining pterygiophores are disposed interneurally singly or in groups of two to five. No pterygiophores are located between the last two neural spines.

Dorsal fin rays develop anterior to posterior except for the first, which is one of the last to develop. It appears as a very small element on the anterior ramus of the first pterygiophore in one 6.5 mm-specimen, but is not developed on any other specimen smaller than 8.4 mm. In small larvae the second dorsal ray is noticeably elongate relative to the more posterior rays (66% SL in a

5.5-mm specimen; Figs. 1–3). By about 8.5 mm the second dorsal ray is approximately the same length as the other rays (Figs. 4–7).

Dorsal fin rays were unclear and difficult to count in many specimens smaller than 7.0 mm. Rapid development of dorsal fin rays appears to take place between 3.1 and 4.5 mm (Table 5). Counts begin to fall into the adult range (71–85) at 6.4 mm; all larvae 7.0 mm and larger have counts within this range. However, two larvae (7.0 and 7.5 mm) with counts within the adult range have not yet developed the first dorsal ray. Only two cleared and stained larvae (15.3 and 19.9 mm) have ossified dorsal rays; the 15.3-mm specimen has all but the last nine rays ossified; the 19.9-mm specimen has all rays ossified. None of the dorsal rays of a 16.5-mm specimen took up stain.

Anal fin.—In the earliest stages, the ventral outline of the body, formed by the base of the anal fin, is deeply concave just posterior to the abdominal cavity (Figs. 1–3). As development proceeds the anal fin moves ventral to the abdominal cavity and the ventral body margin approaches a smooth convex curve (Figs. 4–7). In association with the anterior migration of the anal fin, the enlarged first anal pterygiophore assumes a vertical or slight posterior angle in small larvae and becomes curved anteriorly as development proceeds, following the posterior curve of the abdominal cavity. The first anal pterygiophore is bifurcated distally, supporting the first two anal rays, and rests in a
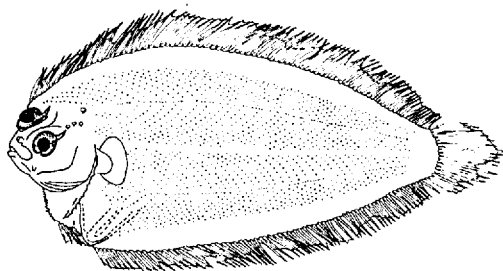
Figure 7. *Engyophrys senta* larva 19.6-mm SL.

deep groove on the anterior surface of the enlarged first hemal spine. Pterygiophores 2–7 articulate with the ventral surface of the first pterygiophore. The eighth directly precedes the second hemal spine, while the rest are disposed interhemally singly or in groups of two to five. No pterygiophores are located between the last two hemal spines. The anteriormost pterygiophore begins to take up stain at 7.7 mm, the remainder do not show signs of ossification until 15.3 mm.

Anal fin rays were unclear and difficult to count in many specimens smaller than 7.4 mm. Rapid development of fin rays takes place between 3.1 and 4.5 mm (Table 5). Counts begin to fall into the adult range (59–69) at 6.3 mm; all larvae 7.0 mm and larger have counts within this range. Only two larvae (15.3 and 19.9 mm) have ossified anal rays. None of the anal rays of a 16.5-mm specimen took up stain. Full development of the anal fin appears coincident with that of the dorsal fin.

Caudal fin.—Development of the caudal fin was interpreted in light of recent studies and models of teleostean (Gosline, 1961a, 1961b, 1965; Greenwood et al. 1966; Patterson, 1968; Monod, 1968; Rosen and Patterson, 1969; Rosen, 1973) and pleuronectiform (Monod, 1968; Amaoka, 1969) evolution. The adult caudal fin complex is characterized typically as follows (Fig. 8G, H): a terminal half-centrum (fusion and/or loss of two ural centra and the first preural centrum); a second preural centrum; a broad hemal spine from the second preural centrum

supporting one caudal ray; an autogenous, proximally free parhypural supporting three caudal rays; an autogenous, broad ventral hypural element (fusion of hypurals 1 and 2) supporting four caudal rays and articulating with the ventral surface of the terminal half-centrum by means of a flattened articulatory process; a broad dorsal hypural element (fusion of hypurals 3 and 4) fused with the tip of the terminal half-centrum and supporting five caudal rays; an autogenous, proximally free second dorsal element (fusion of an epural and hypural 5) supporting three caudal rays; and a broad neural spine from the second preural centrum supporting one caudal ray. Although 82.5% (33) of the juveniles and adults examined have the typical caudal fin formula of 1-3-4-5-3-1, variation is present in the arrangement of rays on the caudal elements and in the number of caudal rays present. Most of this variation is due to differences in placement of one or two rays. Three specimens, however, have only 16 rays. Variation is also present in the morphology of neural and hemal spines of the second preural centrum; approximately 13% of the juveniles and adults examined have neural and/or hemal spines split nearly or completely to the base (Fig. 8H). About 46% of the juveniles and adults have scissures between the rays along the distal margins of the parhypural and the two hypural elements (Fig. 8H). No scissures were seen on the distal margin of the dorsal autogenous element.

