

LARVAE OF *TRICHOPSETTA VENTRALIS* (PISCES: BOTHIDAE), WITH COMMENTS ON INTERGENERIC RELATIONSHIPS WITHIN THE BOTHIDAE

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ABSTRACT

Twenty-seven larvae (6.0–28.5 mm SL) of the bothid flatfish *Trichopsetta ventralis* were discovered in plankton samples from the Gulf of Mexico and Florida's east coast. Identity of these hitherto undescribed larvae is based upon meristics and observed continuity of pigment pattern between larva and adult.

Larvae are thin, greatly compressed, and distinguished by otic, urohyal, cleithral, and basipterygial spination. At about 17 mm SL, pigmentation develops on the left side as three series of spots along dorsal and ventral body margins and along the mid-body axis. Placement of spots is constant. Size at transformation is unknown; largest larva shows no cranial asymmetry.

Adult *Trichopsetta ventralis* occur in the Gulf of Mexico in depths of 33–183 m. Distribution of larvae appears to contrast sharply with adult distribution, suggesting a long-term planktonic existence. Patterns of surface circulation, primarily the Loop Current, probably affect distribution of larvae. Larvae of *T. ventralis* are possibly "bioindicators" of Gulf of Mexico surface circulation systems.

A literature review suggests that larval bothids may be assigned to subfamilies Bothinae or Paralichthinae, based upon relative body thickness, location of cephalic spination, pelvic fin osteology, dorsal fin morphology, and size at transformation. An analysis of larval and adult characters of *Taeniopsetta*, *Engyophrys*, *Trichopsetta*, and *Monolene* indicates bothine affiliation.

Twenty-seven larvae of the bothid flatfish *Trichopsetta ventralis* (Goode and Bean) were discovered in plankton samples from the Gulf of Mexico and Florida's east coast (Fig. 1). Identity of these hitherto undescribed larvae is based upon meristics and observed continuity of pigmentation pattern between larva and adult.

Fishes of the genus *Trichopsetta* have received little attention in the literature. *T. ventralis* was described by Goode and Bean (1885: 592) as *Citharichthys ventralis*. Gill (1889: 603) described the genus *Trichopsetta* to include *Citharichthys ventralis*. Jordan and Goss (1889: 262), apparently unaware of Gill's work, suggested the species be referred to as *Arnoglossus ? ventralis*. Goode and Bean (1895), Jordan and Evermann (1898), and Norman (1934) gave brief diagnoses of the species, adding very little to the original description. Longley and Hildebrand (1941), Hildebrand (1954),

Springer and Bullis (1956), and Bullis and Thompson (1965) documented range extensions of the species. Systematics of the genus received no further attention until Anderson and Guthertz (1967) presented diagnoses and illustrations of *T. ventralis* and three new species, *T. melasma*, *T. caribbaea*, and *T. orbisulcus*. Included was material listed by Bullis and Thompson (1965) as *Trichopsetta ventralis* and/or *Trichopsetta* sp.

METHODS

Terms used are defined below.

STANDARD LENGTH (SL). Tip of snout to tip of notochord in young larvae. Tip of snout to posterior margin of hypural elements in older larvae, juveniles and adults.

HEAD LENGTH (HL). Tip of snout to posterior edge of operculum.

PREANUS LENGTH (PAL). Tip of snout

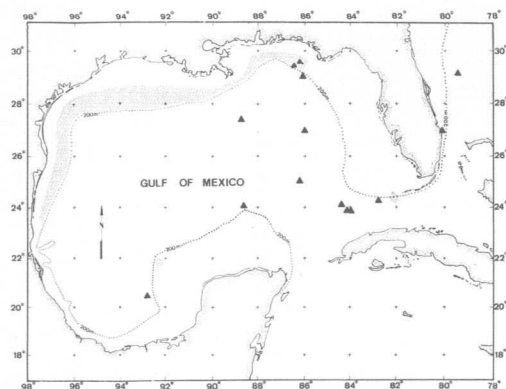


Figure 1. Approximate distribution of adults (stippled area) and capture locations of larvae (triangles) of *Trichopsetta ventralis*.

to a vertical through the anus, along mid-body axis.

BODY DEPTH (BD). Vertical, from anus to dorsal fin base.

EYE DIAMETER (ED). Horizontal diameter of left eye.

JAW LENGTH (JL). Upper jaw, from tip of premaxillary to posterior tip of maxillary.

Measurements were made to the nearest 0.1 mm with ocular micrometer or vernier calipers and relative proportions recorded in percent (Tables 1 and 2). Unless noted otherwise, measurements refer to standard length. Regression lines of morphometrics were calculated from variates transformed to natural logarithms, thus assuring normal distribution. Although Ricker's (1973) "predictive model" of linear regression was used, Table 4 contains necessary information for computation of other models. Analysis of covariance (ANCOVA) was performed on comparable lines of *Trichopsetta ventralis* larvae and juvenile/adults according to procedures of Snedecor and Cochran (1967). Table 4 also contains ANCOVA data so that future comparisons can be made with additional material.

Selected larvae were cleared and stained following Taylor's (1967) method. Osteological terminology follows Futch et al.

(1972) with one exception; caudal fin terminology was synthesized by Hensley (1977).

MATERIAL EXAMINED

Larvae, preserved in 3% buffered Formalin, are in the Florida Department of Natural Resources Marine Research Laboratory Ichthyological Collection, St. Petersburg, FL (FSBC). Juvenile and adult specimens were borrowed from the Florida State University Collection, Tallahassee, FL (FSU) and the United States National Museum, Washington, D.C. (USNM).

Descriptive Material

Trichopsetta ventralis.—*Larvae*: FSBC 8389L, 24°26'N, 82°55'W, 14 June 1963, 1 m plankton net, tow depth 97 m—surface, 1 specimen (11.4 mm); 8390L, 23°54'N, 84°08'W, 15 June 1963, 1 m plankton net, 97 m—surface, 3(6.0–9.0); 8391L, 24°10'N, 84°20'W, 22 June 1963, 1 m plankton net, 97 m—surface, 1(6.4); 8376L, St. Lucie Inlet, FL, 27°10'N, 80°10'W, 14 November 1966, 0.5 m plankton net, surface, 1(10.7); 8392L, HERNAN CORTEZ 64, 29°10'N, 79°33'W, 22 August 1968, 1 m plankton net, 47 m—surface, 1(12.2); 8377L, ALAMINOS 12, Station 6, 20°31'N, 92°53'W, 29 October 1968, 1 m plankton net, 20 m—surface, 1(16.2); 8378L, ALAMINOS 12, Station 8, 24°02'N, 88°35'W, 31 October 1968, 1 m plankton net, 20 m—surface, 3(6.6–14.2); 8379L, ALAMINOS 12, Station 10, 25°01'N, 86°10'W, 31 October–1 November 1968, 1 m plankton net, 60 m—surface, 1(9.4); 8380L, HERNAN CORTEZ 69, 23°50'N, 83°59'W, 24 November 1968, 1 m plankton net, 46 m—surface, 2(16.5, 23.4); 8381L, HERNAN CORTEZ 79, 29°35'N, 86°18'W, 4 September 1969, 1 m plankton net, 73 m—surface, 1(20.6); 8382L, HERNAN CORTEZ 79, 28°40'N, 86°12'W, 7 September 1969, 1 m plankton net, 91 m—surface, 1(18.5); 8349L, HERNAN CORTEZ 81, 29°35'N, 86°18'W, 10 October 1969, 1 m plankton net, 47 m—surface, 2(6.8, 9.7); 8398L, HERNAN CORTEZ 81, 29°25'N, 86°30'W, 10 October 1969, 1 m plankton net, 97 m—surface, 2(6.1, 7.0); 8383L, 27°00'N, 86°00'W, 3 October 1970, 1.8 × 1.8 m Tucker trawl, 50 m—surface, 1(20.2); 8384L, 27°00'N, 86°00'W, 5 October 1970, 1.8 × 1.8 m Tucker trawl, 55 m—surface, 2(22.6, 24.2); 8385L, 27°00'N, 86°00'W, 5 August 1972, 1.8 × 1.8 m Tucker trawl, 60–85 m, 1(27.6); 8387L, 27°00'N, 86°00'W, 9 August 1972, 1.8 × 1.8 m Tucker trawl, 400 m—surface, 1(26.0); 8388L, MIZAR 73-11-09, 27°26'N, 88°

