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DESCRIPTION AND OCCURRENCE OF VEXILLIFER
LARVAE OF *ECHIODON* (PISCES: CARAPIDAE) IN
THE WESTERN NORTH ATLANTIC AND NOTES
ON OTHER CARAPID VEXILLIFERS

John E. Olney and Douglas F. Markle

ABSTRACT

Five hundred twenty-two vexillifers of an unnamed species of the carapid genus *Echiodon* are reported from ichthyoplankton collections made in the Caribbean Sea, Gulf of Mexico, Middle Atlantic Bight, Sargasso Sea, and Scotian Shelf. These are compared with 36 vexillifers and one juvenile of the only other known western Atlantic carapine, *Carapus bermudensis*, as well as two small unidentified western Atlantic vexillifers, and eight eastern Pacific vexillifers of *E. exsilium*. Vexillum placement relative to anal-fin origin, myomeres, and vertebral centra appears to be a useful character for separating *Echiodon* vexillifers from other western Atlantic carapids. The vexillum in *Echiodon* is posteriad of a vertical through the anal-fin origin, over myomeres 9 to 12 and centra 10 or 11.

The vexillum of *Echiodon* sp. was examined in detail and is bilateral, each component of which consists of a distal and proximal element. The paired proximal elements rest on a distal cartilaginous radial which is supported by a slipper-shaped, compound cartilaginous proximal radial (pterygiophore) in *Echiodon* sp. and by a rod-shaped, simple proximal radial in *C. bermudensis*. The structure is covered by a fleshy sheath which is highly ornamented in *C. bermudensis* but less so in *Echiodon* sp. The presumed origin of percoid predorsal bones from an ancestor with vexillar supporting structures is questioned.

Most available vexillifers of *Echiodon* sp. were captured in the eastern Gulf of Mexico. Additional larger size classes were taken from off Bermuda and north of Cape Hatteras to the Scotian Shelf. These and several other subtropical teleost larvae appear to be regularly dispersed northward by the Gulf Stream.

Vexillifers are elongate teleost larvae characterized by a long, ornamented predorsal filament or vexillum which apparently represents a unique larval specialization of the ophidioid Carapidae (Arnold, 1956; Strasburg, 1965). Vexillifer larvae have been described for at least four genera and nine carapid species. Eggs and larvae of the Mediterranean *Carapus acus* (Brunnich) and *Echiodon dentatus* (Cuvier) as well as the northeastern Atlantic *E. drummondi* Thompson have been described by various authors (including Emery, 1880; Ehrenbaum, 1905-1909; Padoa, 1956; Kennedy and Champ, 1971; and see Arnold, 1956 and Wheeler, 1973 for useful summaries of early life history and synonymy). In the western Atlantic, vexillifers of *Carapus bermudensis* (Jones) have been briefly described by Dawson (1971). In the Pacific, the vexillifer of *Snyderidia canina* Gilbert was figured and described by Strasburg (1965) and Trott (1970) illustrated the vexillifer of *Encheliophis jordani* (Heller and Snodgrass). In addition, two Pacific species of *Echiodon* (Trott, 1970; Robertson, 1975) and one Panamanian species originally assigned to *Leptoferasfer* (Meek and Hildebrand, 1928) which Arnold (1956) attributes to *Carapus dubius* have been illustrated. In all of these latter cases however, the identification is not substantiated.

This paper reports the collection in the western Atlantic of 522 carapid vexillifers which we refer to an unnamed species of *Echiodon*. These vexillifers are described and compared with larvae of *Carapus bermudensis* obtained from the Gulf of Mexico and the Sargasso Sea, small unidentified vexillifers taken in the Caribbean Sea, and larvae of the Pacific *Echiodon exsilium*. This larval descrip-

tion and a forthcoming description of adult material from the Gulf of Mexico (Robert Shipp, pers. comm.) confirm earlier suspicions (Rosenblatt, 1961, 1967) that the genus *Echiodon* is present in the western Atlantic.

METHODS

Larvae were measured with an ocular micrometer and dial calipers, using standard ichthyological methods (Hubbs and Lagler, 1958). Twenty vexillifers of *Echiodon* sp., one vexillifer of *E. exsilium*, one unidentified larva, three vexillifers and one juvenile of *Carapus bermudensis* were cleared and stained following Taylor (1967) and Mook and Wilcox (1974). Ossified structures were stained with Alizarin Red S and cartilage was differentially stained in some specimens with Alcian Blue (Dingerkus and Uhler, 1977). Figures were prepared with the aid of a Wild camera lucida.

Abundance estimates were available for some 60 cm bongo collections of *Echiodon* sp. These are compared using the formula: $S = N/V \times D_{\max} \times 100$, where S = the number of larvae per 100 m² of sea surface, N = the number of larvae per tow, V = the volume (m³) of sea water strained, and D_{\max} = the maximum depth (m) reached by the sampler.