Caudal ray counts for larvae are presented in Table 5 and states of notochord flexion are indicated in Table 2. The smallest cleared and stained larva examined (4.6 mm), which has the notochord slightly flexed, has the parhypural, the two compound hypural elements, the epural, and the neural and hemal spines of the second preural centrum (Fig. 8A). All elements are unossified. Six unossified rays are formed. Four of these are supported by the ventral hypural element and two by the dorsal hypural element. A small axial caudal lobe is still present.

Table 5. Meristic and spine counts for larvae of *Engyophrys senta*

SL (mm)	Dorsal Fin Rays	Anal Fin Rays	Caudal Rays	Pelvic Fin Rays*		Otic Spines		Urohyal Spines	Cleithral Spines		Basipterygial Spines
				Left	Right	Left	Right		Left	Right	
3.1	–	–	–	0	0	3	3	10	4	4	3
3.3	5±	0	0	0	0	3	3	7	3	3	0
4.0	–	36	0	0	0	3	3	13	5	5	6
4.3	–	–	–	–	–	3	3	10	–	5	6
4.5	–	55±	–	–	–	3	3	13	–	–	8
4.5	52±	37±	6	0	0	3	3	11	6	6	8
4.6	64–65	44	6	0	0	3	3	17	4	4	10
4.9	–	48±	–	0	0	3	3	–	5	5	–
5.0	–	56	12	0	0	3	3	17	5	6	10
5.2	49	–	0	0	0	3	3	11	4	5	4
5.4	–	–	5	0	0	3	3	17	6	5	11
5.4	62±	51±	7	0	0	3	3	14	4	4	10
5.5	–	–	–	–	–	3	3	16	5	5	9
5.5	60	57	12	0	0	3	3	13	5	6	11
5.5	65	51	6	0	0	3	3	14	4	4	7
5.9	66±	–	12	0	0	3	3	17	6	7	6
6.1	–	–	13	0	0	3	3	16	6	7	11
6.2	–	–	15	0	0	4	4	18	7	7	13
6.3	–	60	15	0	0	3	3	17	5	6	14
6.4	69±	51±	16	0	0	4	4	19	7	7	15
6.4	77	64	17	0	0	3	3	16	5	6	14
6.5	59±	–	–	0	0	3	3	19	6	6	12
6.5	77	66	17	0	0	3	4	17	5	6	10
6.5	79	62	15	3±	–	4	3	20	7	7	13
6.6	77	64	17	0	0	4	4	19	6	7	12
6.7	70	59	16	0	0	4	3	18	6	5	9
6.8	68±	56	16	0	0	3	4	17	7	7	11
7.0	74	60	16	0	0	3	4	21	–	6	7
7.0	76	62	17	0	0	4	3	21	7	7	10
7.2	76	59±	16	P	P	4	4	17	7	7	14
7.2	–	65	17	P	P	4	4	20	7	9	–
7.2	78	65	17	P	P	4	3	16	7	7	14
7.4	–	–	–	0	0	4	4	18	6	7	–
7.5	–	–	–	–	–	4	4	20	7	7	16
7.5	–	60	–	0	0	4	4	18	7	6	–
7.6	77	61	17	5±	5±	4	4	21	7	7	–
7.7	–	–	17	P	P	4	4	23	9	8	15
7.7	76	66	17	4	5±	4	3	17	8	8	17
8.0	76	–	–	P	P	4	4	19	8	7	–
8.0	78	62	17	P	P	4	4	21	7	7	12
8.1	76	60	–	P	P	4	4	21	8	–	13
8.2	80	66	17	P	P	4	4	19	6	5	–
8.4	75	63	17	P	P	4	4	22	8	8	–
8.4	76	65	17	P	P	4	4	23	8	9	17
8.4	80	64	17	4	2±	4	4	18	6	7	15
8.8	79	63	17	P	P	4	4	19	8	8	13
9.0	76	62	17	P	P	4	4	21	8	8	14
9.0	78	63	–	–	–	4	4	22	9	8	–
9.2	78	64	17	P	P	4	4	21	9	9	14
9.8	77	63	17	P	P	4	4	23	8	8	14
10.3	77	61	17	P	P	4	4	21	9	8	14
10.5	75	63	17	4	4	4	4	24	9	8	13
10.5	82	66	17	4	4	4	4	19	7	7	14

Table 5. (Continued)