Table 1. Morphometrics of *Trichopsetta ventralis* larvae

Standard Length (mm)	Head Length		Preamble Length		Body Depth		Eye Diameter			Jaw Length		
	(mm)	(%SL)	(mm)	(%SL)	(mm)	(%SL)	(mm)	(%SL)	(%HL)	(mm)	(%SL)	(%HL)
6.0	1.5	28.1	2.6	48.5	2.3	39.0	0.5	7.8	27.8	0.4	7.8	27.8
6.0	1.6	26.7	3.0	50.0	2.0	33.3	0.5	8.3	31.3	0.5	8.3	31.3
6.1	1.7	27.9	2.9	47.5	2.9	47.5	0.6	9.8	35.3	0.4	6.6	23.5
6.6	1.7	25.8	3.0	45.4	2.6	39.3	0.6	9.0	35.3	0.5	7.6	29.4
6.6	1.8	27.3	2.9	43.9	2.8	42.4	0.5	7.6	27.8	0.4	6.0	22.2
6.8	1.9	27.9	3.0	44.1	2.9	42.6	0.6	8.8	31.6	0.5	7.4	26.3
7.0	2.0	28.6	3.1	44.3	3.1	44.3	0.7	10.0	35.0	0.6	8.6	30.0
9.0	2.3	25.5	3.8	42.2	3.9	43.3	0.7	7.7	30.4	0.7	7.8	30.4
9.4	2.8	29.8	3.2	34.0	6.2	65.9	0.9	9.6	32.1	0.8	8.5	28.6
9.7	2.5	25.8	3.9	40.2	5.3	54.6	0.7	7.2	28.0	0.7	7.2	28.0
10.7	2.5	23.3	3.7	34.6	5.5	51.4	0.9	8.4	36.0	0.7	6.5	28.0
10.8	3.0	27.7	4.0	37.0	6.9	64.0	0.9	8.3	30.0	D A M A G E D		
11.4	2.9	25.4	4.4	38.6	5.8	50.8	0.8	7.0	27.6	0.8	7.0	27.6
12.2	3.1	25.4	4.5	36.8	6.3	51.6	1.0	8.1	32.3	0.8	6.6	25.8
14.2	3.5	24.6	4.5	31.7	9.5	66.9	1.1	7.7	31.4	1.0	7.0	28.6
16.2	4.0	24.7	4.6	28.4	10.1	62.4	1.3	8.0	32.5	1.2	7.4	30.0
16.5	3.6	21.8	4.7	28.5	9.7	58.8	1.1	6.6	30.6	1.0	6.1	27.8
18.5	4.4	25.2	4.8	25.9	11.1	60.0	1.2	6.5	27.3	1.1	5.9	25.0
20.2	4.2	20.7	5.0	24.7	12.9	63.8	1.4	6.9	33.3	1.2	5.9	28.6
20.6	4.6	22.3	4.6	22.3	11.5	44.2	1.3	6.3	28.3	1.2	5.8	26.0
22.6	4.5	19.9	4.5	19.9	13.9	61.5	1.5	6.6	33.3	1.5	6.6	33.3
23.4	5.4	23.1	6.3	26.9	14.0	59.8	1.5	6.4	27.8	1.3	5.5	24.1
24.2	5.4	22.3	5.6	23.1	14.9	61.5	1.6	6.6	29.7	1.4	5.8	25.9
26.0	5.8	22.3	5.0	19.2	15.2	58.5	1.8	6.9	31.0	1.5	5.8	25.8
26.2	5.8	22.1	5.7	21.8	15.0	57.3	1.8	6.9	31.0	1.4	5.3	24.1
27.6	5.9	21.4	5.6	20.3	13.9	50.3	1.9	5.3	32.2	1.7	6.2	28.8
28.5	6.3	23.8	6.5	24.5	15.2	57.4	1.8	6.8	28.6	1.6	5.6	25.4

44°W, 16 August 1973, 1.8 × 3.6 m Tucker trawl, 130–60 m, 2(26.2, 28.5).

Comparative Material

Trichopsetta ventralis.—*Juveniles and Adults*: USNM 117147, south of Tortugas, FL, 30 June 1932, 120–230 m, 3(122.0–146.5); 117148, 16 km south of Tortugas, FL, 26 June 1932, 110–240 m, 2(120.8, 158.2); 156046, PELICAN Station 72-6, 29°11.5'N, 88°52'W, 23 May 1938, try net, 4(46.5–81.4); 156056, PELICAN Station 111-4, 27°17.5'N, 96°25.0'W, 30 June 1939, try net, 150 m, 5(45.4–94.5); 156261, PELICAN Station 112-3, 27°13.5'N, 96°40.0'W, 30 January 1939, try net, 77 m, 3(68.1–99.4); 156263, PELICAN Station 115-5, 26°43'N, 96°51'W, 4 February 1939, try net, 45 m, 1(97.0); FSU 20578, 29°50.3'N, 86°26.1'W, 2 December 1969, 10(35.7–170.5); 21505, TURSIOPS 7120, 29°54.5'N, 86°41.0'W, 20 July 1971, 3(116.6–131.6); FSBC 9076 (formerly FSU

22221), TURSIOPS 7110-08, 29°19.5'N, 87°42.5'W, 9 April 1971, 3(114.6–134.5).

Trichopsetta melasma.—*Adult*: USNM uncataloged, OREGON Station 5956, 13°40'N, 60°54'W, 8 May 1968, tumbler dredge, 228 m, 1(103.3).

Trichopsetta caribbaea.—*Adult*: FSU 13674, OREGON Station 3588, 09°18'N, 80°27'W, 29 May 1962, 1(94.6).

Trichopsetta orbisulcus.—USNM 200422, Holotype, OREGON Station 4394, 12°37'N, 71°10'W, 25 September 1963, 119 m, 1(116.6).

RESULTS

Identification

Caudal ray placement, visible on 16 larvae with the adult complement, were distributed on supporting elements as 1-3-4-5-

Table 2. Morphometrics of *Trichopsetta ventralis* adults

Standard Length (mm)	Head Length		Preanus Length		Body Depth		Eye Diameter			Jaw Length		
	(mm)	(%SL)	(mm)	(%SL)	(mm)	(%SL)	(mm)	(%SL)	(%HL)	(mm)	(%SL)	(%HL)
35.7	10.6	29.7	10.5	29.4	12.5	35.0	3.7	10.4	34.9	4.0	11.2	37.7
43.7	11.8	27.0	11.7	26.8	15.8	36.2	3.6	8.2	30.5	5.8	13.3	49.2
44.9	11.4	25.4	14.8	33.3	17.7	39.4	4.1	9.1	36.0	4.9	10.9	43.0
45.5	11.4	25.1	12.0	26.4	15.0	33.3	3.8	8.4	33.3	5.0	11.0	43.9
46.5	12.9	27.7	11.4	24.5	17.0	36.6	3.9	8.4	30.2	4.8	10.3	37.2
53.6	14.0	26.1	14.6	27.2	18.6	34.7	4.7	8.8	33.6	5.5	10.3	39.3
54.8	14.1	25.7	14.0	25.5	17.8	32.5	4.2	7.7	29.8	5.2	9.5	36.9
59.0	15.8	26.8	14.6	24.7	21.0	35.6	4.6	7.8	29.1	6.8	11.5	43.0
68.1	18.6	27.3	18.6	27.3	24.5	36.0	5.2	7.6	28.1	7.5	11.0	40.3
74.6	21.7	29.1	21.1	28.3	26.6	35.7	5.6	7.5	25.8	8.3	11.1	38.2
81.4	21.7	26.7	21.5	26.4	27.8	34.2	5.8	7.1	26.7	9.0	11.1	41.5
82.9	25.3	30.5	25.4	30.6	30.5	36.8	6.5	7.8	25.7	9.0	10.9	35.6
85.0	22.3	26.2	18.8	22.1	32.1	37.8	5.5	6.5	24.7	9.6	11.3	43.0
88.9	22.2	25.0	21.5	24.2	33.0	37.1	5.7	6.4	25.7	9.7	10.9	43.7
89.2	23.0	35.8	24.4	27.4	32.5	36.4	5.7	6.4	24.8	9.6	10.8	41.7
93.5	26.0	27.8	25.0	26.7	34.8	37.2	6.7	7.2	25.8	10.9	11.7	41.9
94.3	26.7	28.3	25.7	27.3	31.6	33.5	6.2	6.6	23.2	10.1	10.7	37.8
94.5	25.2	26.7	23.7	25.1	33.4	35.3	7.0	7.4	27.8	10.5	11.1	41.7
97.0	26.7	27.5	24.5	25.3	37.5	38.7	6.7	6.9	25.1	11.0	11.3	41.2
99.4	27.6	27.8	27.0	27.2	36.1	36.3	6.7	6.7	24.3	11.0	11.1	39.9
116.6	28.3	24.3	28.3	24.3	37.4	32.1	7.9	6.8	27.9	13.0	11.1	45.9
122.8	30.5	24.8	30.0	24.4	44.2	36.0	7.4	6.0	24.3	13.2	10.7	43.3
129.8	32.0	24.7	32.8	25.3	44.4	34.2	7.3	5.6	22.8	15.2	11.7	47.5
131.6	34.7	26.4	32.0	24.3	46.1	35.0	8.3	6.3	23.9	15.6	11.9	45.0
139.0	36.8	26.5	35.7	25.7	48.2	34.7	7.8	5.6	21.2	15.2	10.9	41.3
170.5	44.4	26.0	47.4	27.8	58.0	34.0	9.1	5.3	20.5	20.2	11.8	45.5

3-1 counting ventral to dorsal (Table 3). This distribution is found only in *Monolene*, *Engyophrys*, and *Trichopsetta* among western Atlantic bothids (Gutherz, 1971:267). The vertebral complement of these larvae (10 + 30-31) excludes their placement in *Monolene* or *Engyophrys*. Specific identification is substantiated by meristics and continuity of pigment patterns between larva and adult. The combination of vertebral and fin ray counts are unique to *T. ventralis* among the genus (Anderson and Gutherz, 1967). All larvae 16.5 mm and larger display melanophore concentrations along dorsal and ventral body margins at regular intervals; 11 adults examined retained areas of dark pigment at comparable intervals (Table 5). Al-

though some specimens did not have the entire series of spots, the correlation appears reliable.

