

## LARVAL AND EARLY JUVENILE DEVELOPMENT OF THE FRILLFIN GOBY, *Bathygobius soporator* (Perciformes: Gobiidae)

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**Abstract:** Larval and early juvenile development of laboratory-reared frillfin gobies, *Bathygobius soporator* (Cuvier and Valenciennes, 1837), is described and figured. One-day-old preserved specimens averaged 2.0 mm SL, had 11-12 preanal myomeres, and 25-26 total myomeres. Caudal fin rays appeared at 3.1 mm SL (10 days), followed by soft dorsal and anal fin rays at 3.4 mm SL (11 days). Dominant larval pigmentation consisted of dense rows of stellate melanophores along the dorsal and anal midlines and later along the lateral midline. The change to juvenile pigmentation and a benthic habit occurred at 4.7-5.4 mm SL (26-31 days). Early juvenile growth was characterized by migration of the eyes to the adult position, rounding of the caudal fin margin, beginning of scale formation, and separation of the upper pectoral fin rays.

Sequence of ossification is described and figured. In one-day-old larvae (2.0 mm SL), only the maxillae and cleithra had started to ossify. Many bones, including the ethmoids, small gill arch elements, nasals, and ribs were not ossified at settling (4.7-5.3 mm SL). With the exception of the adult complement of ribs, all bones were ossified in the largest juvenile (17.6 mm SL, 97 days).

The frillfin goby, *Bathygobius soporator* (Cuvier and Valenciennes, 1837) is a relatively large, robust goby that inhabits shallow coastal waters throughout the southeastern United States. Ginsburg (1947) discusses the specific ranges and adult characteristics of *B. soporator*, its subspecies, and related species in the American *Bathygobius* complex.

The embryonic and early larval development of the frillfin goby is well documented (Breder, 1943; Tavalga, 1950, 1953, 1954). Breder (1943) found late stage *B. soporator* eggs, guarded by the male parent, attached to the underside of a clam shell in shallow water. Eggs were described as elongate and somewhat cigar-shaped with a rounded bulbous distal end into which the head of the embryo fits. The basal end was "roundly pointed" and attached to the shell by a bundle of adhesive threads. Eggs averaged 2.36 mm in length and had small yolk sacs at hatching and were

feeding by the second day. Unfortunately, the rearing had to be terminated on the third day. Tavalga (1950) was able to strip spawn adult *B. soporator* and described the embryonic and early larval development of the species. He found that hatching took place in 96-100 hrs at 27-29°C and that at 20-24 hrs, the embryo undergoes a reversal in orientation from facing the basal end of the egg case to facing the distal end (head down). Apparently, this geotactic response is necessary for successful hatching from the elongate hanging egg. Larvae were 2.3 mm TL at hatching and lived 3-4 days (2.6-2.7 mm TL). These larvae had punctate melanophores "coating the abdominal cavity and thinly scattered over the dorsum." Large stellate melanophores were present on the ventral surface of the hindbrain and in two rows on the dorsal and ventral midline. The swim bladder was highly visible and heavily pigmented. This study was designed to describe

complete development of larval and early juvenile frillfin gobies from laboratory-reared specimens. Other larval *Bathygobius* spp. are probably similar to those described herein and further investigations may be needed to separate them from larval *B. saporator* in areas of overlapping ranges.

## MATERIALS AND METHODS

In mid-October of 1978, an adult male frillfin goby was collected, with its nest, in an oyster shell from Tampa Bay, Florida. The shell contained hundreds of eggs and was returned to the laboratory for rearing of the goby larvae.

Newly-hatched larvae were reared in 30 liter aquaria at temperatures of 24-26°C and salinities of 28-30‰. Larvae were fed rotifers (*Brachionus plicatilis* Müller) until old enough to take newly-hatched brine shrimp (*Artemia salina* L.). Samples of larvae were taken at half-day intervals for the first two weeks, then at daily intervals the third week, and at odd intervals thereafter depending on the number of fish remaining. All larvae were preserved in 5% buffered Formalin, and allowed to stand for several months. Body proportions were then measured on the preserved, shrunken specimens using an ocular micrometer on a Zeiss

dissecting microscope. Mean standard lengths (= notochord lengths in preflexion larvae) were calculated for each day's sample (Table 1). All lengths given refer to standard length (SL) unless otherwise noted. Morphometric measurements follow Peters (1981) and were grouped into the growth stages of preflexion, flexion, postflexion larvae and juveniles to show changes through larval and juvenile growth (Table 2). The growth stages were then further subdivided into 0.5 mm increments to show proportions for the range of larval and juvenile sizes (Tables 3-6).

A developmental series consisting of 83 larval, 13 juvenile, and 5 adult specimens was cleared and differentially stained for bone and cartilage using a method modified from Dingerkus and Uhler (1977). All meristic counts were made on cleared and stained material. Drawings were made using a camera lucida on a Zeiss dissecting microscope.

Osteological abbreviations used in this paper are: AN, angular; AR, anal ray; ART, articular; AS, anal spine; BB, basibranchial; BH, basihyal; BO, basioccipital; BR, branchiostegal; CB, ceratobranchial; CH, ceratohyal; CL, cleithrum; CN, vertebral centrum; COR, coracoid; CPS, cartilaginous pectoral fin support; CR, caudal ray; DEN, dentary;

**Table 1.** Mean Standard Lengths (SL) of laboratory-reared larval and juvenile *Bathygobius saporator* at ages sampled.

Age in Days	Mean SL (mm)	Age in Days	Mean SL (mm)	Age in Days	Mean SL (mm)
1	2.0	15	3.6	29	4.9
2	2.2	16	3.7	30*	5.3
3	2.1	17	3.9	31	5.4
4	2.3	18	3.5	32	5.4
5	2.4	19	3.6	35	5.5
6	2.4	20	4.1	38	6.2
7	2.6	21	4.3	41	6.3
8	2.8	22	4.6	43	7.4
9	2.9	23	5.3	49	8.6
10	3.1	24	4.7	52	8.4
11	3.4	25	4.8	59	8.9
12	3.5	26	4.7	69	11.2
13	3.7	27	5.0	79	14.8
14	3.7	28	5.2	97	16.8

\*Indicates approximate age and size of transition to benthic habit.

**Table 2.** Changes in body proportions (as % SL) of *Bathygobius soporator* larvae and juveniles during four growth stages. Data are mean values  $\pm$  standard deviation, with ranges in parenthesis. Number of specimens measured is given below each stage heading.

	Preflexion 103	Flexion 12	Postflexion 108	Juvenile 20
Total length	106.0 $\pm$ 1.0 (102.9-108.4)	107.1 $\pm$ 3.2 (104.4-123.5)	118.5 $\pm$ 3.0 (106.0-129.1)	123.3 $\pm$ 1.6 (120.4-126.3)
Head length	21.6 $\pm$ 1.6 (15.0-25.6)	22.7 $\pm$ 1.2 (21.0-25.2)	26.7 $\pm$ 2.0 (21.6-31.4)	30.1 $\pm$ 1.6 (27.1-32.8)
Snout length	4.7 $\pm$ 1.0 (1.6-7.3)	4.7 $\pm$ 1.0 (3.6-7.3)	5.3 $\pm$ 0.9 (3.0-8.0)	6.6 $\pm$ 0.7 (5.4-7.9)
Eye diameter	8.5 $\pm$ 0.8 (6.4-10.3)	7.6 $\pm$ 0.4 (6.9-8.4)	8.3 $\pm$ 0.4 (7.9-9.3)	8.3 $\pm$ 0.8 (5.5-9.2)
Prepelvic length	-	-	30.4 $\pm$ 2.5 <sup>1</sup> (26.1-37.3)	31.7 $\pm$ 1.1 (30.3-33.7)
Predorsal length	-	-	41.1 $\pm$ 1.0 <sup>2</sup> (38.9-44.1)	40.3 $\pm$ 0.9 (39.1-42.9)
Preanal length	52.9 $\pm$ 1.7 (46.6-56.5)	54.8 $\pm$ 1.7 (52.0-57.3)	56.0 $\pm$ 1.6 (50.4-64.2)	56.9 $\pm$ 1.2 (54.8-59.0)
Body depth	16.8 $\pm$ 1.3 (14.2-20.1)	16.3 $\pm$ 1.1 (15.1-18.1)	19.3 $\pm$ 1.7 (15.6-23.2)	23.1 $\pm$ 1.3 (20.9-27.2)
Caudal penduncle depth	-	-	9.1 $\pm$ 0.7 <sup>3</sup> (7.3-10.8)	10.9 $\pm$ 0.8 (9.8-12.4)
Pectoral length	11.8 $\pm$ 1.5 (6.8-15.7)	12.2 $\pm$ 1.5 (10.6-12.8)	14.6 $\pm$ 2.9 (10.9-25.5)	24.5 $\pm$ 2.7 (19.1-29.8)
Pelvic length	-	-	11.8 $\pm$ 7.1 <sup>4</sup> (3.3-25.6)	24.8 $\pm$ 2.0 (21.4-28.9)