MATERIALS

All vexillifers of *Echiodon* sp. were taken in plankton tows with the exception of one damaged specimen taken by a 9-m otter trawl fished on the bottom south of Cape Hatteras, North Carolina and three vexillifers taken off Bermuda in Ocean Acre collections with a 3-m Isaacs-Kidd midwater trawl (IKMT). Gear designations listed below are self-evident except for bongo nets. Bongo frames of 18, 20, 50, and 60 cm diameters with nets of 165, 202, 253, 333, or 505 μ m mesh were used for collections. An abbreviation of 18B202 refers to a 12-cm diameter bongo net with 202 μ m mesh.

Institutional abbreviations used are: USNM—United States National Museum of Natural History, Washington, D.C.; VIMS—Virginia Institute of Marine Science, Gloucester Pt., Virginia; GCRL—Gulf Coast Research Laboratory Museum, Ocean Springs, Mississippi; HML—Huntsman Marine Laboratory, St. Andrews, New Brunswick; SEFC—National Marine Fisheries Service, Southeast Fisheries Center, Miami, Florida; SWFC—National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, California.

In the following list of specimens examined, we record, where available, the institutional abbreviation or museum catalog number, specimen head length (HL) or number of specimens and range of head lengths, vessel or cruise designation, station designation, coordinates, station depth (m), date of collection, time of collection, collecting gear, depth of collection (m), surface temperature ($^{\circ}$ C), and surface salinity (ppt.).

Echiodon sp.—Gulf of Mexico—SEFC, 53 specimens 0.85–3.35 mm, R/V OREGON II, Sta. 1, 26 $^{\circ}$ 35'N, 85 $^{\circ}$ 05'W, 190 m, 12–13 September 1970, 24 h collections (hauls = 14), 60B333, 60B505, 20B253 and 20B165, 0–190 m; SEFC, 448 specimens 0.43–3.20 mm, R/V OREGON II, Sta. 2, 26 $^{\circ}$ 47'N, 84 $^{\circ}$ 34'W, 195 m, 13–14 September 1970, 24 h collections (hauls = 20), 60B333, 60B505, 20B253 and 20B165, 0–195 m; SEFC, 2 specimens 1.0 mm, R/V OREGON II, Sta. 31, 15 $^{\circ}$ 00'N, 66 $^{\circ}$ 58'W, 1442 H GMT, 50B505; SEFC, 2.6 mm, R/V TURSIOPS, Sta. 21, 25 $^{\circ}$ 20'N, 85 $^{\circ}$ 08'W, 9 May 1970, 50B505, 40 m.

Echiodon sp.—Sargasso Sea, Ocean Acre—USNM 218376, 2.65 mm, USNS GILLISS, Sta. 3-51S, 32 $^{\circ}$ 54'N, 64 $^{\circ}$ 45'W, 5 July 1968, 2210 h EST, 0.5 m neuston net; USNM 218377, 3.7 mm, R/V TRIDENT, Sta. 4-7B, 32 $^{\circ}$ 05'N, 63 $^{\circ}$ 54'W, 4 September 1968, 1200 h EST, 3 m IKMT, 510–1,300 m; USNM 218378, 4.0 mm, R/V TRIDENT, Sta. 4-18 B and P, 31 $^{\circ}$ 46'N, 64 $^{\circ}$ 08'W, 6 September 1968, 1300 h EST, 3 m IKMT, 0–161 m; USNM 218379, 3.0 mm, Ocean Acre cruise 12, 32 $^{\circ}$ 31'N, 63 $^{\circ}$ 58'W, 31 August 1971, 0330 h EST, 3 m IKMT, 94 m.

Echiodon sp.—Middle Atlantic Bight—USNM 216942, 1.7 mm, R/V GILLISS, Sta. 19, 36 $^{\circ}$ 55.6'N, 74 $^{\circ}$ 37.5'W, 210 m, 11 Sept. 1975, 0600 h, 60B202, 0–150 m, 25.0 $^{\circ}$ C, 34.9‰; USNM 216943, 1.9 mm, R/V GILLISS, Sta. 15, 37 $^{\circ}$ 04.5'N, 74 $^{\circ}$ 32.5'W, 350 m, 10 Sept. 1975, 1303 h, 60B202, 0–150 m, 24.4 $^{\circ}$ C, 34.6‰; USNM 216944, 2.3 mm, R/V GILLISS, Sta. 27, 37 $^{\circ}$ 13.2'N, 74 $^{\circ}$ 20.5'W, 1,450 m, 12 Sept. 1975, 1529 h, 60B333, 0–150 m, 24.9 $^{\circ}$ C, 34.7‰; USNM 216945, 2.3 mm, R/V GILLISS, Sta. 22, 37 $^{\circ}$ 0.17'N, 74 $^{\circ}$ 34.2'W, 985 m, 11 Sept. 1975, 2030 h, 60B333, 0–150 m, 25.0 $^{\circ}$ C, 34.9‰; USNM 216946, 2.5 mm, R/V GILLISS, Sta. 82, 36 $^{\circ}$ 38.8'N, 74 $^{\circ}$ 40.9', 275 m, 17 Sept. 1975, 2024 h, 60B202, 0–150 m, 23.6 $^{\circ}$ C, 35.3‰; USNM 216947, 2.4 mm, R/V GILLISS, Sta. 83, 36 $^{\circ}$ 42.4'N, 74 $^{\circ}$ 32.5'W, 500 m, 17 Sept. 1975, 2240 h, 60B333, 0–150 m, 23.6 $^{\circ}$ C, 35.3‰; USNM 216948, 3.2 mm, R/V GILLISS, Sta. 31, 37 $^{\circ}$ 01.5'N, 74 $^{\circ}$ 32.5'W, 750 m, 13 Sept. 1975, 1203 h, 60B333, 0–150 m, 23.9 $^{\circ}$ C, 34.4‰; USNM 216949, 3.4 mm, R/V PATHFINDER, Sta. 7, 37 $^{\circ}$ 00'N, 74 $^{\circ}$ 30.0'W, ca. 1,200 m, 18 June 1974, 18B202, 0–20 m, 18.8 $^{\circ}$ C, 32.9‰; USNM 216950, 3.9 mm, R/V VIRGINIAN Sea, Sta. N3, 38 $^{\circ}$ 51.3'N, 73 $^{\circ}$ 43.36'W, 45 m, 5 Sept.