SL (mm)	Dorsal Fin Rays	Anal Fin Rays	Caudal Rays	Pelvic Fin Rays*		Otic Spines		Urohyal Spines	Cleithral Spines		Basipterygial Spines
				Left	Right	Left	Right		Left	Right	
10.6	84	69	17	–	–	4	4	24	8	8	–
10.8	80	62	17	6	–	4	4	21	8	10	14
11.5	78	65	17	5	5	4	4	24	9	9	14
11.7	76	60	17	–	–	4	4	22	9	9	–
11.8	79	63	17	5	5	4	4	20	8	7	12
11.8	80	64	17	–	–	4	4	19	10	10	11
12.1	76	60	17	–	–	4	4	24	9	8	14
12.2	79	64	17	–	–	4	4	22	9	9	13
12.3	78	63	17	–	6	4	4	20	9	10	14
12.4	80	64	17	–	–	4	4	24	10	10	–
12.8	78	65	17	–	–	4	4	25	11	11	–
12.8	77	64	17	5	5	4	4	24	9	9	14
12.8	80	64	17	6	6	4	4	23	9	9	16
12.9	83	67	15	–	–	4	4	22	11	12	–
12.9	80	–	–	–	–	4	4	22	8	8	16
15.3	80	66	17	6	6	4	4	26	11	11	–
15.5	80	65	16	6	6	4	4	21	10	10	14
15.6	76	63	17	6	6	4	4	27	10	11	14
15.7	77	63	17	6	6	4	4	21	11	11	–
16.5	76	61	17	6	6	4	4	–	11	11	18
18.9	81	65	17	6	6	4	4	22	8	9	16
19.6	82	67	18	6	6	4	4	15	9	9	11
19.9	78	63	17	5	5	4	4	21	12	12	14

* P = pelvic rays present but not countable.

Notochord flexion takes place between 4.5 and 5.5 mm. All larvae over 5.5 mm have completed notochord flexion and have vertical caudal plate margins (Fig. 8B; Table 2). During notochord flexion the upper hypural element increases in length (dorsoventrally) relatively rapidly as the notochord reaches vertical orientation. The number of caudal rays increases to about 12 (Table 5). Rays develop dorsally and ventrally from the center of the hypural area. Three rays are supported by the parhypural, four by the ventral hypural element, and five by the dorsal hypural element.

At 6.5 mm the fifth hypural begins to appear as a small triangular cartilaginous structure at the tip of the notochord ventral to the spinal cord (Fig. 8C, D). By about 8 mm the fifth hypural and the epural have fused (Fig. 8E). In a 7.7-mm specimen fusion of these elements has occurred but a symphysial line is still visible. In addition, at this stage of development (6.5–8.0 mm), the terminal half-centrum begins to ossify (first seen in a 7.7-mm specimen), the full complement of rays (unstained) is formed, and the parhypural and the dorsalmost compound element become free proximally (Table 5). Spaces begin to appear between caudal elements as they approach their adult configuration, and an articulatory process begins to form on the proximal end of the ventral hy-