Description

Pigmentation

(Figs. 4, 5; Table 5)

Pigmentation consists of three series of spots, left side only, along dorsal and anal fin pterygiophores and along mid-body axis, developed on larvae 16.5 mm and larger. Specific location of spots in relation to pterygiophores and myomeres is summarized in Table 5. The 28.5 mm specimen displays additional pigment (Fig. 5). Eyes of all larvae are pigmented.

Table 3. Meristics of *Trichopsetta ventralis* larvae

SL	Fin Rays			Pelvic		Spination				
	Dorsal	Anal	Caudal	(Left)	(Right)	Otic	Uro-hyal	Basi- ptery- gium	Clei- thrum	Vertebrae/ Myomeres
6.0	*	*	0+3	Bud	Bud	2	0	0	0	*
6.0	76	42	0+2+3+2	Bud	Bud	3	0	0	0	10+30
6.1	72	50	*	Bud	Bud	3	0	0	0	10+30
6.6	68	47	0+2+3+1+1	Bud	Bud	2	0	0	0	10+30
6.6	82	70	*	Bud	Bud	2	0	0	0	10+31
6.8	82	67	0+4+4	Bud	Bud	2	0	0	1	10+30
7.0	78	64	0+3+3+6	Bud	Bud	2	0	0	0	10+30
9.0	93	75	0+4+4+6+2+1	Bud	Bud	3	0	0	1	10+31
9.4	92	75	1+3+5+4+3+1	6	6	3	0	0	3	10+31
9.7	88	71	1+2+4+6+3+1	4	4	2	0	0	1	10+30
10.7	93	73	1+3+4+5+3+1	6	6	2	0	0	1	10+31
10.8	94	72	1+3+4+5+3+1	6	6	3	10	0	3	10+30
11.4	88	70	1+3+4+5+3+1	6	6	3	0	0	1	10+30
12.2	94	73	*	6	6	3	5	1	0	10+30
14.2	94	74	1+3+4+5+3+1	6	6	3	10	0	3	10+31
16.2	93	74	1+3+4+5+3+1	6	6	2	12	3	*	10+30
16.5	93	72	*	6	6	3	7	0	2	10+30
18.5	93	72	1+3+4+5+3+1	6	6	3	9	0	6	10+30
20.2	93	72	1+3+4+5+3+1	6	6	3	13	2	2	10+30
20.6	94	74	1+3+4+5+3+1	6	6	3	11	5	4	10+31
22.6	90	71	1+3+4+5+3+1	6	6	3	10	7	3	10+30
23.4	88	70	*	6	6	3	15	*	5	10+30
24.2	93	73	1+3+4+5+3+1	6	6	3	11	15	*	10+30
26.0	88	71	1+3+4+5+3+1	6	6	3	13	12	6	10+30
26.0	91	72	1+3+4+5+3+1	6	6	3	13	11	7	10+30
27.6	95	73	1+3+4+5+3+1	6	6	3	10	10	5	10+31
28.5	96	76	1+3+4+5+3+1	6	6	3	13	13	8	10+30

* Damaged, or not visible.

Head Development (Figs. 2-5; Tables 1, 3, 4)

The brain is distinctly trilobed throughout the size series. Nasal capsules are evident in the 10.8 mm specimen, dorsal and ventral skin flaps merge forming tubular nostrils by 20.6 mm. Head 19.9-28.9% SL, decreasing slightly with increasing standard length. Eye diameter 5.3-10.0% SL, decreasing with increasing standard length. Eye diameter is fairly constant with respect to head length ($\bar{x} = 31.02\% \text{ HL}$, $S^2 = 6.81$).

Neurocranium.—At 6.1 mm, the supraoccipital is heavily stained, and paired frontals are stained anteriorly. The otic region is swollen; paired autopterotic cartilages, each bearing two swellings, are visible. The para-

sphenoid is lightly stained from its posterior connection with the cartilagenous basioccipital to anterior association with the unossified prevomer. No other neurocranial elements are recognizable. This condition remains much the same until about 10.8 mm. Then, paired parietals are visible, slightly overlapping the frontals. Autopterotics retain stain in the vicinity of the two swellings. Other non-staining elements in the basicranial region, in the area where the prootics and basioccipitals might be expected, are now visible. The parasphenoid has grown in width, and the prevomer retains alizarin. Cartilagenous ethmoid elements lie above the prevomer. At 20.2 mm, parietals and epiotics are completely stained. By 26.2 mm, the frontals project anteriorly to meet

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

Y	X	N	ln \bar{X}	ln \bar{Y}	Σx^2	Σy^2	Σxy	b	a	r	100r ²
Larvae											
lnHL	lnSL	27	2.57	1.16	7.7461	5.5238	6.4872	0.8374	0.3708	0.9917	98.34
lnPAL	lnSL	27	2.57	1.42	7.7461	1.7764	3.5347	0.4563	1.2834	0.9529	90.80
lnBD	lnSL	27	2.57	1.92	7.7461	12.3094	9.5798	1.2368	0.2859	0.9811	96.25
lnED	lnSL	27	2.57	-0.01	7.7461	4.9860	6.1063	0.7883	0.1309	0.9826	96.55
lnJL	lnSL	26	2.57	-0.14	7.7100	5.4639	6.3525	0.8240	0.1042	0.9788	95.80
lnED	lnHL	27	1.16	0.18	5.5238	4.9860	5.1664	0.9353	0.3353	0.9844	96.60
lnJL	lnHL	26	1.15	-0.14	5.5205	5.4639	5.3795	0.9745	0.2806	0.9795	95.94
Juveniles and Adults											
lnHL	lnSL	26	4.38	3.07	4.2671	3.8130	3.9843	0.9337	0.3598	0.9877	97.55
lnPAL	lnSL	26	4.38	3.04	4.2671	3.8569	3.9756	0.9316	0.3353	0.9799	96.02
lnBD	lnSL	26	4.38	3.34	4.2671	4.2000	4.2001	0.9843	0.3801	0.9925	98.50
lnED	lnSL	26	4.38	1.74	4.2671	1.8409	2.7373	0.6415	0.3442	0.9766	95.37
lnJL	lnSL	26	4.38	2.18	4.2671	4.5711	4.3746	1.0252	0.0994	0.9905	98.10
lnED	lnHL	26	3.07	1.74	3.8130	1.8409	2.5997	0.6817	0.7061	0.9812	96.27
lnJL	lnHL	26	3.07	2.18	3.8130	4.5711	4.0920	1.0731	0.3295	0.9801	96.05

X = independent variable.

Y = dependent variable.

N = number of specimens examined.

 \bar{X} = mean value of X. \bar{Y} = mean value of Y. Σx^2 = sum of squares of X. Σy^2 = sum of squares of Y. Σxy = sum of products.

b = slope.

a = y intercept.

r = correlation coefficient.

100r² = percent of variation in Y attributable to variation in X.

ethmoid and prefrontal elements, the latter are lightly stained. Remaining neurocranial bones are poorly ossified, or unrecognizable as such.

Branchiocranium.—**OROMANDIBULAR REGION.** In the 6.1 mm specimen, jaws are symmetric. Premaxillaries, each bearing three teeth, exclude maxillaries from the gape. Each premaxillary bears a well developed medial ascending process. Each maxillary bears two proximal processes, the dorsal cranial condyle, and the ventral premaxillary condyle. Dentaries, each bearing a single tooth, meet in mesial symphysis and arise as lamellae lateral to Meckel's cartilages. Posteriorly, dentaries are overlapped by the angulars. Beneath each angular, Meckel's cartilages curve ventrad, ending in the retroarticulars. Quadrates are visible as cartilages at the dorsoposterior corner of each angular. By 6.8 mm, these elements are more strongly ossified. Each premaxillary and dentary bears four and two larval

teeth respectively. Ectopterygoid cartilages are now visible following the posterior contour of each maxillary. At 10.8 mm, quadrates and ectopterygoids are more heavily ossified. An unossified autopalatine extends from the anterior corner of each ectopterygoid to the maxillary cranial condyles. By 11.4 mm, premaxillaries and dentaries bear four and three teeth. Endopterygoids develop dorsal to the ectopterygoids. By 26.2 mm, premaxillaries and dentaries bear seven

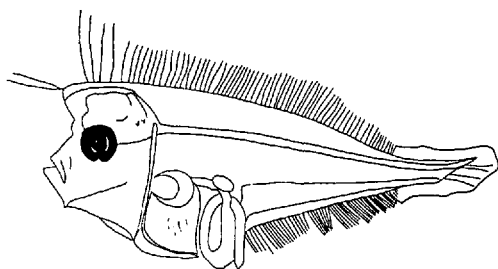
Figure 2. *Trichopsetta ventralis*, 6.4 mm SL; FSBC 8391L.