1976, 2111 h., 60B202, 0–45 m, 21.9°C, 32.1‰; USNM 216951, 3.5 mm, R/V VIRGINIAN Sea, Sta. F2, 38°44.2'N, 73°08.2'W, 106 m, 8 Sept. 1976, 0919 h, 60B505, 0–106 m, 20.8°C, 33.5‰; VIMS 03895, 2.5 mm, R/V FAY, Sta. L6, 37°04.4'N, 74°33.1'W, 300 m, 22 Feb. 1977, 0125 h, 60B202, 0–300 m, 11.6°C, 35.8‰; VIMS 03896, specimen mutilated, R/V GILLISS, Sta. 87, 36°38.5'N, 74°38.5'W, 400–1,000 m, 18 Sept. 1975, 1008 h, 60B202, 0–150 m, 23.1°C, 35.2‰; VIMS 03897, specimen mutilated, R/V EASTWARD, Sta. 22039, 34°03.2'N, 75°52.0'W, 600 m, 28 Apr. 1973, 1745 h., 30 ft. otter trawl, 0–600 m, 24.9°C; VIMS 04910, 4.2 mm, R/V VIRGINIA Sea, Sta. F2, 38°44.1'N, 73°09.1'W, 106 m, 7 Sept. 1976, 2207 h., 60B505, 0–132 m, 20.7°C, 33.2‰.

Echiodon sp.—Scottian Shelf—HML, 3.8 mm, R/V CANSO CONDOR, station 50 set 59, 43°36'N, 59°30'W, 481 m, 2 March 1977, 1110 h., neuston net.

Unidentified Carapidae—Caribbean Sea—SEFC, 2 specimens 1.85 and 2.15 mm, R/V OREGON II, station 165, 17°00'N, 79°57'W, 8 March 1973, 2000 h GMT.

Echiodon exsilium—Eastern Pacific—SWFC, 4.5 mm, 26°4.2'N, 115°45.0'W, 3,980 m, 7 March 1954, 1225 h., CALCOFI net, 0–134 m; SWFC, 3.1 mm, 23°13.5'N, 110°59.0'W, 10 March 1951, 2350 h., CALCOFI net, 0–118 m; SWFC, 1.5 mm, 27°50'N, 112°31'W, 16 June 1957, 0640 h., CALCOFI net, 0–131 m; SWFC, 5.6 mm, 1°50'S, 81°41'W, 1 October 1960, 0035 h., CALCOFI net, 0–368 m; SWFC, 4.2 mm, 3°32'S, 92°05'W, 15 February 1967, 2151 h., CALCOFI net, 0–210 m; SWFC, 4.1 mm; 0°30.6'N, 86°12.8'W, 19 November 1967, 1600 h., CALCOFI net, 0–210 m; SWFC, 4.6 mm, 2°10.0'S, 85°03'W, 24 August 1967, 0300 h., CALCOFI net, 0–210 m; SWFC, 4.8 mm, Sta. 127.60, 26°4.2'N, 115°45.0'W, 7 March 1954, 1225 h., CALCOFI net, 0–134 m.

Carapus bermudensis—Gulf of Mexico—GCRL 5167, two specimens 4.0 and 3.1 mm, R/V GULF RESEARCHER, 29°15.0'N, 88°11.5'W, 91 m, 8 August 1967, 2300 h., meter nekton net, surface collection, 23.9°C, 35.6‰; GCRL V71:6597, 7.3 mm (juvenile), collected by C. E. and E. Dawson at embayment, 9.1 m E of Maria Chiquita on Portobelo Road, Colon, Panama, 3 July 1971.