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Figure 8. Caudal fin structure of *Engyophrys senta* larvae (A–F) and juveniles and adults (G–H). Standard lengths of specimens: A, 4.6 mm; B, 5.5 mm; C, 7.0 mm; D, 7.6 mm; E, 7.7 mm; F, 15.3 mm; G, 45.7 mm; H, 82.4 mm. Abbreviations: al = axial lobe, ep = epural, hs = hemal spines, hy 1–5 = hypurals, nc = notochord, ns = neural spine, ph = parhypural, pu 1–3 = preural centra, u 1 and 2 = ural centra.
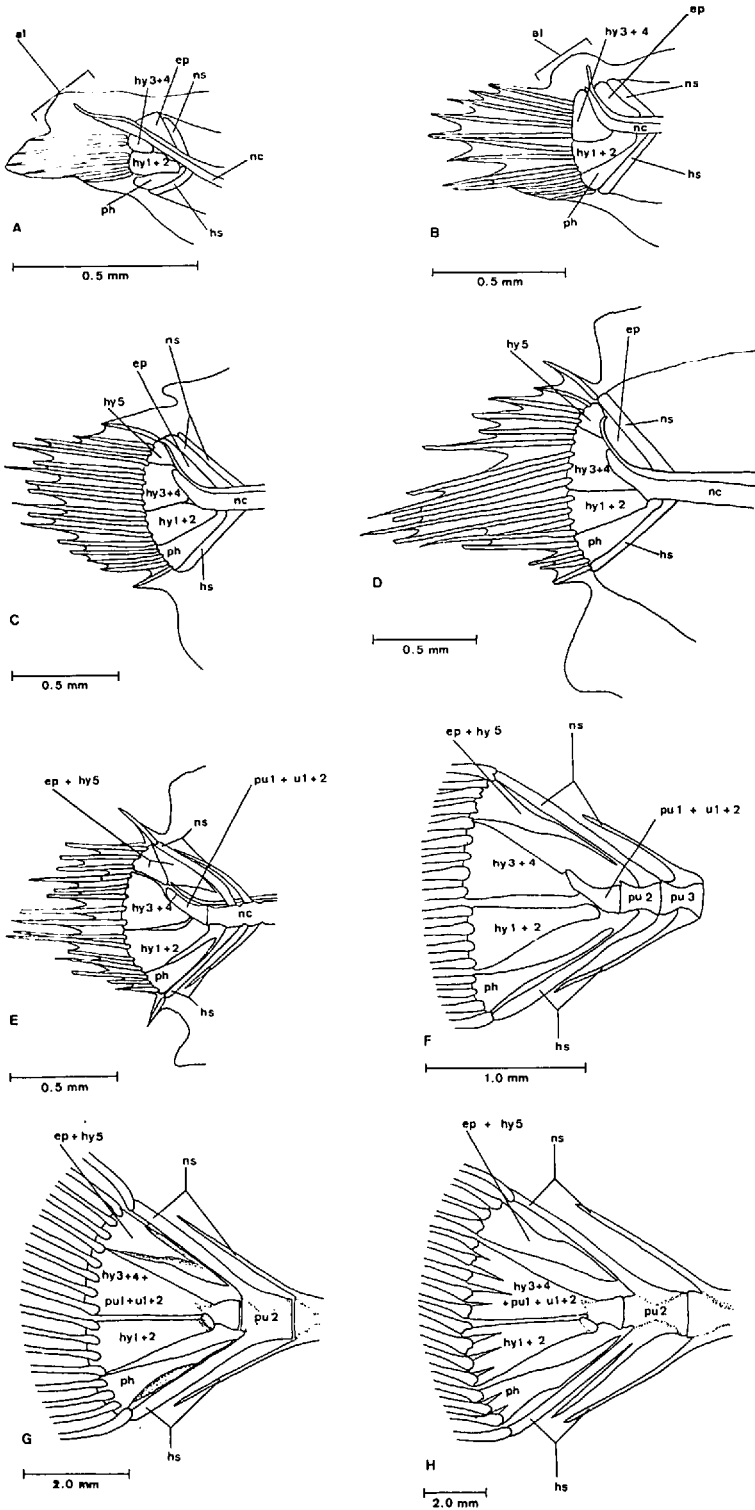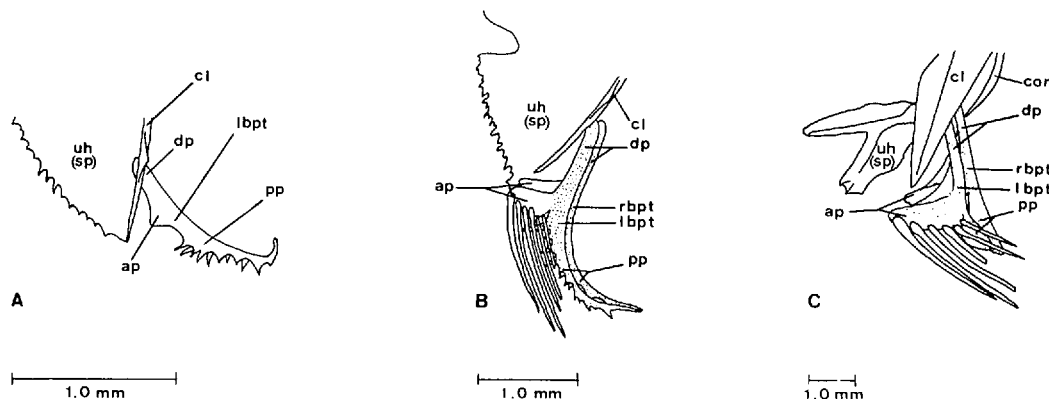
Figure 9. Pelvic fin structure of *Engyophrys senta* larvae (A and B) and juveniles (C). Fin rays of right pelvic fins have been omitted. Stippling indicates areas of ossification of the basipterygia. Standard lengths of specimens: A, 5.4 mm; B, 16.5 mm; C, 38.7 mm. Abbreviations: ap = anterior basipterygial process, cl = cleithrum, cor = coracoid, dp = dorsal basipterygial process, lbpt = left basipterygium, pp = posterior basipterygial process, rbpt = right basipterygium, uh (sp) = urohyal (sciatic portion).

pural element at the point of articulation with the ventral surface of the terminal half-centrum. Three rays develop on the dorsal-most compound element. It appears that four rays develop on the parhypural by about 7 mm, but the ventralmost of these shifts to the hemal spine as development proceeds. The dorsalmost ray, associated with the neural spine, is the last to develop. One 7.0 mm larva has two neural spines (unossified) associated with the area of the notochord where the second preural centrum develops (Fig. 8C).

Between 8 and 10 mm the rays and caudal elements become ossified, the neural and hemal spines becoming broad relative to the more anterior members of the series (Fig. 8F). The parhypural and the dorsalmost compound element become pointed at their proximal ends. In a 10.3-mm specimen and all larger ones, the shapes and arrangement of the caudal elements are those of juveniles and adults, with the exception that the dorsal hypural element has not fused with the terminal half-centrum. This fusion occurs at metamorphosis or shortly thereafter as it has not occurred in a 19.9-mm specimen. None of the larvae show any indications of de-

veloping scissures on the distal margins of the parhypural or hypural elements.