1 n = 83      4 n = 57

2 n = 28

3 n = 86

DH, dorsal hypohyal; DHP, dorsal hypural plate; DPT, distal pterygiophore; DR, dorsal ray; DS, dorsal spine; EB, epibranchial; ECT, ectopterygoid; EH, epihyal; EP, epiotic; EPR, epipleural rib; EPU, epural; EX, exoccipital; F, frontal; HB, hypobranchial; HH, hypohyal; HM, hyomandibula; HY, hypural 5; IH, interhyal; INT, intercalar; IO, interopercle;

LAC, lachrymal; LE, lateral ethmoid; LP, lower pharyngeal; ME, median ethmoid; MET, metapterygoid; MK, Meckel's Cartilage; MPT, medial pterygiophore; MX, maxilla; NA, neural arch; NAS, nasal; NOT, notochord; OP, opercle; PAL, palatine; PALQ, palatoquadrate; PB pharyngobranchial; PC, procurent cartilage; PCR, procurent caudal ray; PEL,

**Table 3.** Changes in body proportions (as % SL) of *Bathygobius soporator* preflexion larvae at 0.5 mm increments of standard length. Data are mean values  $\pm$  standard deviations, with ranges in parenthesis. Number of specimens measured is given below each increment.

	1.8-1.9 16	2.0-2.4 38	2.5-2.9 31	3.0-3.4 15	3.5-3.7 3
Total length	106.8 $\pm$ 0.8 (105.5-108.4)	106.1 $\pm$ 1.2 (102.9-108.1)	105.9 $\pm$ 0.7 (104.8-107.4)	105.6 $\pm$ 0.8 (103.8-106.7)	105.1 $\pm$ 1.7 (103.3-106.6)
Head length	20.2 $\pm$ 2.3 (15.0-23.8)	21.0 $\pm$ 1.2 (17.2-24.2)	21.3 $\pm$ 1.2 (19.3-25.6)	21.0 $\pm$ 1.7 (16.0-23.8)	22.6 $\pm$ 0.6 (21.9-23.0)
Snout length	4.2 $\pm$ 1.4 (1.6-6.2)	4.7 $\pm$ 0.9 (3.4-7.1)	4.7 $\pm$ 0.7 (3.4-6.4)	5.0 $\pm$ 0.5 (4.2-5.8)	5.5 $\pm$ 1.6 (4.4-7.3)
Eye diameter	9.7 $\pm$ 0.4 (8.8-10.3)	8.7 $\pm$ 0.4 (7.7-9.7)	8.0 $\pm$ 0.4 (7.5-8.9)	7.9 $\pm$ 0.5 (6.8-8.8)	7.0 $\pm$ 0.6 (6.4-7.4)
Preanal length	54.0 $\pm$ 1.5 (51.0-55.8)	52.4 $\pm$ 1.7 (48.2-55.5)	53.0 $\pm$ 1.4 (49.8-56.5)	53.3 $\pm$ 1.1 (51.5-55.2)	50.2 $\pm$ 3.7 (46.6-54.0)
Body depth	18.8 $\pm$ 0.9 (17.6-20.1)	16.8 $\pm$ 1.0 (14.5-18.6)	16.1 $\pm$ 1.3 (14.2-18.6)	16.6 $\pm$ 0.9 (15.3-18.0)	15.8 $\pm$ 0.4 (15.2-16.5)
Pectoral length	10.9 $\pm$ 1.3 (8.9-13.4)	12.1 $\pm$ 1.6 (6.8-15.7)	11.7 $\pm$ 1.4 (7.4-14.3)	12.1 $\pm$ 1.2 (9.8-13.8)	11.9 $\pm$ 0.6 (11.5-12.5)

pelvis; PH, parhypural; PL, pleural rib; PM, premaxilla; POP, preopercle; PPT, proximal pterygiophore; PRO, prootic; PS, parasphenoid; PT, posttemporal; PTO, pterotic; PTS, pterosphenoid; Q, quadrate; R, radial; RO, rostral cartilage; SCA, scapula; SCAF, scapular foramen; SCL, supracleithrum; SOC, supraoccipital; SOP, subopercle; SPH, sphenotic; SYM, symplectic; THC, terminal half centrum; UH, urohyal; UP, upper pharyngeal; V, vomer; VH, ventral hypohyal; VHP, ventral hypural plate; ?, anomalous free portion of epural or neural spine.

### External Development (Figures 1 and 2, Tables 1-7)

#### General Development

Preserved one-day-old *B. saporator* larvae ranged from 1.8-2.1 mm and had 11-12 preanal and 25-26 total myomeres. Eyes were pigmented and the digestive tract was functional as evidenced by small particles of food in the gut. A small but distinctive gas bladder was located above the midgut. Dense rows of melanophores covered the ventral midline and central portion of the dorsal midline. The dorsal finfold originated above the second myomere, and was continuous with the caudal and ventral finfolds. The ventral finfold was as long as the dorsal, and already divided at the anus.

Few changes occurred before notochord flexion except for an increase in the degree of pigmentation. Notochord flexion took place from 3.2-3.7 mm (10-12 days) along with the formation of incipient median fin rays and pelvic fin buds. The spinous dorsal, pelvic and pectoral fin rays were forming by 4.4 mm and the caudal fin margin was becoming truncate. Melanophores developed over the brain and in a dashed line midlaterally along the body. The pelagic larval stage

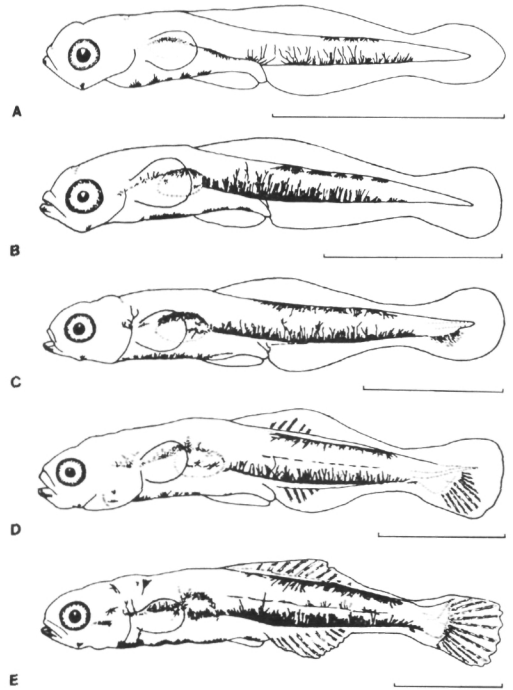


Figure 1. *Bathygobius saporator* larvae. A) 1 day, 1.9 mm SL; B) 6 days, 2.3 mm SL; C) 10 days, 3.1 mm SL; D) 10 days, 3.4 mm SL; E) 12 days, 3.7 mm SL. Horizontal bar represents 1 mm.