Carapus bermudensis—Sargasso Sea, Ocean Acre—USNM 218380, 3.0 mm, Ocean Acre cruise 12, Sta. 12-34A, 32°18'N, 64°03'W, 7 September 1971, 1655 h EST, 3 m IKMT, 62–69 m; USNM 218381, 3.4 mm, Ocean Acre cruise 12, Sta. 12-6 M, 33°19'N, 64°04'W, 28 August 1971, 0530 h EST, 3 m IKMT, 0–633 m; USNM 218382, 4.15 mm, Ocean Acre Cruise 12, Sta. 12-1A, 32°18'N, 64°03'W, 26 August 1971, 1918 h EST, 3 m IKMT, 33 m; USNM, 31 specimens 2.0–3.3 mm, Ocean Acre cruises 1, 3, 4, 6, 9, 12, and 13, at 28 stations within the Ocean Acre study area centered at 32°N, 64°W, November 1968, July, September 1969, March 1970, August 1971 and February 1972, 3 m IKMT, varying depths to 1,200 m.

CONFIRMATION OF IDENTIFICATION

Carapidae is the only family of fishes known to have a vexillifer larva (Strasburg, 1965). Unlike the closely related ophidiids, they lack a supramaxillary and have anal-fin rays longer than opposing dorsal-fin rays (Rosen and Patterson, 1969; Cohen and Nielsen, 1978). Our larvae were not referable to the subfamily Pyramodontinae since pectoral rays numbered less than twenty (but see the following meristic analysis of *E. exsilium*), and the anal-fin origin was anterior to the vexillum and first dorsal ray (Robins and Nielsen, 1970; Strasburg, 1961, 1965; Gosline, 1960). A pronounced gap or diastema (Arnold, 1956, Fig. 3) separating enlarged canines from the smaller teeth in the premaxillary and dentary is characteristic of the genera *Onuxodon* and *Echiodon* (Arnold, 1956; Tyler, 1970; Cohen and Nielsen, 1978). These genera can be distinguished since *Onuxodon* possesses a median rocker bone and lacks transverse processes on the fourth vertebra (Courtenay and McKittrick, 1970). In addition, the rear of the maxillary in *Echiodon* is expanded and its posterior margin is a straight line rather than being slender with a rounded posterior margin as in *Onuxodon* (Cohen and Nielsen, 1978).

Description

The following is a comparative description of western Atlantic vexillifers of *Echiodon* sp. and *Carapus bermudensis* (Fig. 1). Comparative notes on *E. exsilium* are presented where available. Six major aspects are discussed: general morphology and morphometrics, pigmentation, the vexillum, the axial skeleton,

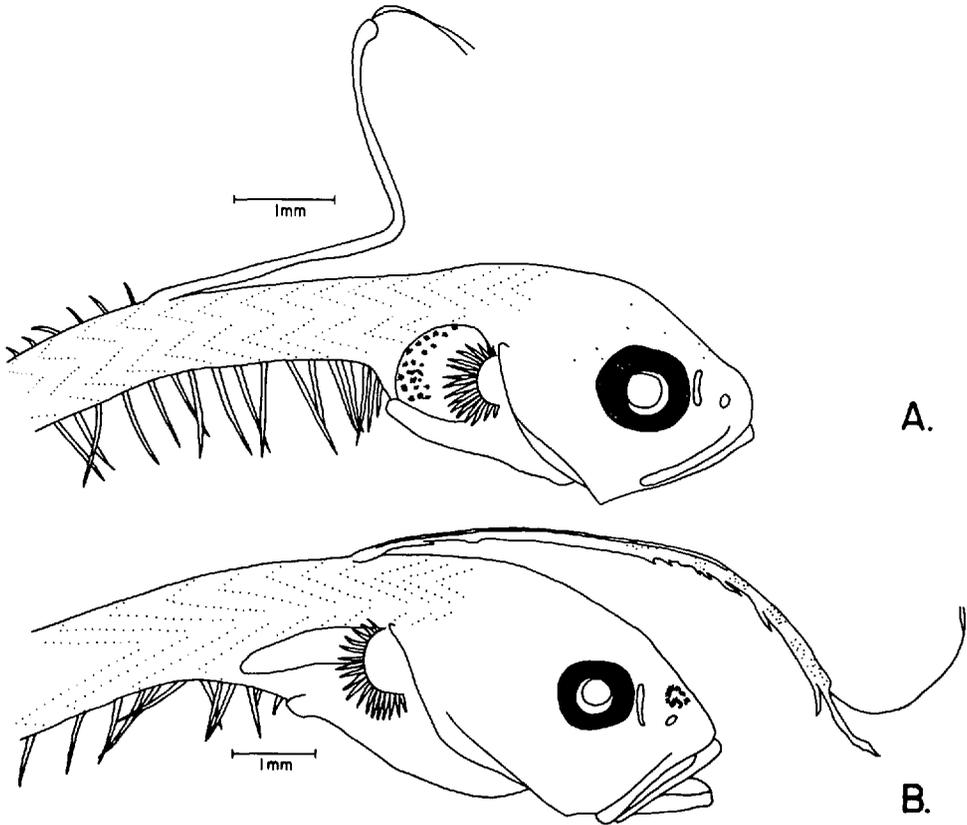


Figure 1. Carapine vexillifers of the western North Atlantic Ocean: (A) *Echiodon* sp. (VIMS 03895), 2.5 mm HL, right lateral view; (B) *Carapus bermudensis* (GCRL 5167), 4.0 mm HL, right lateral view.

meristics, and dentition. Developmental changes are noted through the observed size range. Meristics and observations on the axial skeleton were made from cleared and stained vexillifers of *Echiodon* sp., *E. exsilium*, and *Carapus bermudensis* and a juvenile *C. bermudensis*.