Amaoka (1969) presented a detailed analysis of the evolution of the caudal fin complex in pleuronectiform fishes. The interpretation of the present study, with certain differences in terminology, generally follows that of Amaoka and to some extent Monod's (1968) "hypothesis A." Amaoka interpreted the dorsalmost compound element in bothids as being formed by fusion of a uroneural, an epural, and the fifth hypural. In the present study I have interpreted this element as being a fusion of an epural and the fifth hypural only, as there is no evidence in the larval development of *E. senta* that indicates the presence of a uroneural in this element. The caudal skeleton of *E. senta* corresponds to "type 4" as discussed by Amaoka, an advanced type characterized by a high level of vertical symmetry developed by losses and fusions of elements.

Pectoral fins and girdle.—Cleithra are ossified in the smallest cleared and stained specimen (4.6 mm). The most outstanding feature of the developing pectoral girdle is the presence of pungent spines on lateral surfaces

of the cleithra (Figs. 1–7). Cleithral spines increase in number from 3–6 in 3.1–5.0-mm larvae to 8–12 in 15.3–19.9-mm larvae (Table 5). Spines are greatly reduced in size in the one metamorphic larva (19.6 mm; Fig. 7), and are completely lost during metamorphosis as the cleithra become more massive. Two pairs of postcleithra are present in juveniles and adults. They are closely associated during development and are not distinguishable as separate ossified elements in all specimens where they are developed. Ossified postcleithra first appear in an 8.4-mm specimen but are not consistently present in all larger larvae. Supracleithra are first visible as separate ossified elements in a 7.7-mm specimen. Endochondral elements (scapulas, coracoids, and actinosts) are formed during or shortly after metamorphosis.

The pectoral fins of all larvae examined (3.1–19.0 mm) consist of a large fleshy base bearing a fan-shaped membrane distally (Figs. 1–7). In the larva undergoing metamorphosis (19.6 mm; Fig. 7) the size of these "larval" pectorals (relative to SL) is reduced. Pectoral ray formation occurs during or shortly after metamorphosis, since it is not evident in any of the larvae.

Pelvic fins and girdle.—The pelvic fin complex of juveniles and adults can be characterized as follows (Fig. 9C): (1) Basipterygia have inverted "Y" shapes, each with an anterior, posterior, and dorsal process. (2) Anteroventral areas of the anterior processes remain cartilaginous and support the fin rays. (3) The first ray of the left pelvic fin is located slightly anterior to the ventral tip of the cleithrum; the first ray of the right fin is at the same transverse level as the second ray of the left fin. (4) The left fin base is on the midventral line, the right is dorsal to this line. (5) This asymmetry (3 and 4) is reflected in the basipterygia with the right basipterygium being dorsal and posterior to the left, the ventromedial surface of the posterior process of the right basipterygium articulating with the dorsomedial surface of the posterior process of the left basipteryg-

ium. (6) Dorsal processes of the basipterygia articulate with medial surfaces of the cleithra.

The three basipterygial processes (anterior, dorsal, and posterior) are distinguishable in the smallest specimen examined (3.1 mm). In early stages basipterygia appear as curved rods lying in a nearly horizontal position, and extending from the cleithra (dorsal process) to below the abdominal cavity (posterior process). Anterior processes appear as small projections on anteroventral surfaces of the basipterygia. A conspicuous feature of the developing pelvic girdle is the presence of spines on ventral surfaces of the posterior basipterygial processes. These spines are nearly or entirely confined to the posterior process of the left basipterygium. As development proceeds, anterior processes become larger, basipterygia become elevated anteriorly, and posterior processes become attenuated and curve along the anteroventral margin of the abdominal cavity below the ventral tip of the liver (Fig. 9A, B). As a result of enlargement of anterior processes and elevation of basipterygia anteriorly, anterior processes approach the ventral tips of the cleithra.

Asymmetry of basipterygial placement and morphology are possible. Most adult asymmetry is that of placement; the basipterygia are similar morphologically (Fig. 9C). However, in larval development morphological asymmetry is present in that spines are nearly or entirely confined to the posterior process of the left basipterygium. This asymmetry is present in all larvae examined except one 3.3-mm specimen which lacks basipterygial spines. Spines increase in number until about 6–7 mm (Table 5). In the larva undergoing metamorphosis (19.6 mm), spines are still present but are greatly reduced in size. At some time during metamorphosis, basipterygial spines are lost as posterior processes become more massive and less attenuated. Asymmetry of placement first appears in larvae of about 10 mm. The left basipterygium begins to assume a position more anterior and ventral to the

right, and the right posterior basipterygial process approaches the dorsomedial surface of the left posterior basipterygial process (Fig. 9B). An important result of this movement is location of the anterior tip of the left anterior basipterygial process (insertion of left fin base) slightly anterior to the ventral tip of the cleithrum, and location of the ventral margin of this process along the midventral line of the thoracic region, i.e., the adult condition. Basipterygia begin to take up stain in dorsal and ventral processes at about 10 mm.