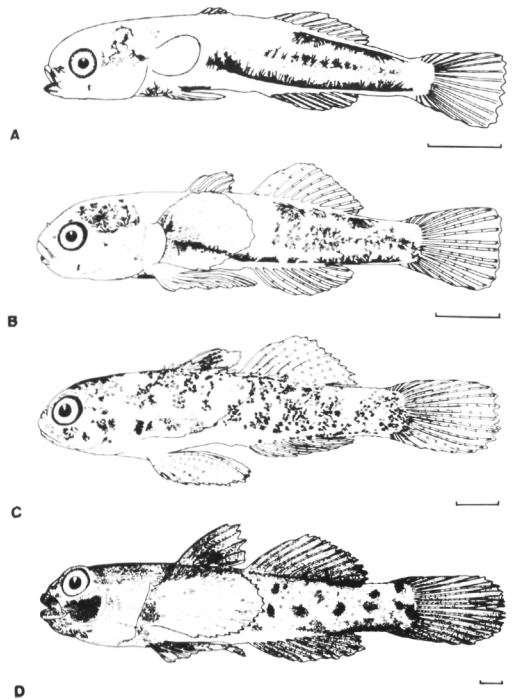


Figure 2. *Bathygobius saporator* larvae and young juveniles. A) 21 days, 5.1 mm SL; B) 41 days, 5.8 mm SL; C) 49 days, 8.1 mm SL; D) 97 days, 17.6 mm SL. Horizontal bar represents 1 mm.

**Table 4.** Changes in body proportions (as % SL) of *Bathygobius soporator* flexion larvae at 0.5 mm increments of standard length. Data are mean values  $\pm$  deviations, with ranges in parenthesis. Number of specimens is given below each increment.

	3.2-3.4 5	3.5-3.7 7
Total length	106.3 $\pm$ 2.6 (104.4-110.8)	107.6 $\pm$ 3.6 (104.9-113.4)
Head length	22.5 $\pm$ 0.7 (21.4-23.3)	22.8 $\pm$ 1.5 (21.0-25.2)
Snout length	4.7 $\pm$ 0.7 (3.9-5.5)	4.7 $\pm$ 1.3 (3.6-7.3)
Eye diameter	7.9 $\pm$ 0.4 (7.5-8.4)	7.4 $\pm$ 0.3 (6.9-7.9)
Preanal length	54.9 $\pm$ 1.5 (53.0-56.7)	54.7 $\pm$ 2.0 (52.0-57.3)
Body depth	16.1 $\pm$ 1.0 (15.3-17.7)	16.4 $\pm$ 1.2 (15.1-18.1)
Pectoral length	12.1 $\pm$ 0.9 (10.6-12.8)	12.2 $\pm$ 0.4 (11.7-12.7)

lasted until larvae were 4.7-5.4 mm (26-31 days) and fins were developed. Standard lengths of larvae during development fit the growth equation:

Standard length (in mm) = 1.92 + 0.11 x Age (in days). Growth was probably slower in the laboratory than in the wild

since it is difficult to duplicate natural food conditions in the lab.

During juvenile development, several changes occurred to ready the gobies for a benthic existence. The truncate caudal fin margin became more rounded and the eyes, having been

**Table 5.** Changes in body proportions (as % SL) of *Bathygobius soporator* postflexion larvae at 0.5 mm increments of standard length. Data are mean values  $\pm$  standard deviations, with ranges in parenthesis. Number of specimens measured is given below each increment.

	3.2-3.4 11	3.5-3.9 34	4.0-4.4 28	4.5-4.9 20	5.0-5.4 14
Total length	116.6 $\pm$ 3.6 (109.1-120.8)	116.6 $\pm$ 2.9 (106.0-120.1)	118.8 $\pm$ 1.6 (115.9-121.1)	120.7 $\pm$ 2.4 (117.3-129.1)	120.5 $\pm$ 2.0 (117.5-123.9)
Head length	25.0 $\pm$ 1.7 (22.2-28.3)	25.6 $\pm$ 1.3 (21.6-27.8)	26.5 $\pm$ 1.4 (25.1-30.3)	28.4 $\pm$ 1.5 (25.8-31.6)	28.9 $\pm$ 1.5 (27.1-31.4)
Snout length	5.0 $\pm$ 0.7 (3.8-6.2)	4.8 $\pm$ 0.8 (3.0-6.4)	5.0 $\pm$ 0.6 (3.8-6.2)	5.8 $\pm$ 0.9 (4.6-7.6)	6.2 $\pm$ 1.0 (4.5-8.0)
Eye diameter	8.6 $\pm$ 0.5 (7.8-9.3)	8.2 $\pm$ 0.5 (7.4-9.0)	8.2 $\pm$ 0.4 (7.0-8.8)	8.3 $\pm$ 0.2 (7.9-8.6)	8.2 $\pm$ 0.4 (7.8-9.3)
Prepelvic length	30.1 $\pm$ 1.1 <sup>1</sup> (28.7-31.5)	28.6 $\pm$ 1.1 <sup>3</sup> (26.1-30.7)	29.1 $\pm$ 1.4 <sup>6</sup> (26.4-32.1)	32.5 $\pm$ 2.7 (28.7-37.7)	32.4 $\pm$ 2.5 (29.1-37.3)
Predorsal length	-	-	41.6 <sup>7</sup>	41.2 $\pm$ 1.3 <sup>8</sup> (38.9-44.1)	40.9 $\pm$ 0.6 <sup>9</sup> (40.0-42.1)
Preanal length	56.7 $\pm$ 1.2 (54.7-59.0)	55.5 $\pm$ 1.5 (50.4-57.8)	56.0 $\pm$ 0.9 (54.8-57.7)	56.1 $\pm$ 2.4 (52.7-64.2)	56.9 $\pm$ 1.8 (54.8-60.9)
Body depth	18.8 $\pm$ 2.1 (16.1-22.8)	18.1 $\pm$ 1.1 (15.6-20.7)	19.1 $\pm$ 1.1 (16.9-21.3)	20.6 $\pm$ 1.1 (18.8-22.7)	21.2 $\pm$ 1.3 (19.1-23.2)
Caudal peduncle depth	9.0 $\pm$ 0.8 <sup>2</sup> (8.5-9.9)	8.6 $\pm$ 0.5 <sup>4</sup> (7.5-9.5)	8.8 $\pm$ 0.6 (7.3-10.0)	9.5 $\pm$ 0.6 (8.5-10.3)	9.7 $\pm$ 0.5 (9.1-10.8)
Pectoral length	13.3 $\pm$ 1.1 (11.2-15.8)	13.1 $\pm$ 1.3 (11.1-15.8)	13.8 $\pm$ 1.5 (10.9-17.7)	16.7 $\pm$ 2.4 (12.8-22.3)	18.1 $\pm$ 4.0 (12.7-25.5)
Pelvic length	-	4.1 $\pm$ 0.6 <sup>5</sup> (3.3-5.4)	8.1 $\pm$ 4.8 (4.0-22.0)	16.8 $\pm$ 4.8 (5.9-22.3)	18.4 $\pm$ 5.7 (9.1-25.6)

1 n=6      6 n=26  
2 n=3      7 n=1  
3 n=17     8 n=15  
4 n=20     9 n=12  
5 n=10

**Table 6.** Changes in body proportions (as % SL) of *Bathygobius saporator* juveniles at 0.5 mm increments of standard length. Data are mean values  $\pm$  standard deviations, with ranges in parenthesis. Number of specimens measured is given below each increment.

	5.3-5.4 7	5.5-5.9 8	6.0-6.5 5
Total length	122.6 $\pm$ 1.6 (121.6-124.8)	123.6 $\pm$ 1.7 (120.4-125.1)	124.9 $\pm$ 0.9 (124.1-126.3)
Head length	29.9 $\pm$ 1.2 (22.2-28.3)	29.4 $\pm$ 1.4 (21.6-27.8)	31.6 $\pm$ 1.7 (25.1-30.3)
Snouth length	6.8 $\pm$ 0.6 (5.9-7.9)	6.2 $\pm$ 0.7 (5.4-7.7)	6.9 $\pm$ 0.7 (6.2-7.8)
Eye diameter	8.5 $\pm$ 0.4 (7.8-8.8)	8.0 $\pm$ 1.1 (5.5-9.2)	8.4 $\pm$ 0.7 (7.3-9.0)
Prepelvic length	31.2 $\pm$ 0.8 (30.3-32.2)	31.7 $\pm$ 1.3 (30.3-32.7)	32.5 $\pm$ 1.0 (31.7-33.7)
Predorsal length	41.0 $\pm$ 1.1 (39.4-42.9)	39.9 $\pm$ 0.7 (39.2-41.4)	39.8 $\pm$ 0.5 (39.1-40.3)
Preanal length	57.0 $\pm$ 1.5 (54.8-58.4)	56.8 $\pm$ 1.0 (55.5-59.0)	56.9 $\pm$ 1.2 (55.1-57.4)
Body depth	22.8 $\pm$ 0.7 (22.1-23.9)	22.7 $\pm$ 1.1 (20.9-24.8)	24.2 $\pm$ 1.8 (22.4-27.2)
Caudal peduncle depth	10.6 $\pm$ 0.4 (10.0-11.2)	10.6 $\pm$ 0.6 (9.8-11.5)	11.8 $\pm$ 0.7 (10.9-12.4)
Pectoral length	23.5 $\pm$ 2.1 (21.2-23.9)	24.0 $\pm$ 2.5 (19.1-26.6)	26.8 $\pm$ 3.0 (22.8-29.8)
Pelvic length	24.2 $\pm$ 2.3 (22.4-28.9)	24.3 $\pm$ 1.6 (21.4-26.1)	26.4 $\pm$ 1.8 (23.4-27.9)

midlateral on the head since hatching, became situated more dorsad on the head in the adult position. Pigment filled in and covered most of the body and fins in a mottled pattern. Scales began to develop on the caudal peduncle at about 6.3 mm (42 days) and had reached, but not covered, the head by 17.6 mm. Upper pectoral fin rays began separating from the rest of the fin at about 8.1 mm.