General Morphology and Morphometrics

Vexillifers of *C. bermudensis* and *Echiodon* sp. may be characterized as follows: body elongate, tapering to a filamentous tip; head large; eye prominent; nares well developed; nasal rosette large, occupying most of the snout; a minute pore, perhaps associated with the cephalic lateralis system, located near the dorsal edge of the rosette; otoliths large, both sagitta and lapillus relatively well developed in *Echiodon* sp. only; gut short, bulbous and in a flat coil; air bladder conspicuous; dorsal-fin and anal-fin bases long; pelvic fins absent; pectoral-fin base lobate; vexillum (as described below) conspicuous.

Vexillifers of *C. bermudensis* captured in the Gulf of Mexico and the Sargasso Sea varied in total length (TL) from 37–137 mm and in head length (HL) from 2.0–4.1 mm. Vexillifers of *Echiodon* sp. from the Middle Atlantic Bight, the Sargasso Sea, and the Scotian Shelf ranged from 27–64 mm TL and 1.7–4.0 mm HL. Those from the Gulf of Mexico ranged from 2.9 to 6.7 mm TL and 0.4–3.4 HL.

Table 1. Statistics of selected morphometrics of vexillifers of *Echiodon* sp. and *Carapus bermudensis**

Selected Measurements	<i>Echiodon</i> sp.				<i>C. bermudensis</i>			
	N	\bar{x}	range	S _x	N	\bar{x}	range	S _x
Snout length	20	0.26	0.20–0.32	0.03	10	0.27	0.23–0.32	0.03
Undamaged vexillum length	19	1.70	0.88–2.58	0.41	6	2.91	1.90–3.44	0.56
Orbit diameter	20	0.36	0.25–0.45	0.06	10	0.24	0.22–0.27	0.02
Snout to anus	20	1.34	1.19–1.66	0.12	10	1.33	1.20–1.41	0.07
Snout to vexillum base	20	1.99	1.77–2.28	0.13	10	1.28	1.13–1.37	0.07
Predorsal length	12	2.08	1.91–2.40	0.16	8	2.53	2.27–2.90	0.22
Preanal length	12	1.35	1.20–1.50	0.09	10	1.41	1.28–1.50	0.08
Upper jaw length	20	0.47	0.37–0.58	0.05	10	0.45	0.40–0.50	0.03
Lower jaw length	20	0.68	0.54–0.89	0.09	10	0.53	0.47–0.58	0.03
Maximum depth	19	0.88	0.54–1.14	0.15	8	0.79	0.71–0.85	0.05
Snout to v_{\max}	19	0.81	0.30–1.13	0.19	8	0.64	0.36–0.91	0.19

* Morphometrics are expressed as a ratio to head length; N = number of specimens, \bar{x} = mean, S_x = Standard deviation, v_{\max} = vertical through the point of greatest depth.

Total length was not suitable for morphometric comparisons due to the fragile nature of the caudal filament. In Table 1, the mean, range and standard deviation of selected measurements are presented for vexillifers of *Echiodon* sp. (N = 20, 0.5–3.9 mm HL) and *C. bermudensis* (N = 10, 2.1–4.0 mm HL). The mean, range and standard deviation of the head length as a percent of total length was 9.26, 5.21–13.8, 3.42 for *Echiodon* sp. vexillifers and 3.66, 2.50–5.68, 0.97 for *C. bermudensis*. Morphometrics of *E. exsilium* (N = 7, 1.5–4.6 mm HL) fell within the ranges of selected measurements for *Echiodon* sp. vexillifers in the western Atlantic.

For vexillifers of *Echiodon* sp., most morphometric values remained constant relative to head length throughout the size range observed. Three values (orbit diameter, lower jaw length and vexillum length) changed ontogenetically with ratios decreasing relative to increasing HL. In addition, HL as a percent of TL decreased with increasing total length.

In *C. bermudensis*, ontogenetic trends were noted in two selected measurements. Snout length relative to HL decreased with increasing HL, and HL as a percent of TL decreased with increasing TL.

Vexillifers of *Echiodon* sp. and *C. bermudensis* are easily separable morphometrically (Table 1). In *Echiodon* sp., the orbit diameter, lower and upper jaw lengths are larger and vexillar length smaller relative to head length than in vexillifers of *C. bermudensis*. In addition, vexillifers of *Echiodon* sp. are smaller in TL than those of *C. bermudensis* at corresponding HL resulting in a larger value for HL as a percent of TL, especially in the smallest size classes. Most conspicuous, however, is the difference in vexillum placement and predorsal length. In *Echiodon* sp., the vexillum inserts well behind the insertion of the first anal ray at a point about twice (1.77–2.28 times) the head length from the snout or a distance greater than the snout to anus length (Fig. 1A, Table 1). In *C. bermudensis*, the vexillum is placed anterior to a vertical through the first anal ray and posterior to a vertical through the base of the pectoral fin (Fig. 1B), at a point 1.13–1.37 HL from the snout or a distance less than the snout to anus distance. Finally, predorsal length relative to HL is greater in vexillifers of *C. bermudensis* since the first dorsal ray inserts well behind the vexillum (Figs. 1B, 2). In *Echiodon* sp., the first dorsal ray inserts immediately posterior to the vexillum (Fig. 3).