Table 5. Pigment location in relation to pterygiophores and myomeres in *Trichopsetta ventralis* larvae, juveniles, and adults (pigment spots numbered anterior to posterior)

Size (mm SL)	Dorsal Series (Pterygiophore Number)						Ventral Series (Pterygiophore Number)				Mid-Body Series (Myomere Number)		
	1	2	3	4	5	6	1	2	3	4	1	2	3
Larvae													
16.5	—	—	25-26	—	—	—	—	20-21	—	—	8	23-24	37
18.5	—	16	26-27	41-42	—	—	—	20-21	38	—	—	22-23	—
20.2	—	—	26-27	42-43	62-63	—	—	22-24	44-45	—	—	26	—
20.6	—	—	27	42-43	61	—	6-7	22-24	42-43	—	7-8	24-25	35-36
22.6	—	14	24-26	39-41	57-58	71	5-6	20-23	38-40	52-53	7-9	23-25	36-37
23.4	—	13-14	25-26	38-39	—	—	4-5	20-22	—	—	9	24	38
24.2	—	15-16	25-27	41-43	60-62	—	6	22-24	42-44	—	8-9	24-25	36-37
26.0	—	—	25-26	39-40	58	—	7	22-24	42-43	—	—	23-24	36
26.2	—	15-16	20-27	40-41	60-62	75-76	6-7	22-24	42-44	58	9	23-24	36-37
27.6	—	—	27-28	42-43	62-64	78-79	8	20-22	42-44	58-59	8-9	24-25	37-38
28.5	8	15-16	27-29	41-43	60-62	77-78	6-8	22-25	43-45	57-59	9	23-24	37-38
Juveniles and Adults													
54.8	8	15	26-28	41-44	58-60	77-78	—	21-22	43-44	56	—	—	—
85.0	—	15	25-27	40-41	58-59	—	—	22-24	42-44	54-56	—	—	—
88.9	—	—	26-27	41-43	59-60	75	—	—	—	—	—	—	—
89.2	8-9	—	25-27	42-44	59-60	74	—	—	—	—	—	—	—
94.3	—	15-16	26-28	41-43	57-59	76-78	7-9	21-23	43-46	—	—	—	—
116.6	7-8	15	25-26	39-40	57-58	72	—	20-21	43-44	57-58	—	—	—
122.8	8	14-15	26-27	41-43	60-61	74-75	8	20	42-43	—	—	—	—
129.8	—	15	22	40-41	59-60	75	8	21	41	60	—	—	—
131.6	—	15-16	26-27	40-41	58-59	72-74	—	22-24	43-44	56-57	—	—	—
139.0	8-9	14-16	27-28	41-42	58-59	73-74	—	21-22	41-42	56-58	—	—	—
170.5	8	—	25-27	41-42	60-61	75-76	—	21-22	40-41	55-56	—	—	—

and six teeth. No other significant changes in jaw morphology occur throughout the size series.

Jaw length ranges from 5.3-8.6% SL, percentage generally decreasing with increasing standard length. Jaw length as a percentage of head length is fairly constant ($\bar{x} = 27.4\%$ HL, $S^2 = 6.73$).

HYOID REGION. Ossified hyoid elements in the 6.1 mm specimen include preoperculars, operculars, suboperculars, hyomandibulars, seven pairs of branchiostegals and the median urohyal. By 6.8 mm, symplectics and interoperculars are visible, but not ossified. At 11.4 mm, epihyals and ceratohyals are ossified. Interhyals and hypohyals are ossified in the 20.2 mm specimen. The most striking feature of the hyoid region is urohyal spination. First spines appear at 9.0 mm and increase in number with standard

length. The six largest specimens bear 13-15 urohyal spines.

BRANCHIAL REGION. Branchial arches of the 20.2 mm specimen were removed and examined. The arches are lightly stained, making it difficult to determine number and placement of certain elements. Nevertheless,

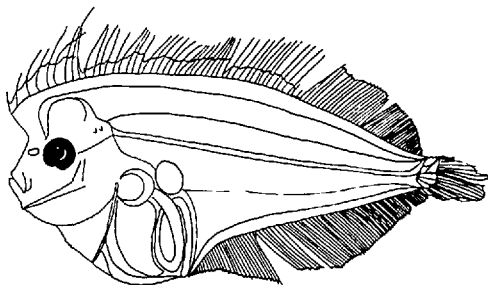


Figure 3. *Trichopsetta ventralis*, 9.0 mm SL; FSBC 8390L.

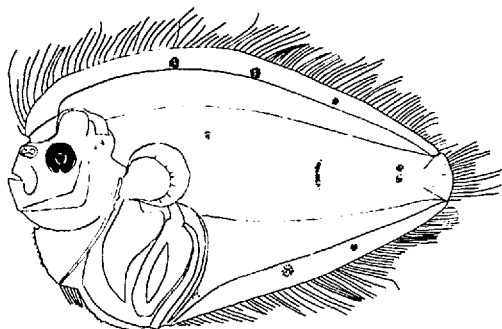


Figure 4. *Trichopsetta ventralis*, 20.6 mm SL; FSBC 8381L.

basic gill arch structure is similar to that of 24 species of Japanese flounders described and figured by Amaoka (1969). The basihyal is long and pointed. Three, possibly four, basibranchials lie along the floor of the pharyngeal cavity. Adpharyngeal components of gill arches 1–3 are hypobranchials, each associated with the basibranchials. Distally, they articulate with the ceratobranchials. Ceratobranchials 4 and 5 have no hypobranchials, but are associated proximally with a round cartilagenous element appearing to be a basibranchial. Its identity and homology are uncertain. Arches 1–4 articulate distally with epibranchials; the first three bear pharyngobranchial tooth plates. Ceratobranchial 5, bearing a tooth plate, has no distal elements. The adult complement of nine gill rakers is present on gill arch 1, distributed as two on the hypobranchial and seven on the ceratobranchial.

Body Development (Figs. 2–6; Tables 1, 3, 4)

The body is greatly compressed and diaphanous. Preanus length:standard length ratio (19.2–50.0% SL) decreased with increasing standard length. Body depth is variable ($\bar{x} = 53.1\%$ SL, $S^2 = 89.20$), probably caused by shrinkage and distortion in preservation and storage. The gut is a single loop to the left. The liver is large, occupying most of the body cavity anterior to

the gut. The mesonephric duct follows the posterior contour of the body cavity, ending at the vent. The swimbladder is visible in all larvae, slightly displaced to the right side of the body.

Vertebral Column.—Myomeres/vertebrae in all specimens number 10 + 30–31, including the terminal half-centrum. At 6.1 mm, distinct constrictions in the notochord mark developing vertebral centra, though none are ossified. Neural spines of trunk vertebrae 2–10 are ossified, and neural elements of 27 caudal vertebrae are present. The notochord is flexed slightly dorsad. By 10.7 mm, neural and hemal elements of all caudal vertebrae are ossified. The neural arch of the atlas and hemal elements of remaining trunk vertebrae are unossified, but recognizable. By 11.4 mm, the terminal half-centrum is ossified. At 14.2 mm, hemal arches of trunk vertebrae 5–10 and dorsal portions of all vertebral centra are ossified. By 26.2 mm, all centra are ossified, with heaviest concentrations of stain occurring at neural and hemal arch bases. The atlas is now visible as a very small centrum with a neural spine extending only slightly dorsad of the arch. Hemal arches on trunk vertebrae 5–10 are now heavily ossified; each arch is closed. The first hemal spine is very large and concave anteriorly to accommodate the first anal pterygiophore.

Caudal Skeleton.—The notochord of the 6.0 mm specimen (Fig. 6A) is flexed slightly dorsad. Primordial hypural elements, including the parhypural, hypural 1+2 and hypural 3+4, are visible emanating from the ventral aspect of the notochord. About three lepidotrichs are located on hypural 1+2. By 6.1 mm (Fig. 6B), the hemal spine of the second preural centrum and hypural 5 are developed. About 7 lepidotrichs are present. At 6.8 mm (Fig. 6C), the notochord is flexed more sharply, and the neural spine of the as yet unossified second preural centrum is visible. The epural lies dorsal to the notochord. About 14 lepidotrichs are present. By 9.0 mm (Fig. 6D), the adult com-

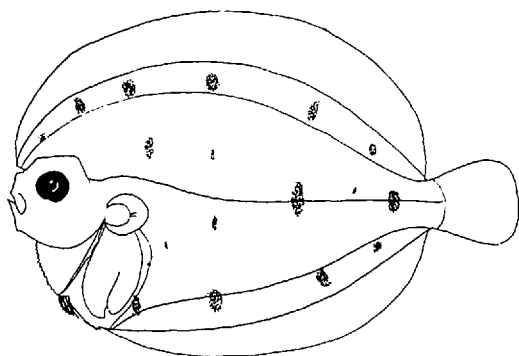


Figure 5. *Trichopsetta ventralis*, 28.5 mm SL; FSBC 8388L. Pigmentation pattern in largest larval specimen.

plement of 17 lepidotrichs is present, but not yet arrayed in the adult configuration. By 10.7 mm (Fig. 6E), the adult arrangement is present (1-3-4-5-3-1, counted from hemal spine to neural spine). Hypural 5 has migrated dorsal to the notochord tip and fused, or otherwise closely associated with the epural. The parhypural arises in close association with the second preural centrum. The terminal half-centrum (assumed to be composed of first and second ural centra and first preural centrum) ossifies between 10 and 12 mm, and remaining caudal elements begin to absorb stain shortly thereafter. By 20.2 mm (Fig. 6F), union of the epural and hypural 5 is complete, and the compound nature of the bone is unrecognizable. One anomalous condition was noted; the second preural centrum of the 20.2 mm specimen bears two neural spines.

Appendicular Skeleton.—Adult *Trichopsetta ventralis* have paired pectoral fins, bearing 12–13 and 8–10 lepidotrichs on left and right fins. Radiographs suggest a typical bothid arrangement of supporting bones, including cleithrum, supracleithrum, postcleithra, coracoid, scapula and radials (Woolcott et al., 1968; Richardson and Joseph, 1973).