### Fin Development (Table 7)

Principal caudal rays were the first fin rays to form (3.1 mm) and developed from the central rays toward both ends just prior to and during notochord flexion. Larvae reached the typical laboratory-reared larval count of 7 + 6 rays at 3.6-3.8 mm. From then on, procurrent caudal rays formed and continued to increase in number until the larvae had reached 5.2-5.5 mm and a count of 9-10 upper and 8-9 lower rays. Four cleared and stained adult specimens from

Tampa Bay all had 8 + 7 principle rays and from 8-9 upper and 6-8 lower procurrent rays.

Soft (second) dorsal and anal fin rays developed simultaneously starting at 3.6 mm and formed first near the anterior end of the fin base. The single spines associated with these fins developed along with the segmented rays. Both completed development as early as 3.7 mm. The spinous first dorsal formed next beginning at about 4.1 mm. All six spines had formed by 4.3 mm, but remained quite short. The proportional adult height of the spinous dorsal was not reached until well into the juvenile stage.

The pelvic fin buds were first evident at 3.7 mm and fin rays were forming by 4.4 mm. Pectoral and pelvic fin rays developed concurrently. Pelvic and pectoral fins lengthened during early juvenile growth and reached their proportional adult lengths by 5.0-5.4 mm and

**Table 7.** Meristics of *B. saporator* from laboratory-reared larvae and locally collected adults. All counts were made on cleared and stained specimens. Larvae between the dotted lines were undergoing notochord flexion.

Standard length(mm)	Age (days)	Princ. caudal fin rays	Procurent caudal fin rays	1st dorsal fin rays	2nd dorsal fin rays	Anal fin rays	Pectoral fin rays	Pelvic fin rays	Vertebral centra	Pleural ribs	Epipleural ribs
3.1	10	~3							10+6		
3.3	10	~3							10+11		
3.4	10	5							10+14		
3.6	11	4+5			~3	~4			10+14		
3.6	13	6+6			1,6	1,6			10+14		
3.6	14	7+6	1+2		1,9	1,8			10+15		
3.7	12	6+6	—		1,6	1,6			10+17		
3.7	16	7+6	2+3		1,9	1,8			10+17		
3.8	15	7+6	2+2		1,9	1,8			10+17		
3.8	16	7+6	1+2		1,8	1,8			10+17		
3.9	13	7+6	0+1		1,7	1,7			10+17		
3.9	14	7+6	2+3		1,8	1,7			10+17		
3.9	15	7+6	2+3		1,9	1,8			10+17		
3.9	19	7+6	3+3		1,9	1,8			10+17		
4.0	17	7+6	3+4		1,9	1,8			10+17		
4.1	18	7+6	3+4	IV	1,9	1,9			10+17		
4.1	18	7+6	3+3	IV	1,9	1,8			10+17		
4.2	17	7+6	4+4	—	1,10	1,9			10+17		
4.3	21	7+6	4+4	VI	1,9	1,9			10+17		
4.4	20	7+6	5+6	VI	1,9	1,8			10+17		
4.4	22	7+6	4+5	VI	1,9	1,9	~8	1,5	10+17		
4.6	21	7+6	5+6	VI	1,9	1,8	~9	1,5	10+17		
4.6	22	7+6	5+6	VI	1,9	1,8	~9	1,5	10+17		
4.6	26	7+6	8+8	VI	1,9	1,8	~15	1,5	10+17		
4.9	24	7+6	7+7	VI	1,9	1,8	~16	1,5	10+17		
4.9	24	7+7	7+7	VI	1,9	1,8	~15	1,5	10+17		
4.9	31	7+6	8+8	VI	1,9	1,8	18	1,5	10+17		
5.0	26	7+6	8+8	VI	1,9	1,8	~18	1,5	10+17		
5.2	31	7+6	9+8	VI	1,9	1,8	~17	1,5	10+17		
6.3	41	7+6	10+8	VI	1,9	1,8	19	1,5	10+17		2
6.8	41	7+6	9+8	VI	1,9	1,8	19	1,5	10+17		2
9.1	49	7+6	9+9	VI	1,9	1,8	19	1,5	10+17	6	7
17.6	97	7+6	8+8	VI	1,10	1,8	19	1,5	10+17	6	9
37.8	adult	8+7	8+8	VI	1,9	1,8	18/17 <sup>1</sup>	1,5	10+17	7	11
43.6	adult	8+7	9+6	VI	1,9	1,8	18/17 <sup>1</sup>	1,5	10+17	7	11
43.8	adult	8+7	8+8	VI	1,9	1,8	18	1,5	10+17	7/8 <sup>1</sup>	11
44.6	adult	8+7	8+8	VI	1,9	1,8	18	1,5	10+17	7	12

<sup>1</sup> Left and right sides different.

6.4-6.6 mm respectively. The upper rays began separately from the pectoral fin membrane at 8.1 mm and reached the adult state by about 17 mm.

### Pigmentation

One-day-old larvae had a small melanophore at the symphysis and posterior angle of the lower jaw and five large stellate melanophores ventrally along the robust midgut. Internal pigment lined the dorsal abdominal cavity from the pharyngeal region to the gas bladder. A single row of dense melanophores extended from the hindgut to the caudal peduncle and reached dorsally to the midline. The individual melanophores in this row were so close, they could not be counted. A shorter dorsal series of melanophores was present midway between the anus and caudal

peduncle. In a few specimens, the dorsal series was preserved in a punctate condition and about 20 melanophores could be counted.

As larvae grew, the melanophores along the dorsal and especially the ventral midline increased in length and density and continued to dominate larval pigmentation. The ventral series remained as a single row, but the dorsal series split anteriorly around the soft dorsal fin base. By 3.4 mm, melanophores appeared in the horizontal septum in a linear or sometimes dashed pattern. This midlateral series lengthened anteriorly and became somewhat hidden by the opaqueness of the body. At the same time, the posterior portion expanded toward the body surface and formed a stellate pattern along the lateral midline.

Head, gut and caudal fin pigment in-

creased slowly during the larval stage. Melanophores at the angle and symphysis of the lower jaw remained throughout the larval growth. Pigment beneath the auditory vesicles often was visible near the surface of the skin in a branching pattern. By 3.7 mm, single melanophores were occasionally seen over the hindbrain and midway along the upper jaws. Dorsal gut pigment formed branching patterns near the surface after 3.1 mm in the region of the cleithra and gas bladder. The number of melanophores along the ventral gut had increased to 8-12 by 3.6 mm, but were rarely countable and usually coalesced into a single line extending from the isthmus to a point near the anus. The ventral caudal fin rays of specimens with flexed notochords usually had a single branching melanophore at their base. Occasionally, this spot was missing or in such a punctate condition that it was barely visible.

In the early juvenile stages, the number of melanophores increased rapidly on the head and posterolateral portion of the tail. The size of individual melanophores decreased and the mottled juvenile pigment pattern became evident between 8.4 and 11.2 mm. As scales formed, tiny dots of pigment outlined their posterior margins. The characteristic dark diagonal band of melanophores on the spinous dorsal fin developed at about 8.0 mm and was clearly visible by 9.0 mm.