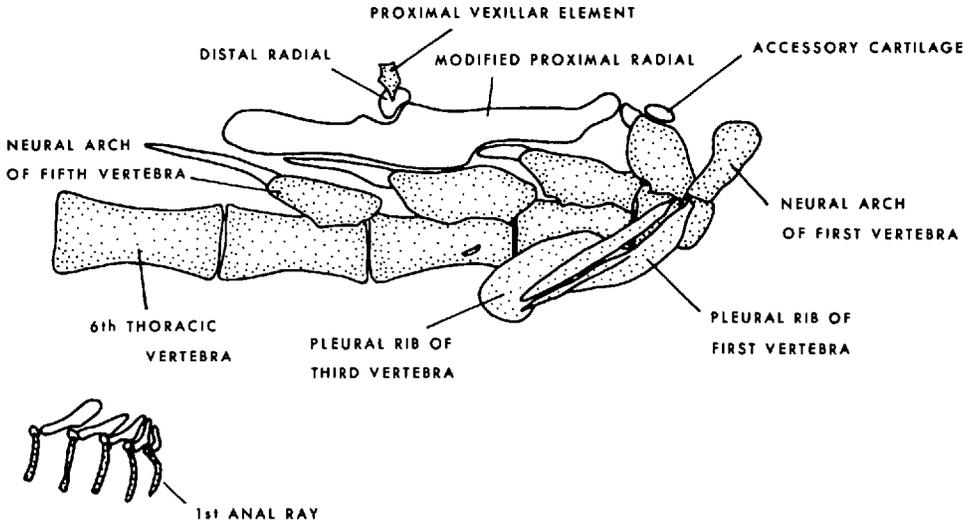


Figure 2. Lateral view of the modified proximal radial supporting the vexillum in *Carapus bermudensis* (USNM 218382, 4.1 mm HL). Stippling indicates ossification.

Pigmentation

Vexillifers of *C. bermudensis* and *Echiodon* sp. are sparsely pigmented although some differences were noted (Fig. 1). Only black melanophores are present on preserved material, but red chromatophores (erythrophores) were plainly visible in one freshly preserved *Echiodon* sp. vexillifer (VIMS 03895). In this specimen, erythrophores were found on the base of each anal-fin ray; in a line of 8 to 10 along the posterior edge of the vexillum; in a scattered arrangement of 18 to 20 on the belly; in a small group on the cheek; and in a scattered arrangement of about 12 erythrophores on the dorsal surface of the head. Some of the latter were superimposed over cranial melanophores shown in Fig. 1. Two melanophores were seen on the tip of the lower jaw (not in Fig. 1) and four were found in a diamond arrangement on the forebrain just posterior to the nasal rosette. A few internal melanophores are visible in lateral view under the hindbrain and melanophores are variably present on the distal swelling of the vexillum sheath. The most conspicuous pigment in some, but not all, *Echiodon* sp. was peritoneal (Fig. 1A). This character is variable in our material and, therefore, cannot be used with certainty in identification. Vexillifers of *E. exsilium* had less pigment which was restricted to the brain and peritoneum but this difference could be due to longer preservation.

In *C. bermudensis*, pigment is sparse, principally occurring on the head and vexillum (Fig. 1B). A few faded internal melanophores are visible under the hindbrain and a ring of 8 to 10 stellate melanophores are located antero-dorsal to the nasal rosette. The latter were described as a "minute subcircular ring of micromelanophores on the preorbital" by Dawson (1971). The vexillum of *C. bermudensis* is ringed distally with four bands of small stellate melanophores. The posterior vexillar edge is covered with a dense pattern of smaller melanophores. No peritoneal chromatophores are present in our *C. bermudensis* material. On a few specimens with intact caudal filaments, dorsal and ventral concentrations of small melanophores extending to the filamentous tip were present.