Cleithra are heavily ossified in the 6.1 mm specimen, and a supracleithral cartilage is attached to each cleithrum dorsally. A

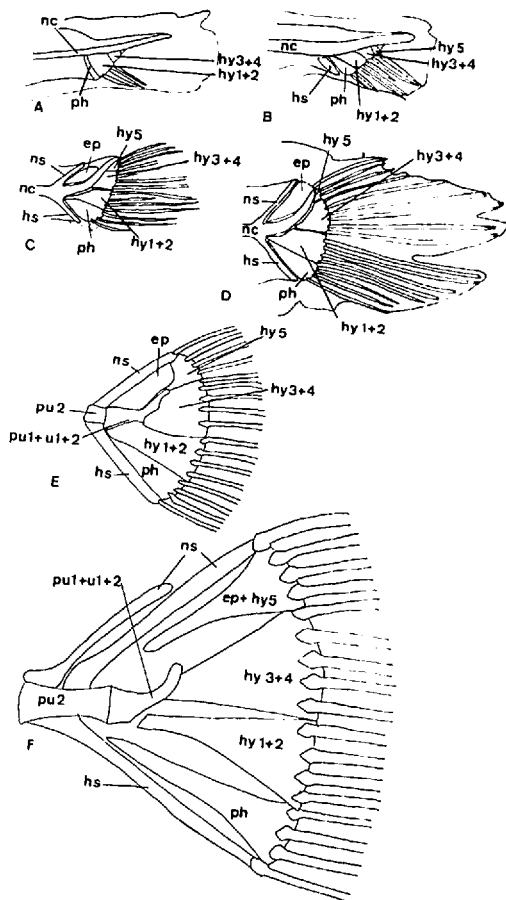


Figure 6. Developmental series of caudal fin development in *Trichopsetta ventralis*. A, 6.0 mm SL; B, 6.1 mm SL; C, 6.8 mm SL; D, 9.0 mm SL; E, 10.7 mm SL; F, 20.2 mm SL. Abbreviations: nc = notochord; ph = parhypural; ns = neural spine; hs = hemal spine; hy = hypural; ep = epural; pu2 = second preural centrum; pu1+ul+2 = terminal half-centrum.

series of cleithral spines first develop at 6.8 mm. Although spines are variable in number, there is a general increase with increasing standard length. Largest number of spines was eight. Cleithra become larger and postcleithral elements appear by 10.7 mm. At 11.4 mm, supracleithra and posttemporals are ossified. No other significant changes occur throughout the larval series examined. The largest larva retains the

typical fan-shaped larval pectoral fin, and no other pectoral bones are present.

In adult *Trichopsetta ventralis* pelvic fins, the first ray of the left fin is inserted 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. The left fin base is on the ventral median line; the right fin base lies above this line. Paired basipterygial cartilages are present in smallest larvae, emanating from ventroposterior surfaces of the cleithra, curving beneath the body cavity, and ending anterior to the vent. Small primordial buds, later developing into fins, are present. Pelvic fins develop rapidly; the 9.0 mm specimen has only buds, the 9.7 mm specimen has four lepidotrichs on each fin, and the 10.7 mm specimen bears the adult complement of six lepidotrichs each. By this size, the left fin is located anterior to the right fin, the first indication of basipterygial asymmetry. By 12.2 mm, asymmetry is more pronounced, the left basipterygium becoming larger than the right. Ventrally directed spines develop on a keel-like process of the left basipterygium. The number of spines increases with standard length; the largest specimen bears 13.

Transformation

Size at transformation is unknown. The largest larva examined is 28.5 mm, and the smallest juvenile is 35.7 mm. Nevertheless, certain changes in morphometrics, osteology and pigmentation at transformation can be inferred.

ANCOVA of comparable regression lines between larvae and juvenile/adults indicated the following: Significant differences ($P = .05$) between mean square residuals of SL:BD and SL:JL; significant differences between slopes of SL:HL, SL:PAL, SL:ED, and HL:ED. The remaining lines, HL:JL, differed in elevation (y-intercept). Accordingly, the head length-jaw length relationship, an adult diagnostic character, changes

the least of all morphometric relationships examined (Tables 1, 2, 4).

Osteological changes through transformation include initiation of cranial torsion and asymmetry associated with eye migration; increased ossification of syncranial elements; development of postcleithra, coracoids, scapulae, radials, and the associated adult-type pectoral fin; loss of basipterygial, cleithral, and otic spination; and reduction of urohyal spination to three blunt projections.

There are changes in the mid-body series of pigmentation, but the dorsal and ventral series of spots remains constant (Table 5). Relationship of mid-body pigmentation between larva and adult is not clear. Apparently, the small spot at myomeres 7-9 becomes the large spot at the juncture of curved and straight segments of the lateral line. The large spot at myomeres 35-38 most certainly becomes the one on the lateral line immediately anterior to the caudal peduncle.

DISCUSSION

Distribution

General morphology and distribution of *Trichopsetta ventralis* larvae indicates they are "long-distance" or "teleplanic" (Scheltema, 1971) larvae. The thin, greatly compressed body provides a large surface area-to-volume ratio, a well documented flotation mechanism. Furthermore, larvae are diaphanous until about 17 mm and lightly pigmented thereafter, another adaptation to planktonic life (Breder, 1962).

The three largest larvae were captured in closing nets at depths between 60 and 130 m; all others were taken in oblique tows made from as deep as 400 m to surface. Concomitant surface tows at several collection locations captured no *Trichopsetta ventralis* larvae, suggesting their exclusion from uppermost surface waters. There is no data to speculate upon vertical migrations. However, presence of a swimbladder throughout the size series indicates an ability to adjust depth.

Juvenile and adult *Trichopsetta ventralis* are known from the Gulf of Mexico continental shelf off Tamaulipas, Mexico, to Panama City, Florida. The species has also been collected off Tortugas, Florida (Longley and Hildebrand, 1941:45). Bullis and Thompson (1965) recorded *T. ventralis* from one location on the Yucatan shelf (identity unconfirmed). They further listed *T. ventralis* outside the Gulf of Mexico, but Anderson and Guthertz' (1967) study strongly indicates these records pertain to other *Trichopsetta* species. Topp and Hoff's (1972: 107) listing of *T. ventralis* outside the Gulf of Mexico is spurious; they were unaware of the Anderson and Guthertz (1967) treatment of the genus. *Trichopsetta ventralis* are most frequently captured in depths of 33–183 m. However, Bullis and Thompson (1965) list *T. ventralis* from two northern Gulf of Mexico locations at depths of 320 and 402 m (OREGON Stations 1095 and 541).

Capture locations of larvae appear to contrast sharply with known adult distribution (Fig. 1). Smallest larvae have been taken near the continental shelf in the northeastern Gulf, Florida Straits, and off Yucatan. Distribution of larger larvae over deep water further suggests their dispersal by surface currents. Additional western Gulf of Mexico collections should clarify larval distribution and dispersal patterns.

Recent investigations have elucidated general patterns of surface circulation in the Gulf of Mexico and adjacent waters. The Caribbean Current flows northward through the Yucatan Straits into the eastern Gulf of Mexico basin. It then forms a clockwise loop (the Loop Current) and flows southward into the Florida Straits where it joins the Florida Current. During spring, the Loop Current intrudes increasingly northward, reaches northernmost penetration by autumn, and recedes during winter (Leipper, 1970). Annual and seasonal variation in this sequence has been documented (Maul, 1974). Meanders in the main current body sometimes detach as eddies and wash into

the western Gulf (Nowlin, 1971) or onto the Florida shelf (Jones et al., 1973). Surface circulation in the western Gulf is poorly known. It is thought to consist of generally minor currents and a clockwise cell oriented northeast to southwest (Nowlin, 1971:32). This cell is probably generated and driven by the Loop Current (Jones et al., 1973: IIB-4).

Small *Trichopsetta ventralis* larvae were taken in the northern Gulf during autumn when the Loop Current typically attains northernmost penetration. Small larvae from the southern Gulf and Florida Straits were clearly in areas influenced by the Loop Current and Florida Current. Thus, small larvae had access to a current system as a means of dispersal.

I have no information on length of larval life of *Trichopsetta ventralis*; samples were occasional and contained too few larvae for length frequency analysis. There is no data on spawning time of adults. Occurrence of large and small larvae from comparable months suggests either a protracted spawning season, or long-term planktonic existence. The latter postulate is favored judging from morphological evidence alone.

That adult *Trichopsetta ventralis* have been taken only from the Gulf of Mexico suggests suitable habitat does not exist elsewhere. The northern Gulf shelf contains a warm temperate fauna and is included in Briggs' (1974) Carolina Warm Temperate Region as the "north Gulf of Mexico section." Topp and Hoff (1972) in their treatment of zoogeography of Gulf of Mexico flatfishes point out that two species, *Scophthalmus aquosus* and *Etropus microstomus* (Gill), exhibit a disjunct distribution, occurring in the northern Gulf of Mexico and along the east coast of the United States from Cape Canaveral to north of Cape Hatteras. Perhaps *Trichopsetta ventralis* conforms to a similar distribution. However, extensive sampling by the United States Fish and Wildlife Service and others along the Atlantic coast has failed, to my knowledge, to yield *T. ventralis* juveniles or adults.

Occurrence of two larvae (FSBC 8376L and 8392L) offshore Stuart and Daytona Beach, Florida (Fig. 1) indicates that larvae can reach the Atlantic seaboard. The mechanism for entrainment and transport of organisms from the eastern Gulf of Mexico to the Atlantic Ocean might be by normal merging of the Loop Current and Florida Current. Alternatively, Murphy et al. (1975) documented entrainment and transport of the dinoflagellate *Gymnodinium breve* Davis from the Florida lower west coast to the lower east coast by an unexpected degradation of the main body of the Loop Current. There are records of several species of distinctly tropical fishes carried to the New England area by the Gulf Stream. These include Smith (1902a; 1902b), Colton (1961), and Alperin and Schaefer (1964). Nevertheless, existence of a dispersal mechanism does not assure dispersal of the species.