Fin buds begin to appear at about 4.5 mm. Fin rays can be seen beginning to develop in 6.5–10.3-mm larvae, but are not countable with certainty until 10.5 mm (Table 5). The anterior four rays are the first to develop in both fins. One 12.8-mm specimen and all specimens 15.3 mm and larger have the adult complement of fin rays (six) in both fins. An aberrant 19.9-mm larva has five rays in both fins. In larvae with the adult complement of pelvic rays, basipterygia have become positioned so that the first ray of the right fin is at the same transverse level as the second ray of the left fin. Only two cleared and stained larvae (15.3 and 19.9 mm) have ossified pelvic rays. None of the pelvic rays of a 16.5-mm specimen took up stain.

Development of the vertebral column

Many adult vertebral characters do not develop prior to metamorphosis. Important characters apparent in larvae are the lack of a neural spine on the first precaudal vertebra, development of parapophyses on precaudal vertebrae 5–10, those on precaudal vertebrae 6–10 fusing ventrally to form hemapophyses, and the concave (groove-like) anterior surface of the first hemal spine supporting the first anal pterygiophore.

Notochord flexion occurs between 4.5 and 5.5 mm (Table 2). Developing centra, most neural and hemal arches and spines, and parapophyses on precaudal vertebrae 5–10 are visible but unstained in the smallest cleared and stained larva (4.6 mm). In a 7.7-mm specimen most of the neural and

hemal arches and spines and the terminal half-centrum have started to ossify. The first hemal spine is longer and more stout than the others and is always in contact with the first anal pterygiophore throughout development, the concave (groove-like) anterior surface becoming apparent at about 7 mm. Centra are cylindrical in shape during early stages of development, becoming noticeably spool shaped at about 10 mm. Dorsal and ventral surfaces of centra are the first areas to become ossified, first taking up stain in a 10.3-mm specimen (except terminal half-centrum). Parapophyses of precaudal vertebrae 6–10 appear to close to form hemapophyses at about 8 mm.

Development of the branchiocranium

Only development of the hyoid and oromandibular regions were studied.

Hyoid region.—Essential features of most of the hyoid region of adult bothids were given by McAllister (1968). In *E. senta* 3½ branchiostegals insert on the epihyal and 3½ on the ceratohyal, i.e., one straddles the epihyal-ceratohyal joint. The sciatic portion of the urohyal (see Amaoka, 1969) of juveniles and adults bears 2–3 low spines (Fig. 9C).

Most elements of the hyoid region, except the opercular elements (operculars, suboperculars, and interoperculars) and the preoperculars, are present in the smallest cleared and stained larva (4.6 mm). An outstanding feature of the hyoid region is the presence of spines on the anteroventral margin of the urohyal (Fig. 9A, B). Urohyal spines increase in number from 7–17 in 3.1–5.0-mm larvae to 21–27 in 15.3–19.9-mm larvae (Table 5). An exception is the 19.6-mm metamorphic specimen in which the urohyal spines are markedly reduced in size and number (15) (Fig. 7). The urohyal begins to absorb stain at 5.0 mm. During metamorphosis the expansive sciatic portion of the urohyal becomes reduced in size relative to the remaining portions, and loses all spines except possibly the anteriormost 2–3 which

may form the low spines found in juveniles and adults (Fig. 9C).

Hyomandibulars, epihyals, and ceratohyals begin to ossify in 7–9-mm larvae. Interhyals, upper and lower hypohyals, and the basihyal first show ossification in a 15.3-mm specimen. Symplectics are ossified in only one specimen (19.9 mm), the largest examined. The anteriormost branchiostegal is the last to develop as it is not visible with certainty in some of the smaller larvae. Branchiostegals begin to ossify in 6–8-mm larvae, ossifying in a posterior to anterior sequence. Preoperculars and opercular elements appear to be the last elements of the hyoid region to develop. Preoperculars first appear as ossified elements at 15.3 mm, the operculars, suboperculars, and interoperculars appearing as partially ossified elements in a 16.5-mm specimen. This apparent late development of preopercular and opercular elements is in contrast to the early development of these structures in *Cyclopsetta fimbriata, Etropus microstomus*, and *Citharichthys arctifrons* (Gutherz, 1970; Richardson and Joseph, 1973).

Oromandibular region.—The sequence of ossification for elements of the oromandibular region is similar to that given for *Etropus microstomus* and *Citharichthys arctifrons* by Richardson and Joseph (1973). Meckel's cartilage is visible in all cleared and stained specimens (4.6–19.9 mm). No bones of this region show evidence of ossification before 7.7 mm. However, in all smaller larvae (4.6–7.6 mm) maxillaries and premaxillaries are distinct, and in two (7.5 and 7.6 mm) ectopterygoids can be distinguished. In a 7.6-mm larva dentaries and angulars are distinguishable as separate structures. All 4.6–7.6-mm larvae have 2–4 conical teeth on margins of each premaxillary and dentary, or areas where dentaries will develop.