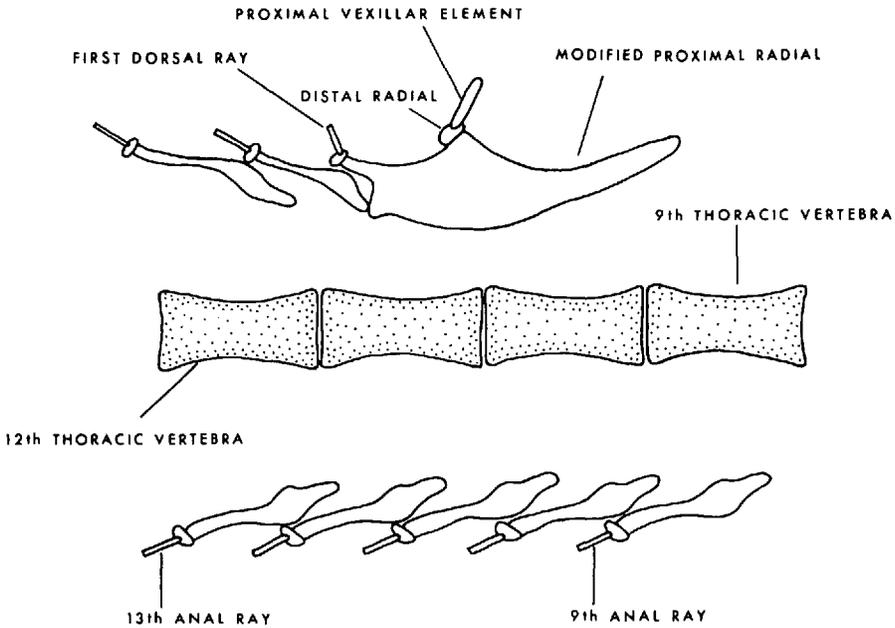


Figure 3. Lateral view of the modified proximal radial supporting the vexillum and first dorsal ray in *Echiodon* sp. (VIMS 04910, 4.2 mm HL). Stippling indicates ossification.

Vexillum

The vexillum of *Echiodon* sp. is bilateral and appears distally as two cartilaginous threads exiting through a fleshy sheath (Figs. 1A, 4). Each bilateral component has a proximal and distal element which meet in a flat joint at a height roughly equal to the height of the first dorsal-fin ray. The fleshy sheath of the vexillum terminates in a slightly bulbous tip (Fig. 1A). Other ornamentations were not seen. The length of undamaged vexilla, including distal threads, in *Echiodon* sp. varied from 0.50 mm in a 0.43 mm HL specimen to 6.65 mm in a 3.35 mm HL specimen. Vexillum length increased with increasing HL up to about 2.5 mm HL. From this size to the largest specimens observed, vexilla lengths remained between 4.0 and 6.65 mm.

In the largest cleared and stained vexillifers of *Echiodon* sp., the vexillum inserted over vertebrae 10 or 11 (Fig. 3) and in all other specimens, over myomeres 9 to 12 (Fig. 1A).

The paired proximal elements of the vexillum are supported by a small cartilaginous distal radial and a modified proximal radial (Figs. 3, 4). The cartilaginous proximal radial is slipper-shaped and extends from the ninth to the eleventh thoracic vertebra. It is clearly a compound structure since it also supports the distal radial and first fin ray of the dorsal fin (Fig. 3). Cleared and stained vexillifers of *Echiodon exsilius* revealed no differences in the morphology or placement of the vexillum and its supporting radials.

Although the general morphology of the vexillum of *Carapus bermudensis* was identical to that observed in *Echiodon* sp. (Fig. 4), conspicuous differences were noted in relative vexillar length, ornamentation, placement, and the morphology of its supporting proximal radial. The vexillum of *C. bermudensis* is larger and more highly ornamented than in larvae of *Echiodon* sp. Vexillar lengths ranged

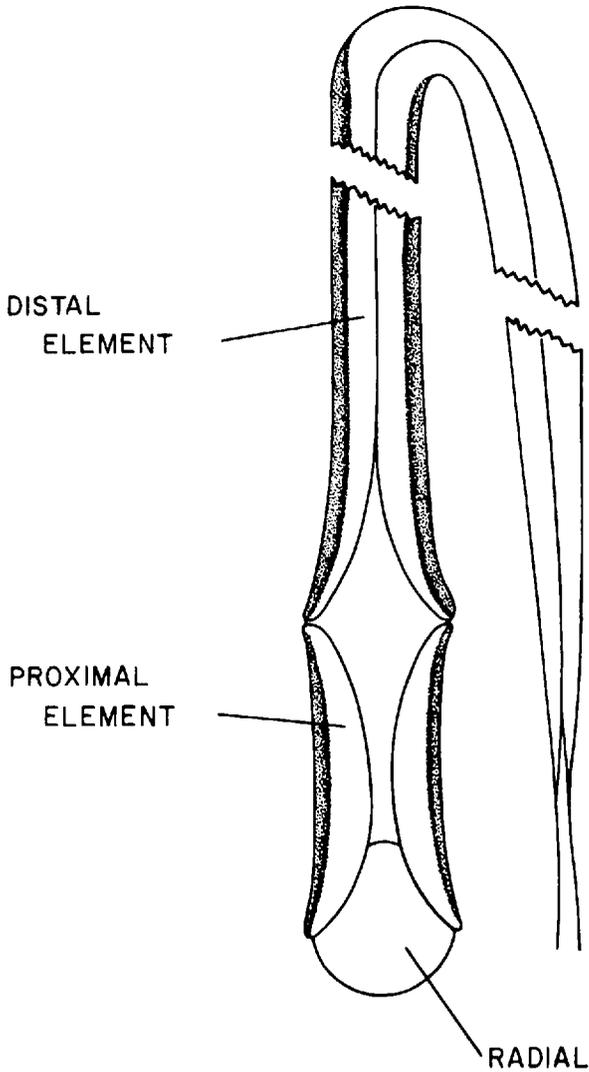


Figure 4. Diagrammatic representation of a 4.3 mm vexillum of *Echiodon* sp. (USNM 216951, 3.5 mm HL), viewed along a longitudinal axis. Stippling indicates ossification. Only ossified or cartilaginous elements are shown. The fleshy sheath surrounding these elements is omitted.