Recruitment of fish eggs and larvae from the Caribbean Sea through the Yucatan Straits into Florida and adjacent waters is well documented (Caldwell, 1959; Dawson, 1962; Caldwell, 1963; Eldred, 1968; Starck, 1968; Haburay et al., 1969; Eldred, 1971; Smith and Castle, 1972). Caribbean recruitment of palinurid and scyllarid lobsters has been treated in detail by Ingle et al. (1963), Sims and Ingle (1967) and Hammer (1974). None of approximately 300 samples taken by Marine Research Laboratory sampling in the Yucatan Straits, however, yielded any *Trichopsetta ventralis* larvae, and no adults are known from the Caribbean Sea.

Accordingly, an assumption of long distance dispersal of *Trichopsetta ventralis* remains unconfirmed and fate of larvae is undetermined. It is tempting to speculate that the rather large individuals (ca. 20–28 mm) captured well seaward of the continental shelf are trapped in unfavorable eddies or currents, exhibiting continued growth with retardation of transformation in absence of suitable habitat. Kyle (1913:5) first presented evidence that *Bothus* may have a larval period of indefinite length, and stated (p. 39) that metamorphosis in *Arnoglossus*

and *Pleuronectes* was governed by proximity to deep water. Colton (1961) found larvae of *Bothus ocellatus* (Agassiz) in the Gulf Stream off Georges Bank, larvae larger than known size at metamorphosis. Topp and Hoff (1972) attributed this disparity in size to retardation of metamorphosis. However, evidence at hand suggests that *Trichopsetta ventralis* larvae are not abnormally large and that transformation has not been retarded. Morphometric analysis shows no overlap in sizes of largest larva and smallest juvenile. Moreover, allometry between larvae and juvenile/adults does not appear to be any greater than larval and adult allometry reported for *Syacium papillosum* (Linné) [Futch and Hoff, 1971], *Citharichthys arcifrons* Goode and Bean and *Etropus microstomus* (Gill) [Richardson and Joseph, 1973]. Thus, the most likely assumption is that larval *Trichopsetta ventralis* in deeper Gulf waters are returned to the Gulf of Mexico shelf; occasionally, larvae may be lost to the Gulf Stream.

Recent interest in use of plankters as indicators of current systems has been thoroughly discussed by Hammer (1974). Present knowledge of *Trichopsetta ventralis* biology does not fulfill sufficient criteria to accord the species a "bio-indicator" status, but there is a distinct possibility it could be established as such. Needed are additional samples from year-round sampling so that length-frequency analyses might determine growth rates. Relationship of capture location with known current location would be essential. A complete size series demonstrating size at transformation would settle any questions regarding arrested development.

Phyletic Considerations

The bothid genera *Trichopsetta* and *Engyophrys* are very closely related. Anderson and Gutherz (1967) considered placing *Trichopsetta orbisulcus* in *Engyophrys*, but ultimately decided its characters favored *Trichopsetta*. Gutherz (1971:267) demon-

strated similarities in caudal skeleton morphology between the genera. Larvae of each are remarkably similar. Ahlstrom (1971:41) described larvae of *Engyophrys sanctilaurentii* Jordan and Bollman as having "heavy serrations on the ventral edge of the body fore and aft of the cleithrum," with three small otic spines. He did not mention cleithral spination. Larvae of *E. senta*, Ginsburg, described by Hensley (1977), possess urohyal, basipterygial, cleithral, and otic spination similar to that of *Trichopsetta ventralis*. There are other similarities between the larvae. The supraoccipital in early larvae of each is heavily ossified, and striking similarities in development of the caudal fin further suggest a close relationship. Regression lines of measurements for both *Trichopsetta ventralis* and *Engyophrys senta* were compared by ANCOVA using data from Hensley (1977: Table 4). Although all comparable lines appeared similar, only eye diameter on standard length lines did not differ significantly. The two lines clearly the most different were those of jaw length on standard length, and jaw length on head length. The latter is an important character distinguishing adults of *Engyophrys senta* and *Trichopsetta* species (Anderson and Gutherz, 1967).

Moser and Ahlstrom (1974) used larval characters in combination with adult characters to define two distinct subgroupings of myctophid larvae consonant with the existing subfamilial scheme based upon adult characters. This study of *Trichopsetta ventralis* suggests that relationships among bothid genera might be derived in similar fashion.

Norman's (1934) monograph of the flatfishes is generally regarded as the baseline for subsequent studies of Bothidae. He recognized three subfamilies, Paralichthyinae, Bothinae, and Scopthalminae, each distinguished by pelvic fin morphology and structure of vertebral centra. Hubbs (1945), Hubbs and Hubbs (1945), and Greenwood et al. (1966) recognized the latter subfamily as a separate family, Scopthalmidae. Amaoka (1969:65) in his study of the sinistral

flounders of Japan, recounted several authors' suggestions relating to bothid phylogeny and concluded that it was unsatisfactorily understood "because of poor osteological studies of the flatfishes and because of the special emphasis each author placed on a few characters." His studies of comparative osteology elevated Paralichthyinae to family status [Paralichthyidae (Jordan, 1923; Chabanaud, 1949a; 1949b)] and erected a new bothid subfamily, Taeniopsettiniae. Scopthalmid fishes are not known from Japan and were not treated.

Amaoka's (1969) concept of bothid phylogeny is the most detailed in terms of adult characters, but exclusion of taxa not occurring in Japan limits its direct application elsewhere. Until cosmopolitan review of Norman's (1934) Bothidae by use of Amaoka's (1969) criteria, I refer to subfamilies Paralichthyinae and Bothinae, yet recognize Scopthalmidae based upon comprehensive reappraisal (Hubbs, 1945).

Presently, any synthesis relating adult and larval characters to derive relationships among bothid genera is subject to formidable constraints. Osteology of many species is poorly known or unknown. Larvae of most bothid taxa are undescribed, and some larval descriptions are superficial or questionable. Nevertheless, there is evidence that known larval bothids do constitute at least two natural and logical subgroups.

Differences between bothine and paralichthyne larvae can be demonstrated. Okiyama (1974:39-40) listed several larval characters diagnostic of Paralichthyinae [Amaoka's (1969) Paralichthyidae]. The following tentative subfamilial diagnoses are proposed, drawing from Okiyama's (1974) diagnosis, and other larval fish literature including: Weber (1913), Regan (1916), Hildebrand and Cable (1930), Hubbs and Chu (1934), Uchida (1936), Bruun (1937), Hsiao (1940), Gopinath (1946), John (1951), Padoa (1956), Jones and Pantulu (1958), Colton (1961), Nielsen (1961; 1963a; 1963b), Jutare (1962), Amaoka (1963; 1964; 1970; 1971; 1972; 1973;

1974; 1976), Balakrishnan (1963), Ochiai and Amaoka (1963), Ahlstrom (1965; 1971), Pertseva-Ostroumova (1965; 1971), Aboussouan (1968; 1969; 1972), Smith and Fahay (1970), Futch (1971), Futch and Hoff (1971), Guthertz (1971), Leonard (1971), Richardson and Joseph (1972), and Hensley (1977).

Paralichthinae.—Body thickened, not diaphanous; spination usually present on opercular series, sometimes present on frontals and posttemporals; posterior processes of basipterygia short, not extending beneath body cavity to vent; 0–11 elongate anterior dorsal rays, usually with sheathing membranes densely pigmented; transformation evident, sometimes nearly complete by 15 mm.

Bothinae.—Body thin, diaphanous; spination absent, or present only on urohyal, basipterygia, cleithra, or otic series; posterior process of basipterygia long, extending beneath body cavity almost, or completely to vent; second dorsal ray long, sheath sometimes pigmented; transformation not evident at 15 mm.

The value of other less trenchant characters is not clear. Relative size and placement of pelvic fins deserve closer scrutiny. Consistent differences in pigmentation between subfamilies are not evident.

Consideration of adult and larval morphology of *Taeniopsetta ocellata* (Günther), *Engyophrys senta*, *Trichopsetta ventralis*, and *Monolene sessilicauda* Goode indicates that Norman's (1934) *Paralichthinae* is polyphyletic. Presence of intermuscular bones and transverse apophyses on caudal vertebrae (Amaoka, 1969; Hensley, 1977) in adults of these species fulfill Amaoka's (1969) criteria for affiliation with *Bothinae*. Larval morphology of each (Amaoka, 1969; Hensley, 1977; this paper; Futch, 1971) suggests bothine affinity. Otherwise, descriptions and/or illustrations of genera including *Hippoglossina*, *Paralichthys*, *Pseudorhombus*, *Tarphops*, *Syacium*, *Cyclopsetta*, *Citharichthys*, *Etropus*, and *Dorsopsetta* generally follow the diagnosis for paralich-

thyne genera. Descriptions of *Arnoglossus*, *Psettina*, *Engyprosopon*, *Crossorhombus*, *Bothus*, *Chascanopsetta*, and *Laeops* unquestionably fulfill proposed bothine requirements, in addition to *Taeniopsetta*, *Engyophrys*, *Trichopsetta*, and *Monolene* as discussed above.