From 8.0 mm to my oldest specimens (16.8 mm), the entire fish, except the stomach, was covered with tiny spots of pigment. The body contained large patches of concentrated pigment down its sides and the pelvic, dorsal and anal fins were noticeably darkened.

### Morphology

Eight of the eleven measured mor-

phological characters increased in relations to standard length from preflexion larvae to early juveniles. Increases in fin lengths accounted for three of the eight increases. The caudal fin length, as indicated by the total length measurement, increased from 6.0 to 23.3% SL mainly during postflexion larval and juvenile growth (Table 2). Pectoral fin lengths increased from 10.9% SL in early preflexion larvae to 26.8% SL in juveniles (Tables 3-6), while the pelvic fin increased from a small bud in early postflexion larvae to 26.4% SL in juveniles (Tables 5, 6).

An increase in head length from 21.6 to 30.1% SL (Table 2) took place mainly during postflexion larval and early juvenile growth. Snout length increased from 4.2 to 6.9% SL during growth (Tables 3-6), while eye diameter decreased from 9.7% SL in the smallest larvae to 7.4% SL in flexion larvae (Tables 3, 4) and then stabilized around 8.3% SL (Table 2).

Prepelvic and predorsal lengths remained nearly constant at about 30.6 and 41.0% SL, respectively, after those fins developed in postflexion larvae (Table 2). Preanal length increased slightly from 52.9 to 56.9% SL during larval growth (Table 2). Both the body and the caudal peduncle depths also increased during growth from 16.8 to 23.1% SL and 9.1 to 10.9% SL, respectively (Table 2). The high percentage of body depth in the early preflexion larvae (Table 3) was due to a small yolk sac.

### DEVELOPMENTAL OSTEOLOGY

(Table 8, Figures 3-9)

Table 8 summarizes the ossification sequence of *Bathygobius soporator*. A brief summary of each developing bone is given below.

### Neurocranium (Figure 3)

*Parasphenoid (Figure 3A-E)*. A thin parasphenoid, first ossified at 2.2 mm, was bifid posteriorly and narrowed to a point anteriorly. The posterior half grew rapidly to cover the anteromedial portion of the myodome and met the basioccipital by 4.6 mm. By 9.1 mm, the parasphenoid met the prootic forming the internal carotid foramen.

*Basioccipital (Figure 3A-E)*. The basioccipital was first ossified at 2.7 mm around the anterior tip of the notochord. Lateral ossification met the parasphenoid and exoccipitals by 4.6 mm, the prootics and intercalars by 9.0 mm.

*Exoccipitals (Figure 3B-E)*. The exoccipitals, first visible at 3.7 mm, ossified around the posteroventral margins of the occipital arches. By 6.3 mm, the exoccipitals extended dorsally and met above the foramen magnum. Posteroventrally, ossification extended down a condyle which abutted the medial portion of the basioccipital. Anteriorly, the exoccipital had surrounded the vagal nerve foramen. By 9.0 mm, a second condyle, originating from the first, had formed an articulation with the first vertebrae.

*Frontals (Figure 3B-E)*. The frontals, first ossified at 3.7 mm, formed anterodorsal to the orbits along the supraorbital cartilage. Ossification spread over the braincase and reached its adult limits by about 4.6 mm. The relative width of ossification between the orbits (about 3/5 the orbit diameter in larvae) decreased to about 1/5 the orbit diameter at 16.8 mm.

*Pterotics (Figure 3C-E)*. The pterotics first ossified at 3.9 mm. They formed as thin, oval-shaped ossifications over the middle of the horizontal semicircular canals. Development was slow; the bony sides of the latero-sensory canal and fossa for articulation with the

hyomandibula were not well formed until 16.8 mm.

*Epiotics (Figure 3C-E)*. The epiotics first ossified at 3.9 mm, and lay over the dorsal portion of the posterior semicircular canals. The epiotics also developed slowly, attaining adult shape by about 16.8 mm.

*Supraoccipital (Figure 3C-E)*. The supraoccipital was first visible at 4.4 mm as an ossified portion of the vertical septum. By 6.3 mm, the oval base had ossified on the skull between the frontals and epiotics. The base met the exoccipitals posteriorly, but did not participate in the foramen magnum.

*Vomer (Figure 3C-E)*. The vomer, first ossified at 4.6 mm, was centered beneath the ethmoid cartilage and extended caudad to meet the parasphenoid. By 9.0 mm, the vomer had grown to lateral edges of the ethmoid plate and articulated with the palatine.

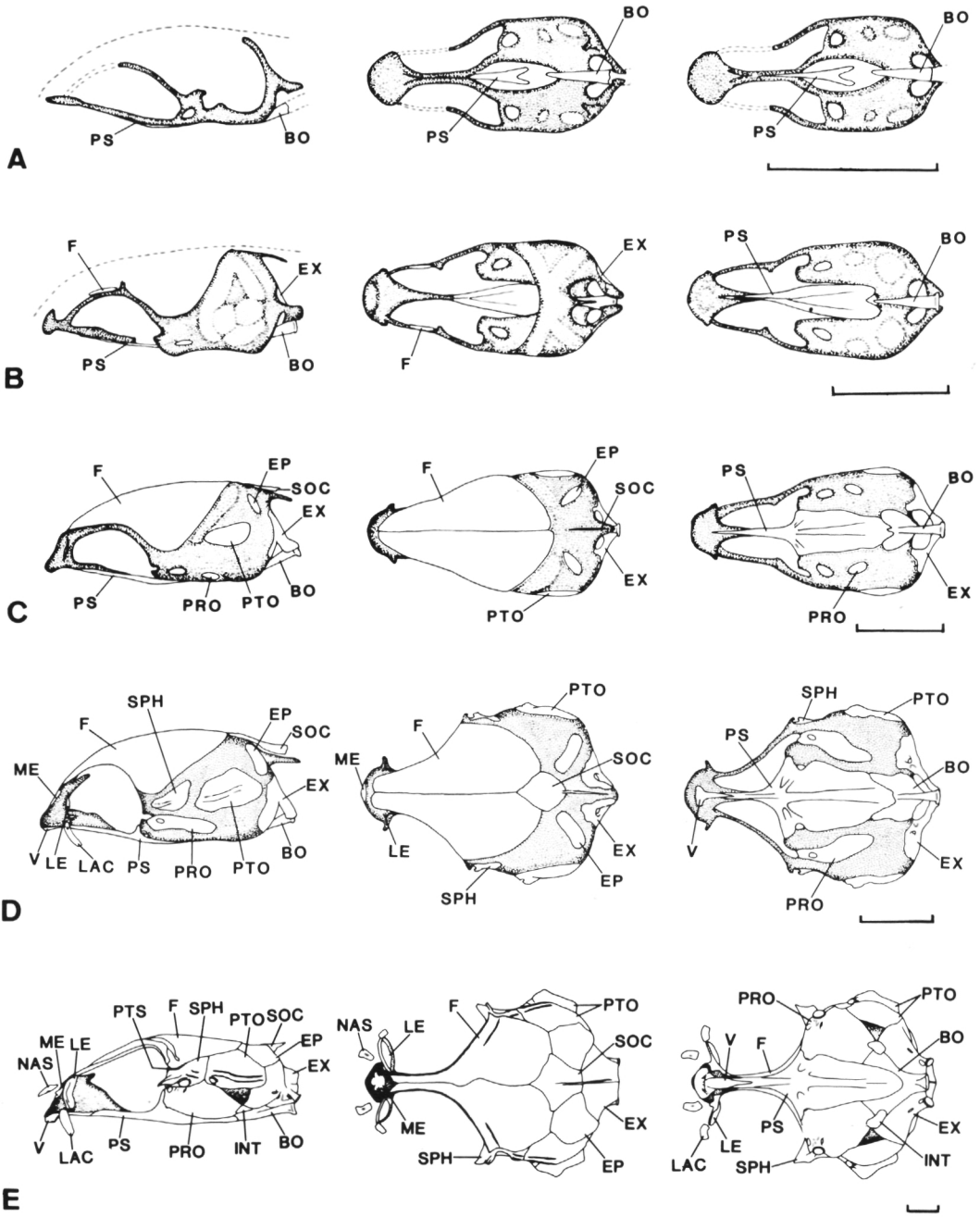
*Lachrymals (Figure 3C-E)*. Lachrymals were first ossified at 4.6 mm. They remained weakly ossified in all specimens.