Premaxillaries, maxillaries, dentaries, and angulars first show ossification in a 7.7-mm specimen. Retroarticulars, although difficult to see, are visible as distinct ossified structures in an 8.4-mm specimen. This specimen is also first to show ossification of the

ectopterygoids. Quadrates become distinct and ossified at about 8 mm. Endopterygoids are distinct at 7.7 mm and usually become ossified at about 10 mm, although in one 16.5-mm specimen they are still unossified. Autopalatines are distinct cartilaginous structures at about 15 mm, but apparently ossify during or shortly after metamorphosis. Metapterygoids are distinct (unossified) only in the largest specimen examined (19.9 mm). Larval teeth on premaxillaries and dentaries become slightly more numerous (3–9 on each) in the 7.7–19.9-mm size range.

Distribution of teeth in juvenile and adult *E. senta* is asymmetrical, almost entirely (or entirely) confined to the right premaxillary and dentary. Larvae examined in this study indicate that this asymmetry begins as metamorphosis is approached, the distribution of larval teeth remaining symmetrical until this time. Replacement teeth on medial surfaces of the right premaxillary and dentary first appear in a 16.5-mm larva. They are caniniform teeth angled dorsomedially on the premaxillary and ventromedially on the dentary. Replacement teeth are also present on a 19.9-mm premetamorphic and the 19.6-mm metamorphic specimen. During metamorphosis replacement teeth apparently rotate to positions on the dorsal margin of the dentary and ventral margin of the premaxillary. In the right dentary of the 19.9-mm specimen, replacement teeth can clearly be seen nearing the dorsal margin of this bone. The number of replacement teeth in the right premaxillary and dentary range from 13 to 16 on each. This approaches the range of visible teeth on these bones in juveniles and adults (14–26 one each; counts from five specimens). Apparently all larval teeth are lost (resorbed or shed) at or near metamorphosis.

Comments on the neurocranium

The neurocranium was not studied in detail. However, the otic region deserves comment, since the epiotics and autosphenotics of larvae bear prominent spines. All 3.1–

6.1-mm larvae have three spines on each epiotic (Figs. 1–3; Table 5). The dorsalmost of the epiotic spines is the largest and is frequently curved ventrad. Between 6.2 and 7.7 mm a fourth spine develops on each autosphenotic; all larvae 8.0 mm and larger bear four otic spines (Figs. 4–7; Table 5). As metamorphosis is approached, the spines become reduced in size and are lost during metamorphosis.

COMMENTS ON INTERMUSCULAR BONES IN FLATFISHES

Because most systematic studies of flatfishes have been limited to a few, mostly external, characters, the phylogeny of this group is still poorly known. Norman (1934) recognized three subfamilies within the Bothidae, the Bothinae, Paralichthyinae, and Scophthalminae. Hubbs (1945) and Hubbs and Hubbs (1945) have since recognized the Scophthalminae at the familial level, and shown that it is probably more closely related to the citharids than to the remaining bothids. Norman used morphology of the pelvic fins and caudal vertebrae as diagnostic characters to separate the Bothinae and Paralichthyinae: The Paralichthyinae usually have short-based pelvic fins, the exceptions being some genera in which the base of the ocular pelvic fin is slightly extended anteriorly; have both pelvic fins inserted behind the cleithra; have pelvic rays supported by the pelvic bones; and lack transverse apophyses on the caudal vertebrae. The Bothinae have a short-based pelvic fin on the blind side; an ocular pelvic fin base elongated anteriorly; pelvic rays of the ocular side supported by a cartilaginous plate extended anteriorly onto the urohyal; pelvic rays of the blind side supported by the pelvic bone; and transverse apophyses on the caudal vertebrae.

Amaoka (1969) reviewed the sinistral flounders of Japan using many osteological characters. Among Japanese species of Bothidae (*sensu* Norman, 1934), Amaoka's conclusions generally support Norman's subfamilial groupings (i.e., the Bothinae and Paralichthyinae). In fact, Amaoka inter-

preted the divergence between these two groups to be great enough to recognize them as families. An important difference between the groupings of Amaoka and Norman is that Amaoka showed the Indo-West Pacific genus *Taeniopsetta*, considered by Norman to be a paralichthyine, has its true affinities with Norman's Bothinae.