Amaoka (1969) placed *Taeniopsetta* in a new subfamily, *Taeniopsettinae*. The striking similarity of larvae of *Taeniopsetta ocellata*, *Engyophrys senta*, and *Trichopsetta ventralis* (Amaoka, 1970; Hensley, 1977; this paper) suggested that presence or absence of otic, cleithral, urohyal, and basipterygial spination could serve as a key character for a category below the family level. A review of the literature revealed several taxa whose larvae bear some combination or urohyal, cleithral, and basipterygial, but not otic spination. These include *Arnoglossus*, *Psettina*, *Engyprosopon*, and *Crossorhombus*. Not all descriptions of each taxon describe or illustrate consistent presence or absence of spination. For example, Weber (1913), John (1951), Jones and Pantulu (1958), and Balakrishnan (1963) described *Arnoglossus* with spination, but Kyle (1913), Padoa (1956), and Amaoka (1973; 1974) did not describe such spination. Also, Pertseva-Ostroumova (1965) showed spination in *Psettina*, but Amaoka (1976) did not. Despite uncertainty of identifications and incomplete descriptions in certain instances, it is possible to surmise a relationship among bothid taxa bearing spines during the larval life.

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LITERATURE CITED

- Aboussouan, A. 1968. Oeufs et larves de téléostéens de l'Ouest Africain. VII. Larves de *Syacium guineensis* (Blkr.) [Bothidae]. Bull. Inst. Fr. Afr. Noire. Sér. A, 30: 1188-1197.
- . 1969. Sur une petite collection de larves de téléostéens récoltée au large du Brésil (Campagne "Calypso" 1962). Vie Milieu Sér. A: Biol. Mar. 20: 595-610.
- . 1972. Oeufs et larves de téléostéens de l'Ouest Africain. XII. Les larves d'*Heterosomata* récoltées aux environs de l'île de Gorée (Sénégal). Bull. Inst. Fr. Afr. Noire. Sér. A, 34: 974-1003.
- Ahlstrom, E. H. 1965. Kinds and abundance of fishes in the California Current region based on egg and larval surveys. Calif. Coop. Oceanic Fish. Invest. Rep. 10: 31-52.
- . 1971. Kinds and abundance of fish larvae in the eastern tropical Pacific, based on collections made on EASTROPAC I. Fish. Bull. 69: 3-86.
- Alperin, I. M., and R. H. Schaefer. 1964. Juvenile bonefish (*Albula vulpes*) in Great South Bay, New York. N.Y. Fish Game J. 11: 1-12.
- Amaoka, K. 1963. A revision of the flatfish referable to the genus *Engyprosopon* found in the waters around Japan. Bull. Misaki Mar. Biol. Inst. Kyoto Univ. 4: 107-121.
- . 1964. Development and growth of the sinistral flounder, *Bothus myriaster* (Temminck and Schlegel) found in the Indian and Pacific Oceans. Bull. Misaki Mar. Biol. Inst. Kyoto Univ. 5: 11-29.
- . 1969. Studies on the sinistral flounders found in the waters around Japan. Taxonomy, anatomy, and phylogeny. J. Shimonoseki Univ. Fish. 18: 65-340.
- . 1970. Studies on the larvae and juveniles of the sinistral flounders. I. *Taeniopsetta ocellata* (Gunther). Jap. J. Ichthyol. 17: 95-104.
- . 1971. Studies on the larvae and juveniles of the sinistral flounders. II. *Chascanopsetta lugubris*. Jap. J. Ichthyol. 18: 25-32.
- . 1972. Studies on the larvae and juveniles of the sinistral flounders. III. *Laeops kitaharae*. Jap. J. Ichthyol. 19: 154-163.
- . 1973. Studies on the larvae and juveniles of the sinistral flounders. IV. *Arnoglossus japonicus*. Jap. J. Ichthyol. 20: 145-156.
- . 1974. Studies on the larvae and juveniles of the sinistral flounders. V. *Arnoglossus tenuis*. Jap. J. Ichthyol. 21: 153-157.
- . 1976. Studies on the larvae and juveniles of the sinistral flounders. VI. *Psettina iijimai*, *P. tosana*, and *P. gigantea*. Jap. J. Ichthyol. 22: 201-206.
- Anderson, W. W., and E. J. Gutherz. 1967. Revision of the flatfish genus *Trichopsetta* (Bothidae) with descriptions of three new species. Bull. Mar. Sci. 17: 892-913.
- Balakrishnan, K. P. 1963. Fish eggs and larvae collected by the Research Vessel *Conch*. 2. Larvae of *Arnoglossus tapeinosoma* Blkr., *Bothus ocellatus* Agassiz, *Laeops guentheri* Alc., *Solea ovata* Rich., and *Cynoglossus monopus* Blkr. Bull. Dept. Mar. Biol. Oceanogr., Univ. Kerala. 1: 81-96.
- Breder, C. M., Jr. 1962. On the significance of transparency in osteichthid fish eggs and larvae. Copeia. 1962: 561-567.
- Briggs, J. C. 1974. Marine zoogeography. McGraw-Hill, Inc. 475 pp.
- Bruun, A. F. 1937. *Chascanopsetta* in the Atlantic; a bathypelagic occurrence of a flatfish, with remarks on distribution and development of certain other forms. Vidensk. Medd. Dan. Naturhist. Foren. Kbh. 101: 125-136.
- Bullis, H. R., Jr., and J. R. Thompson. 1965. Collections by the exploratory fishing vessels *Oregon*, *Silver Bay*, *Combat* and *Pelican* made during 1956-1960 in the southwestern North Atlantic. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. No. 510. 130 pp.
- Caldwell, D. K. 1959. Observations of tropical marine fishes from the northeastern Gulf of Mexico. Quart. J. Fla. Acad. Sci. 20: 126-128.
- . 1963. Tropical marine fishes in the Gulf of Mexico. Quart. J. Fla. Acad. Sci. 26: 188-191.
- Chabanaud, P. 1949a. Le problème de la phylogénèse des Heterosomata. Bull. Inst. Oceanogr. (Monaco) 950: 1-24.
- . 1949b. Contribution à l'anatomie et à la systématique de la famille des Bothidae, s. str. Bull. Soc. Zool. Fr. 74: 246-253.
- Colton, J. B., Jr. 1961. The distribution of eyed flounder and lanternfish larvae in the Georges Bank area. Copeia 1961: 274-279.
- Dawson, C. E. 1962. New records and notes of fishes from the North Central Gulf of Mexico. Copeia 1962: 442-444.

- Eldred, B. 1968. Larvae and glass eels of the American freshwater eel, *Anguilla rostrata* (Lesueur, 1817), in Florida waters. Fla. Bd. Conserv. Mar. Lab., Leaflet Ser., Vol. IV, Pt. 1, No. 9. 4 pp.
- . 1971. First records of *Anguilla rostrata* larvae in the Gulf of Mexico and Yucatan Straits. Fla. Dep. Nat. Resour. Mar. Res. Lab., Leaflet Ser., Vol. IV, Pt. 1, No. 19. 3 pp.
- Futch, C. R. 1971. Larvae of *Monolene sesilicauda* Goode, 1880 (Bothidae). Fla. Dep. Nat. Resour. Mar. Res. Lab., Leaflet Ser., Vol. IV, Pt. 1, No. 21. 14 pp.
- , and F. H. Hoff, Jr. 1971. Larval development of *Syacium papillosum* (Pisces: Bothidae), with notes on adult morphology. Fla. Dep. Nat. Resour. Mar. Res. Lab., Leaflet Ser., Vol. IV, Pt. 1, No. 20. 22 pp.
- , R. W. Topp, and E. D. Houde. 1972. Developmental osteology of the lined sole, *Achirus lineatus* (Pisces: Soleidae). Contrib. Mar. Sci. 16: 33–58.
- Gill, T. H. 1889. Gleanings among the pleuronectids, and observations on the name *Pleuronectes*. Proc. U.S. Nat. Mus. 11: 593–608.
- Goode, G. B., and T. H. Bean. 1885. Descriptions of new fishes obtained by the United States Fish Commission mainly from deep water off the Atlantic and Gulf coasts. Proc. U.S. Nat. Mus. 8: 589–605.
- . 1895. Oceanic ichthyology, a treatise on the deep-sea and pelagic fishes of the world, based chiefly upon the collections made by the Steamers *Blake*, *Albatross*, and *Fish Hawk* in the northwestern Atlantic. Smithsonian Inst., U.S. Nat. Mus., Spec. Bull. 553 pp.
- Gopinath, K. 1946. Notes on the larval and post-larval stages of fishes found along the Trivandrum coast. Proc. Nat. Inst. Sci. India. 12: 7–21.
- Greenwood, P. H., D. E. Rosen, S. H. Weitzman, and G. S. Myers. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bull. Amer. Mus. Nat. Hist. 131: 341–455.
- Guthertz, E. J. 1967. Field guide to the flatfishes of the family Bothidae in the western North Atlantic. U.S. Fish Wildl. Serv., Cir. 263. 47 pp.
- . 1971. Characteristics of some larval bothid flatfish, and development and distribution of larval spotfin flounder, *Cyclopsetta fimbriata* (Bothidae). Fish. Bull. 68: 261–283.
- Haburay, K., C. F. Crooke, and R. Hastings. 1969. Tropical marine fishes from Pensacola, Florida. Quart. J. Fla. Acad. Sci. 31: 213–219.
- Hammer, R. M. 1974. Distribution of phyllosoma lobster larvae (Crustacea: Decapoda: Reptantia: Scyllaridea) in the Gulf of Mexico in relation to currents and recruitment potential. M.S. Thesis, Texas A&M University, College Station, Texas. 215 pp.
- Hensley, D. A. 1977. Larval development of *Engyophrys senta* (Bothidae), with comments on intermuscular bones in flatfishes. Bull. Mar. Sci. 27: 681–703.
- Hildebrand, H. H. 1954. A study of the fauna of the brown shrimp (*Penaeus aztecus* Ives) grounds in the western Gulf of Mexico. Publ. Inst. Mar. Sci. Univ. Tex. 3: 233–366.
- , and L. E. Cable. 1930. Development and life history of fourteen teleostean fishes at Beaufort, N.C. Bull. U.S. Bur. Fish. 46: 383–488.
- Hubbs, C. L. 1945. Phylogenetic position of the Citharidae, a family of flatfishes. Misc. Publ. Mus. Zool. Univ. Mich. No. 63. 38 pp.
- , and Y. T. Chu. 1934. Asiatic fishes (*Diploprion* and *Laeops*) having a greatly elongated dorsal ray in very large postlarvae. Occas. Pap. Mus. Zool., Univ. Mich. 299: 1–7.
- , and L. C. Hubbs. 1945. Bilateral asymmetry and bilateral variation in fishes. Pap. Mich. Acad. Sci. Arts Lett. 30: 229–310.
- Hsiao, S. C. T. 1940. A new record of two flounders, *Etropus crossotus* Goode and Bean and *Ancylosetta dilecta* (Goode and Bean), with notes on postlarval characters. Copeia. 1940: 195–198.
- Ingle, R. M., B. Eldred, H. W. Sims, and E. A. Eldred. 1963. On the possible Caribbean origin of Florida's spiny lobster populations. Fla. State Bd. Conserv. Mar. Lab., Tech. Ser. No. 40. 12 pp.
- John, M. A. 1951. Pelagic fish eggs and larvae of the Madras coast. J. Zool. Soc. India. 3: 1–221.
- Jones, J. I., J. J. O'Brien, and Y. Hsueh. 1973. Physical oceanography of the northeast Gulf of Mexico and Florida Continental Shelf area. In A summary of knowledge of the eastern Gulf of Mexico, J. I. Jones, R. E. Ring, M. O. Rinkel, and R. E. Smith, eds.
- Jones, S., and V. R. Pantulu. 1958. On some larval and juvenile fishes from the Bengal and Orissa coasts. Indian J. Fish. 5: 118–143.
- Jordan, D. S. 1923. A classification of fishes including families and genera as far as known. Stanford Univ. Publ., Univ. Ser., Biol. Sci. 3: 77–243.
- , and B. W. Evermann. 1896–1900. The fishes of North and Middle America. Bull. U.S. Nat. Mus. 47: 1–3313.