*Prootics (Figure 3C-E)*. The prootics, first visible at 4.6 mm, developed as thin, oval ossifications posterior to the facial nerve foramina. They became elongate, surrounded the facial nerve foramina, and reached the orbit by 6.3 mm.

*Sphenotics (Figure 3D, E)*. Sphenotics, first visible at 4.9 mm, formed as oval ossifications just anterior to the pterotics. They soon extended below the ventral-most tip of the frontal, nearly reaching the orbit.

By 6.3 mm, lateral shelves along the entire length of the sphenotic had formed the laterosensory canal trough and fossa for articulation with the anterior arm of the hyomandibula.

*Lateral ethmoids (Figure 3D, E)*. Lateral ethmoids were first visible at 6.3 mm. Each consisted of one ossification



**Figure 3.** Development of *Bathygobius soporator* neurocranium (left side, dorsal and ventral views). A) 10 days, 3.1 mm SL; B) 13 days, 3.9 mm SL; C) 26 days, 4.6 mm SL; D) 41 days, 6.3 mm SL; E) 97 days, 16.8 mm SL. Stippled, cartilage. Horizontal bar represents 0.5 mm.

in the lamina orbitonasalis and another in the membrane lateral to it. Ossification strengthened the lamina orbitonasalis, but the lateral membrane remained thin.

*Median ethmoid* (Figure 3D, E). The median ethmoid, first visible at 6.3 mm, formed as an oval ossification in the ethmoid cartilage dorsomedial to the olfactory nerve foramina. By 16.8 mm,

two strong anterolateral processes had formed for ligamentous attachment to the lateral heads of the maxillae.

**Intercalars (Figure 3E).** Intercalars, first visible at 17.6 mm, were oval in shape and overlapped the prootics, basioccipitals and exoccipitals.

**Nasals (Figure 3E).** Nasals, first present at 17.6 mm, formed as wide, thin troughs below the nasal pits, and each had a small foramen near its center.

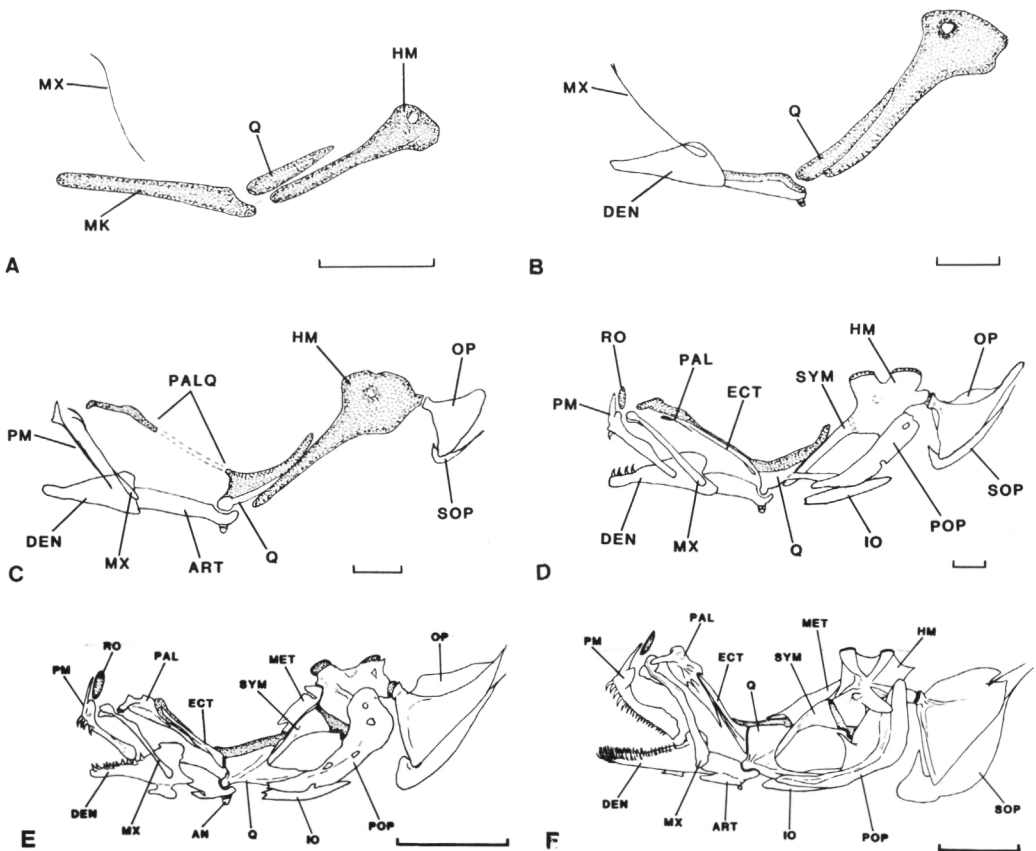
### Jaws and Suspensorium (Figure 4)

**Maxillae (Figure 4A-F).** Maxillae were first seen as thin ossifications in the dorsal lips at 1.8 mm. By 3.3 mm, the posteroventral end had expanded into an oval in the membrane lateral to the dentary. By 3.9 mm, medial and lateral pro-

cesses were forming at the dorsal end. The shaft of the maxilla was heavily ossified by 4.6 mm and resembled the adult structure.

**Dentaries (Figure 4B-F).** The dentaries, first visible at 2.1 mm, ossified along the anterolateral edge of Meckel's Cartilage. By 3.9 mm, the posterodorsal portion had become greatly expanded around the tip of the articular. By 6.3 mm, nine teeth were present in the left dentary. The oldest reared juvenile (17.6 mm), had about 60 teeth in each dentary which were arranged in one or two rows posteriorly and three or four rows anteriorly.

**Articulars (Figure 4B-F).** The articulars first ossified at 3.1 mm along the posterolateral edge of Meckel's Car-



**Figure 4.** Development of jaws and suspensorium (left side) of *Bathygobius soporator*. A) 1 day, 1.9 mm SL; B) 10 days, 3.3 mm SL; C) 13 days, 3.9 mm SL; D) 26 days, 4.6 mm SL; E) 41 days, 6.3 mm SL; F) 97 days, 16.8 mm SL. Stippled, cartilage. Horizontal bar represents 0.1 mm in A-D, 0.5 mm in E and F.

tilage. By 3.9 mm, the articular inserted into the dentary anteriorly, articulated with the quadrate posteriorly, and had begun to surround Meckel's Cartilage medially.

*Angulars* (Figure 4B-F). The angulars ossified at 3.6 mm on the posteroventral tips of Meckel's Cartilage.

*Premaxillae* (Figure 4C-F). The premaxillae, first visible at 3.6 mm, ossified along the extreme anterior margin of the upper lip. By 3.9 mm, the ascending process was forming and the alveolar process reached posteroventrally to the dentary. A tooth appeared at 4.2 mm and by 6.3 mm, there were four teeth on the heavily ossified alveolar process. In the oldest reared juvenile (17.6 mm) there were about 30 teeth in each premaxilla arranged in two rows posteriorly and three rows anteriorly.

*Quadrates* (Figure A-F). Small cartilaginous quadrates were present in the smallest larva (1.8 mm). Each was rod-shaped and lay dorsal to the ventral tip of the hyomandibular cartilage. By 3.6 mm, ossification had begun anteroventrally. The anterior end became enlarged and the pterygoid process was developing. This process joined with the palatine to form the palatoquadrate. By 4.6 mm, a long, posterior process had ossified and met the preopercle.

*Symplectics* (Figure 4D-F). The symplectic formed from the ventral portion of the hyomandibular cartilages in close association with the posterodorsal process of the quadrate cartilages. The symplectic was first ossified at 3.7 mm. By 16.8 mm, it was tightly joined to the metapterygoid anterodorsally and to the quadrate anteroventrally.

*Hyomandibulae* (Figure 4A-F). In the smallest larva (1.8 mm), cartilaginous hyomandibulae with small facial nerve foramina were present. By 3.6 mm, the opercular condyle was forming and the

facial nerve foramen was distinct. Ossification, first present at 3.7 mm, began as a thin layer over the lateral face of the cartilage. The dorsal condyles ossified soon after they formed from cartilage. By 16.8 mm, the hyomandibula had intramembranous ossification between the condyles and processes. A posterolateral flange formed and restricted lateral movement of the preopercle.