One of the diagnostic characters used by Amaoka (1969) to separate his Bothidae from his Paralichthyidae is the presence of five series of intermuscular bones in the Bothidae. The Paralichthyidae lack these intermuscular bones but have pleural and epipleural ribs, which are absent in the Bothidae. Amaoka presents detailed descriptions of the intermuscular bones. He has implied homologies of three of these series (epimerals, epicentrals, and hypomerals) with those of lower fishes (see Phillips, 1942). However, the homologies here may not be strict. The two remaining series he called "myorhabdoi." The bones in four of these series are highly branched (brush like); those of the epicentral series are often unbranched. Chabanaud (1940) claimed to have seen these bones in *Bothus podas* (Delaroche) (Bothidae), *Brachypleura novaezeelandiae* Günther (Citharidae), and *Samaris cristatus* Gray (Pleuronectidae). Later he states these bones are absent in *B. novaezeelandiae* (Chabanaud, 1949a). Intermuscular bones of *S. cristatus* were briefly described later by Chabanaud (1969) as being in two series. *S. cristatus* should be reexamined to determine the nature of these bones. Chabanaud's (1940) early description was clearly in reference to *Bothus podas*. Chabanaud (1949a, 1949b), like Amaoka, elevated Norman's (1934) Bothinae and Paralichthyinae to the familial level. His primary justification for this was the presence of intermuscular bones in Norman's Bothinae.

During the course of the present study, I found that juvenile and adult *Engyophrys senta* have five series of intermuscular bones. They were not present in any of the cleared and stained larvae examined. Their presence in *E. senta* prompted me to examine cleared

and stained specimens of all bothid (*sensu* Norman, 1934) genera from the western North Atlantic except *Chascanopsetta*, which was discussed by Amaoka (1969). In addition to *Engyophrys*, intermuscular bones are found in *Bothus*, *Trichopsetta*, and *Monolene*; Amaoka found them in *Chascanopsetta*. *Engyophrys*, *Trichopsetta*, and *Monolene* were considered by Norman to be paralichthyines. Intermuscular bones are absent and pleural and epipleural ribs are present in the remaining Paralichthyinae (i.e., *Paralichthys*, *Syacium*, *Etropus*, *Cyclopsetta*, *Ancylopsetta*, *Citharichthys*, and *Gastropsetta*).

Chabanaud (1949a) and Amaoka (1969) considered intermuscular bones in flatfishes an ancestral character. The presence of these bones was one of the main reasons they hypothesized a group lower than percoids as ancestral to pleuronectiforms. Considered as such, the presence of intermuscular bones should not be used to define taxa (Hennig, 1966; Mayr, 1969), i.e., the Bothidae *sensu stricto*. There are, however, several arguments against interpreting the presence of these bones as an ancestral character: (1) They are not found in the conservative families Psettodidae and Citharidae (Chabanaud, 1949a; Amaoka, 1969). (2) They are not found in percoids from which pleuronectiforms presumably arose. (3) Within the order Pleuronectiformes they are not widely distributed among the taxa (in this regard *S. cristatus* should be reexamined). (4) Due to the highly branched (brush-like) condition of bones in at least four of the series, they do not resemble intermuscular bones found in other fish groups (see Chabanaud, 1949b, Figs. 3–8; Amaoka, 1969, Figs. 120–122, 125). (5) Distribution of these bones is strongly symmetrical vertically. The dorsal- and ventralmost series, the "myorhabdoi" of Amaoka, apparently lack homologues in lower fishes. The vertical (dorsoventral) symmetry and the apparent lack of homologues for at least two of the series suggest that this group of fishes evolved these structures independently in conjunction with adaptive refinements of undulatory swimming and the trend toward secondary bilateral (dorsoventral) symmetry. It is not the purpose of this discussion to show that the presence of intermuscular bones in flatfishes is a derived character, but only to show that the possibility should be considered.

Several other observations are relevant to this discussion. I have found that *Engyophrys*, *Trichopsetta*, and *Monolene* have transverse apophyses on most of the caudal vertebrae; Amaoka (1969) found them in *Taeniopsetta*. Norman (1934) apparently failed to detect the presence of transverse apophyses on the caudal vertebrae in these genera since this is a character he used as diagnostic for his Bothinae. Although *Engyophrys*, *Trichopsetta*, *Monolene*, and *Taeniopsetta* (see Amaoka, 1969) do not have the greatly elongated left ventral fin base (extending to the urohyal) as found in typical bothines (*sensu* Norman), fin rays are supported by the cartilaginous region of the anterior basipterygial process which extends slightly anterior to the tip of the cleithrum (see Fig. 9C). The *Bothus*-type support for this fin differs only in degree of development (i.e., anterior extension) of this cartilaginous region. Futch (1977) has made a comparative study of larval bothids (*sensu* Norman). He has found that larvae seem to form two groups which generally correspond with Norman's Bothinae and Paralichthyinae. However, there are differences; larval characters of *Engyophrys*, *Trichopsetta*, *Monolene*, and *Taeniopsetta* indicate a closer relationship of these genera with Norman's Bothinae than his Paralichthyinae.

A major limitation of Amaoka's (1969) classification and phylogenetic model is its restriction to Japanese species. Similar studies are needed in other areas before his classification can be applied on a worldwide basis. The present study merely emphasizes an analysis of one character used by Amaoka. This analysis suggests the possibility that within the western North Atlantic bothids (*sensu* Norman, 1934), *Engyophrys*, *Trichopsetta*, and *Monolene* may be more

closely related to Norman's Bothinae than the Paralichthyinae, much as Amaoka found in regard to *Taeniopsetta*.

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