- , and D. K. Goss. 1889. A review of the flounders and soles (Pleuronectidae) of America and Europe. Rep. U.S. Comm. Fish and Fish., for 1886, App. B: 225–342.
- Jutare, T. 1962. Studies on the biology of *Bothus ocellatus* with a description of a related new species. M.S. Thesis, Univ. Miami. 97 pp.
- Kyle, H. M. 1913. Flatfishes (Heterosomata). In Report on the Danish Oceanographic Expeditions 1908–10 to the Mediterranean and adjacent seas. Vol. II. Biology. Copenhagen. 150 pp.
- Leipper, D. F. 1970. A sequence of current patterns in the Gulf of Mexico. J. Geophys. Res. 75: 637–657.
- Leonard, S. B. 1971. Larvae of the fourspot flounder, *Hippoglossina oblonga* (Pisces: Bothidae), from the Chesapeake Bight, western North Atlantic. Copeia. 1971: 676–681.
- Longley, W. H., and S. F. Hildebrand. 1941. Systematic catalogue of the fishes of Tortugas, Florida. Pap. Tortugas Lab., Carnegie Inst., Washington, 34. 331 pp.
- Maul, G. E. 1974. A time series of the Loop Current: an interim report. Trans. Amer. Geophys. Un. 55: 283. (Abstr.).
- Moser, H. G., and E. H. Ahlstrom. 1974. Role of larval stages in the systematic investigations of marine teleosts: The Myctophidae, a case study. Fish. Bull. 72: 391–413.
- Murphy, E. B., K. A. Steidinger, B. S. Roberts, J. Williams, and J. W. Jolley, Jr. 1975. An explanation for the Florida east coast *Gymnodinium breve* red tide, November 1972. Limnol. Oceanogr. 20: 481–486.
- Nielsen, J. 1961. Heterosomata (Pisces). Galathea Rep. 4: 219–226.
- . 1963a. Description of two large unmetamorphosed flatfish-larvae (*Heterosomata*). Vidensk. Medd. Dan. Naturhist. Foren. Kbh. 125: 401–406.
- . 1963b. Notes on some Heterosomata (Pisces) from N-W South America with the description of a new genus and species and a new subspecies of *Paralichthinae*. Vidensk. Medd. Dan. Naturhist. Foren. Kbh. 125: 377–400.
- Norman, J. R. 1934. A systematic monograph of the flatfishes (Heterosomata). 1. Psetto-
didac, Bothidae, Pleuronectidae. Brit. Mus. 459 pp.
- Nowlin, W. D. 1971. Water masses and general circulation of the Gulf of Mexico. Oceanol. International 6: 28–33.
- Ochiai, A., and K. Amaoka. 1963. Description of larvae and young of four species of flatfishes referable to subfamily Bothinae. Bull. Jap. Soc. Sci. Fish. 29: 127–134.
- Okiyama, M. 1974. Studies on the early life history of a flounder, *Paralichthys olivaceus* (Temminck et Schlegel). II. Descriptions of juveniles and the comparison with those of the related species. Bull. Jap. Sea. Fish. Res. Lab. 25: 39–61.
- Padoa, E. 1956. Heterosomata. Pages 783–877 in S. LoBianco, ed. Fauna e flora del Golfo di Napoli: Uova, larve e stadi giovanili di Teleostei. Stn. Zool. Napoli Publ. Monogr. 38.
- Pertseva-Ostroumova, T. A. 1965. Flatfish larvae from the Gulf of Tonkin. Trud. Inst. Okeanol. 80: 177–220.
- . 1971. Unusual flounder larvae (Pleuronectiformes, Pisces). J. Ichthyol. 11: 817–822.
- Regan, C. T. 1916. Larval and post-larval fishes. Brit. Antarctic "Terra Nova" Exped., 1910, Brit. Mus. Natur. Hist., Zool. 1: 125–155.
- Richardson, S. L., and E. B. Joseph. 1973. Larvae and young of western North Atlantic bothid flatfishes *Etropus microstomus* and *Citharichthys arcifrons* in the Chesapeake Bight. Fish. Bull. 71: 735–767.
- Ricker, W. E. 1973. Linear regression in fishery research. J. Fish. Res. Bd. Can. 30: 409–434.
- Scheltzma, R. S. 1971. Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. Biol. Bull. 140: 284–322.
- Sims, H. W., Jr., and R. M. Ingle. 1967. Caribbean recruitment of Florida's spiny lobster population. Quart. J. Fla. Acad. Sci. 29: 207–242.
- Smith, D. G., and P. H. J. Castle. 1972. Biological results of the University of Miami Deep-Sea Expeditions. 88. The eel genus *Neconger* Girard: Systematics, osteology, and life history. Bull. Mar. Sci. 22: 196–249.
- Smith, H. M. 1902a. Additions to the fish fauna in 1900. Biological Notes, No. 2. Bull. U.S. Fish Comm. 21: 32.
- . 1902b. Notes on the subtropical fishes observed in 1900. Biological Notes, No. 2. Bull. U.S. Fish Comm. 21: 32–33.
- Smith, W. G., and M. P. Fahay. 1970. Description of eggs and larvae of the summer flounder, *Paralichthys dentatus*. U.S. Fish Wildl. Serv., Res. Rep. 75. 21 pp.
- Snedecor, G. W., and W. G. Cochran. 1967. Statistical methods. Sixth Edition. The Iowa State Univ. Press, Ames, Iowa. 593 pp.
- Springer, S., and H. R. Bullis, Jr. 1956. Collections by the Oregon in the Gulf of Mexico.

- U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. No. 196. 134 pp.
- Starck, W. A., II. 1968. A list of fishes of Alligator Reef, Florida with comments on the nature of the Florida reef fish fauna. *Undersea Biol.* 1: 4-40.
- Taylor, W. R. 1967. An enzyme method of clearing and staining small vertebrates. *Proc. U.S. Nat. Mus.* 122: 1-17.
- Topp, R. W., and F. H. Hoff, Jr. 1972. *Memoirs of the Hourglass Cruises: Flatfishes (Pleuronectiformes). Vol. IV, Pt. II.* Fla. Dep. Nat. Resour. Mar. Res. Lab. 135 pp.
- Uchida, K. 1936. Note on two remarkable heterosomatous postlarvae with a greatly elongated and branched dorsal ray. *Zool. Mag.* 48: 497-501.
- Weber, M. 1913. *Die Fische der Siboga-Expedition.* Leiden. 710 pp.
- Woolcott, W. S., C. Beirne, and W. M. Hall, Jr. 1968. Descriptive and comparative osteology of the young of three species of flounders, genus *Paralichthys*. *Chesapeake Sci.* 9: 109-120.

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