*Ectopterygoids* (Figure 4D-F). The ectopterygoids, first ossified at 4.4 mm, lay ventral to the thin pterygoid processes of the quadrates. The posterior end became enlarged ventrally at the quadrate. The anterior portion lay dorsal to the palatine and later inserted into an open groove in the palatine near the ethmoid cartilage.

*Palatines* (Figure 4D-F). The cartilaginous palatines were first visible at 3.6 mm and chondrified separately from the pterygoid processes of the quadrates. Ossification was first visible in the membrane below the cartilage at 4.6 mm and fused with the cartilage as it ossified. The ossified palatine was broadly attached to the vomer dorsomedially and to the anteroventral face of the ectopterygoid.

*Sesamoid articulators* (not figured). The small sesamoid articulators, first visible at 6.3 mm, ossified dorsomedial to Meckel's Cartilage halfway along the articulators.

*Metapterygoids* (Figure 4E,F). The metapterygoids first ossified at 6.3 mm along the anterior margins of the hyomandibulae and symplectics. By 16.8 mm, the metapterygoid also extended along the dorsal edge of the quadrate above the remaining cartilage.

#### **Opercular Series (Figure 4B-F)**

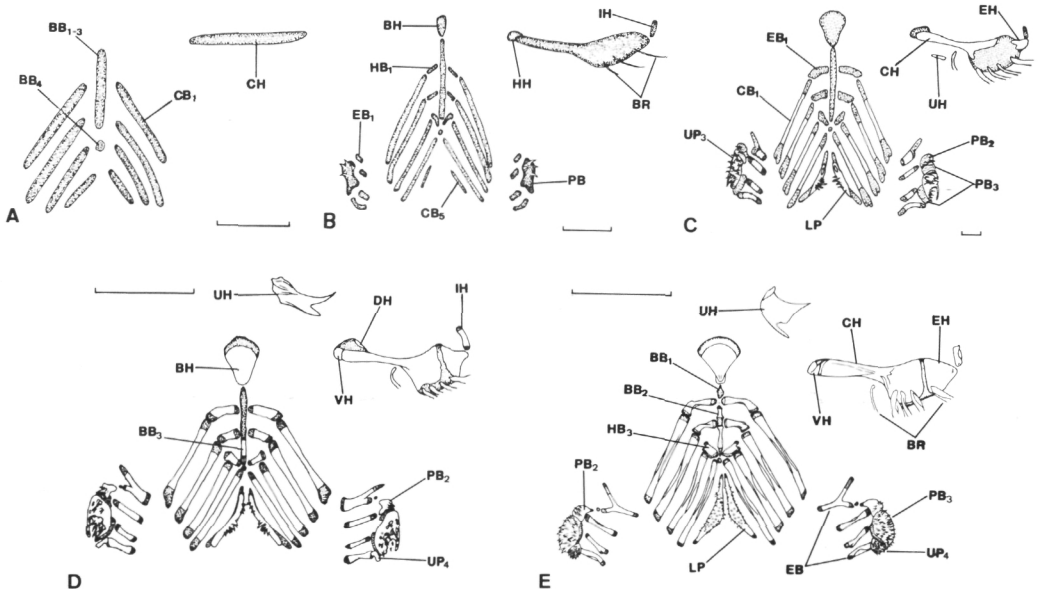
The opercle was first ossified at 3.6 mm at the condyle. Its blade formed in

a posterior direction first and then expanded ventrally. The thin preopercle, first visible at 3.7 mm, lay in its adult position well away from the symplectic. By 16.8 mm, the preopercle adhered closely to the posterior arm of the quadrate and had developed a strong symplectic process halfway up to the anterior margin. The subopercle and interopercle were first ossified at 3.8 and 3.9 mm, respectively. Both had their adult shape early in development.

### Hyoid Arch (Figure 5)

Brachioptegals ossified in a posterior to anterior direction. The first was visible at 3.3 mm and all were ossified by 3.8 mm. A narrow ceratohyal cartilage, present in the smallest larva (1.8 mm), had expanded posteroventrally by 3.3 mm. Ossification of the ceratohyal, first present at 3.7 mm in the shaft and anterior end, was nearly complete by 16.8 mm. The epihyal, first visible at 3.9 mm, ossified from the posterior

tip of the ceratohyal cartilage and had not met the ceratohyal by 16.8 mm. The urohyal, first ossified at 4.6 mm, formed as an elongate plate in the median septum below the basibranchials. The majority of the urohyal remained thin developing a convex margin anteriorly, tapering to one or two points posteriorly. The anterodorsal portion became heavily ossified and developed a concave trough below the reduced cartilage of basibranchial 1. The hypohyal cartilage was visible at 3.1 mm. The ventral hypohyal, first present at 4.4 mm, ossified from the anteroventral tip to the cartilage. The dorsal hypohyal, first present at 6.8 mm, ossified from the posteromedial portion of the cartilage. The interhyal, present as cartilage in the smallest larva (1.8 mm), was first ossified at 6.3 mm. The basihyal cartilage, first present at 3.1 mm, was triangular in dorsal view. Ossification began posteriorly at 6.3 mm and spread anteriorly over the dorsal and ventral surfaces of the



**Figure 5.** Development of gill arches (dorsal view) and hyoid arch (left side) of *Bathygobius soporator*. A) 1 day, 1.9 mm SL; B) 10 days, 3.3 mm SL; C) 26 days, 4.6 mm SL; D) 41 days, 6.3 mm SL; E) 97 days, 16.8 mm SL. Stippled, cartilage. Horizontal bar represents 0.1 mm in A-C, 0.5 mm in D, and 1.0 mm in E. Urohyal displaced in D and E.

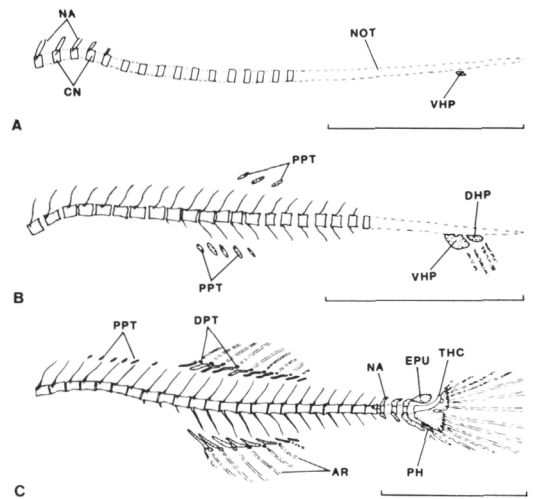
cartilage.

### Gill Arches (Figure 5)

Ceratobranchials 1-4, the combined cartilage of basibranchials 1-3, and a separate basibranchial 4 were all present in the smallest larva (1.8 mm). Hypobranchial cartilages 1-3 were visible at 2.1 mm. Epibranchials 1-4, ceratobranchial 5 and pharyngobranchial 3 were present as cartilage at 3.3 mm. The cartilaginous pharyngobranchial 2 was present at 3.6 mm. Ossification of the gill arches began on the upper pharyngeals. Three teeth were present on pharyngobranchial 3 by 3.3 mm. By 3.9 mm, 10 teeth were visible, with ossification around their bases. By 6.8 mm, pharyngobranchial 2 and the upper pharyngeal tooth plate 4 were also ossifying. Teeth on pharyngobranchials 2 and 3 were relatively larger and fewer than those on upper pharyngeal tooth plate 4. Ossification of the lower pharyngeal tooth plate began at 3.7 mm over the midportion of cartilaginous ceratobranchial 5 and teeth were first noted at 4.4 mm. The posteriormost ceratobranchials ossified first beginning at 3.8 mm. Basibranchial 3 was beginning to ossify at 6.8 mm. By 9.0 mm, basibranchial 2 was also ossifying, although it was still connected to basibranchial 3 by cartilage. Basibranchial 1 separated from basibranchials 2 and 3 at 9.0 mm, but remained cartilaginous and became reduced as did basibranchial 4. The epibranchials and hypobranchials were ossified by 6.3 mm.

### Laterosensory Canal System

The laterosensory canal system of *B. saporator* is much reduced and lies in an open bony trough. Shelves which make up the troughs for the supraorbital, postorbital, and preopercular portions of the canal were first visible at 6.3 mm. The posttemporal shelves were first present

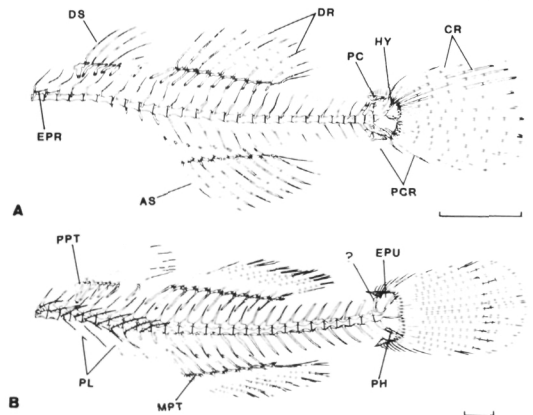


**Figure 6.** Development of axial skeleton of *Bathygobius saporator*. A) 10 days, 3.1 mm SL; B) 10 days, 3.3 mm SL; C) 13 days, 3.9 mm SL; Stippled, cartilage. Horizontal bar represents 1 mm.

at 16.8 mm and by this time, all sensory canal troughs were well defined.

### Vertebral Column and Median Fins (Figures 6, 7)

**Caudal Fin (Figures 6, 7).** Principal caudal fin rays began ossification at 3.1 mm with median rays forming first. Procurrent caudal fin rays were first ossified at 3.6 mm. The ventral hypural cartilage (fused hypurals 1 and 2) and dorsal hypural cartilage (fused hypurals 3 and



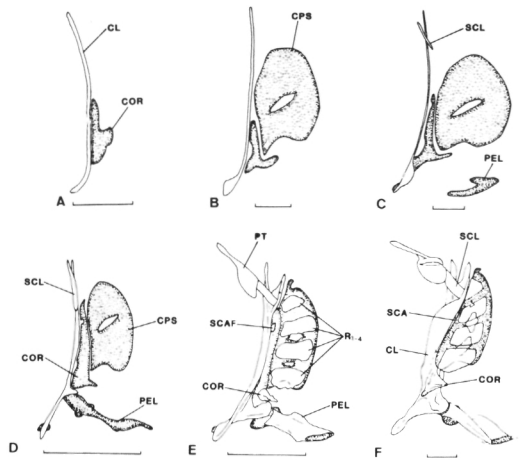
**Figure 7.** Development of axial skeleton of *Bathygobius saporator*. A) 41 days, 6.3 mm SL; B) 97 days, 16.8 mm SL. Stippled, cartilage. Horizontal bar represents 1 mm.

4) were first visible at 3.1 mm beneath the unflexed notochord. The dorsal hypural cartilage was visible as a separate cartilage that sometimes fused to the ventral cartilage near the notochord later in development. The notochord underwent flexion between 3.2 and 3.7 mm. During the same period, epural and parhypural cartilages became visible and the terminal half centrum began to ossify. The epural cartilage was often fused to the penultimate neural spine (also cartilaginous). The hypural plates began to ossify by 3.9 mm. A cartilaginous fifth hypural was present by 4.4 mm. The fifth hypural, epural, and parhypural were all ossifying at 6.8 mm.

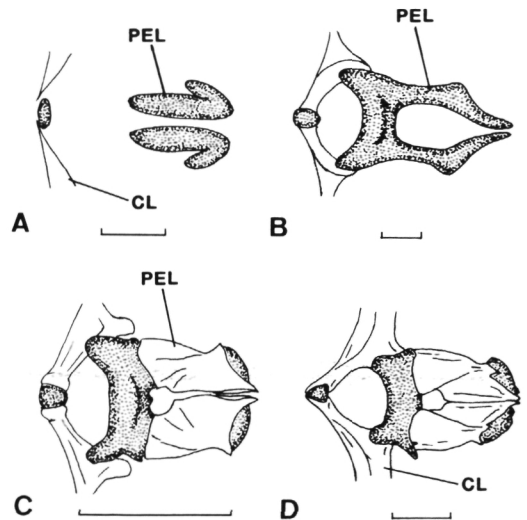
**Vertebral Column (Figures 6, 7).** Vertebral centra ossified from anterior to posterior except for the terminal half centrum which ossified somewhat before those just anterior to it. The centra were first ossified at 3.1 mm. Sixteen centra were visible, the first five with neural arches. All neural and haemal arches except the last three formed, beginning at the centra, with no cartilaginous precursor. Haemal arches and parapophyses were present by 3.3 mm, and developed first on the anterior caudal centra. By 3.9 mm, all vertebral centra and all except the last three neural and haemal arches were ossifying. The last three neural and haemal arches were preformed in cartilage and ossified much later (9.1 mm), after the spines had ossified. The anteriormost of these arches ossified first. Epipleural and pleural ribs ossified from anterior to posterior beginning at 6.3 mm and 9.1 mm respectively. By 16.8 mm, nine epipleural and six pleural ribs were present. Ribs did not have cartilaginous precursors.

**Dorsal and Anal Fins (Figures 6, 7).** Dorsal and anal proximal pterygiophores were developing as cartilage as 3.3 mm. The pterygiophores for the anterior soft rays formed first. By 3.6 mm, all proximal

and most distal pterygiophores were present. Dorsal and anal proximal pterygiophores began to ossify at 4.6 mm and 5.0 mm respectively. Medial pterygiophores of the dorsal and anal fins, first present at 6.3 mm, ossified from the distal end of the proximal pterygiophore cartilages. Distal



**Figure 8.** Development of pectoral girdle (left side) of *Bathygobius soporator*. A) 1 day, 1.9 mm SL; B) 10 days, 3.1 mm SL; C) 13 days, 3.9 mm SL; D) 23 days, 5.4 mm SL; E) 41 days, 6.3 mm SL; F) 97 days, 16.8 mm SL. Stippled, cartilage. Horizontal bar represents 0.1 mm in A-C, 0.5 mm in D-F.



**Figure 9.** Development of pelvic girdle (dorsal view) of *Bathygobius soporator*. A) 13 days, 3.9 mm SL; B) 23 days, 5.4 mm SL; C) 41 days, 6.3 mm SL; D) 97 days, 16.8 mm SL. Stippled, cartilage. Horizontal bar represents 0.1 mm in A and B, 0.5 mm in C and D.



pterygiophores of the dorsal and anal fins first ossified at 17.6 mm. Soft dorsal and anal fin rays first ossified at 3.6 mm. The anterior spinous rays associated with each fin formed along with the soft rays. The four anterior dorsal spines first ossified at 4.1 mm, with all six ossified by 4.3 mm.

### Paired Fins (Figures 8, 9)

The cleithrum was ossified in the smallest larva (1.8 mm). The ventral tips of the cleithra became enlarged early and by 4.9 mm, the main body had become thickened. A posteroventral flange developed with a large recess for the pelvic cartilage. By 6.3 mm, the dorsal end of the cleithrum had divided and the posterior branch received the posterior tip of supracleithrum.

The supracleithrum and dorsal arm of the posttemporal were first ossified at 3.6 mm. Both developed slowly and the ventral arm of the posttemporal had not yet formed by 17.6 mm. The coracoid cartilage was visible in the smallest larva (1.8 mm). The posterior process of the coracoid developed early, but was not large. By 3.9 mm, the scapular portion of the cartilage had formed and the scapular foramen was visible. Ossification of the coracoid, first present at 6.3 mm, originated in the posterior process. The scapula remained cartilaginous until 16.8 mm.

The cartilaginous pectoral fin support, barely visible in newly-hatched larvae, was distinct by 3.1 mm. It was a single block of cartilage with one oblong foramen between future radials 2 and 3. Foramina formed between the other radials as they ossified at 6.3 mm.

The pelvic cartilage was first visible at 3.4 mm as two separate hook-shaped bars in the posterior pelvic region. As these cartilages expanded anterodorsally, they met the cleithra and joined together anteromedially. Ossification

began posteriorly at 4.6 mm and surrounded the two posterior columns.

Pectoral and pelvic fin rays were first ossified at 4.4 mm. Nine middle and upper pectoral rays were present, while all five pelvic soft rays and the single pelvic spine had formed. By 4.9 mm, all 17-19 pectoral rays were ossified.

### ACKNOWLEDGMENTS

I am indebted to Ken Halscott for culturing the rotifers and helping to rear the larvae.

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