from 7.0 mm at 2.1 mm HL to 11.0 mm at 3.2 mm HL in *C. bermudensis*. Ornamentation consists of about seven fleshy tabs on the distal half of the structure in most specimens examined (Fig. 1B). In three cleared and stained vexillifers of *C. bermudensis*, the vexillum inserted over the posterior portion of the fourth vertebral centrum (Fig. 2), and in all other specimens, over myomeres 3 to 5 (Fig. 1B). The paired proximal elements of the vexillum are supported by a small cartilaginous distal radial (Fig. 2) as in *Echiodon* sp., but the modified proximal radial in *C. bermudensis* is rod-shaped and extends from the third to the fifth thoracic vertebra. In addition, the structure is not compound as in *Echiodon* sp. (Fig. 3) and overlies the distal portion of the neural arches of vertebrae 2-5 (Fig. 2).

Axial Skeleton and Fins

Echiodon sp.—Observations on the axial skeleton and fins were made on twenty cleared and stained specimens of *Echiodon* sp. ranging in HL from 0.8–3.9 mm. With the exception of the vexillum which was evident on the smallest *Echiodon* sp., differentiation of rays in both dorsal and anal fins was first observed between 0.9 and 1.1 mm HL. Ray formation commences in the posterior mid-portions of the fin bases and proceeds anteriorly and posteriorly. The most posteriad rays in both dorsal and anal fins are the last to develop. By 1.7 mm HL, all anterior dorsal and anal fin rays are formed and the caudal portion terminates in a filamentous tip of notochord tissue. A caudal skeleton was not seen in any of our *Echiodon* sp. material. In *Echiodon* sp. vexillifers over 1.7 mm HL, the first dorsal ray inserts over vertebrae 11–12 (Fig. 3) and the first anal ray under vertebrae 5–7.

Differentiation of pectoral-fin rays begins between 2.0–3.0 mm HL. By 3.5 mm HL, the full compliment of pectoral rays is apparent.

Ossification of the first three thoracic vertebral centra in *Echiodon* sp. commences between 1.3 and 1.4 mm HL and proceeds posteriorly. By 3.5 mm HL, all vertebrae up to the damaged caudal tip can be detected. Ossification of neural arches and pleural ribs begins around 2.0 mm HL. By 3.9 mm HL, neural arches and cartilaginous spines are present on the first ten vertebrae and pleural ribs are present on the first five vertebrae. Haemal spines are not apparent in the cleared and stained series.

By 3.5 mm HL the third pleural rib is prominently recurved (Fig. 5A). In two species of *Onuxodon* illustrated by Courtenay and McKittrick (1970) the recurved third rib is greatly expanded, presumably fusing with the fourth rib which is absent in that genus. Both illustrated species of *Onuxodon* possess a unique structure, the median rocker bone, associated with the modified ribs and swim-bladder (Courtenay and McKittrick, 1970). Until vexillifer material of *Onuxodon* is available for study it is difficult to decide if these differences are ontogenetic or represent derived characteristics in *Onuxodon* which may prove useful in delimiting these genera. Identification of larval *Onuxodon* should be facilitated by the observations of Courtenay and McKittrick (1970, Fig. 3), which indicate that the predorsal bone is above thoracic vertebrae 4 to 6.

Echiodon exsiliium.—In one cleared and stained vexillifer (4.8 mm HL), the first dorsal ray inserts over vertebra 11 and the first anal ray under vertebra 7. Neural arches and cartilaginous spines are present on the first seven vertebrae and pleural ribs on the first four vertebrae.

Carapus bermudensis.—In three cleared and stained specimens (3.0, 3.4 and 4.2 mm HL), the first dorsal ray inserts over vertebrae 10 or 11 and the first anal ray under vertebra 6 (Fig. 2). In one juvenile specimen (GCRL 6597, 7.3 mm HL), the first anal ray inserts under thoracic vertebra 3, an anterior displacement perhaps due to changes in body depth and vertebral curvature at metamorphosis.

Meristics

Echiodon sp.—Counts on the largest cleared and stained specimens (2.0–4.2 mm HL) were: anal rays, 127⁺–139; dorsal rays, 127⁺–140; pectoral rays, 17–19; total vertebrae, 100⁺–123; branchiostegal rays, 7 (5 on the ceratohyal, 2 on the epihyal).

Echiodon exsiliium.—Counts on one cleared and stained specimen (4.8 mm HL) were: anal rays, 193⁺; dorsal rays, 190⁺; total vertebrae, 132⁺; branchiostegal rays, 7; pectoral rays, 24, 25. In two additional vexillifers (SWFC) and four adult

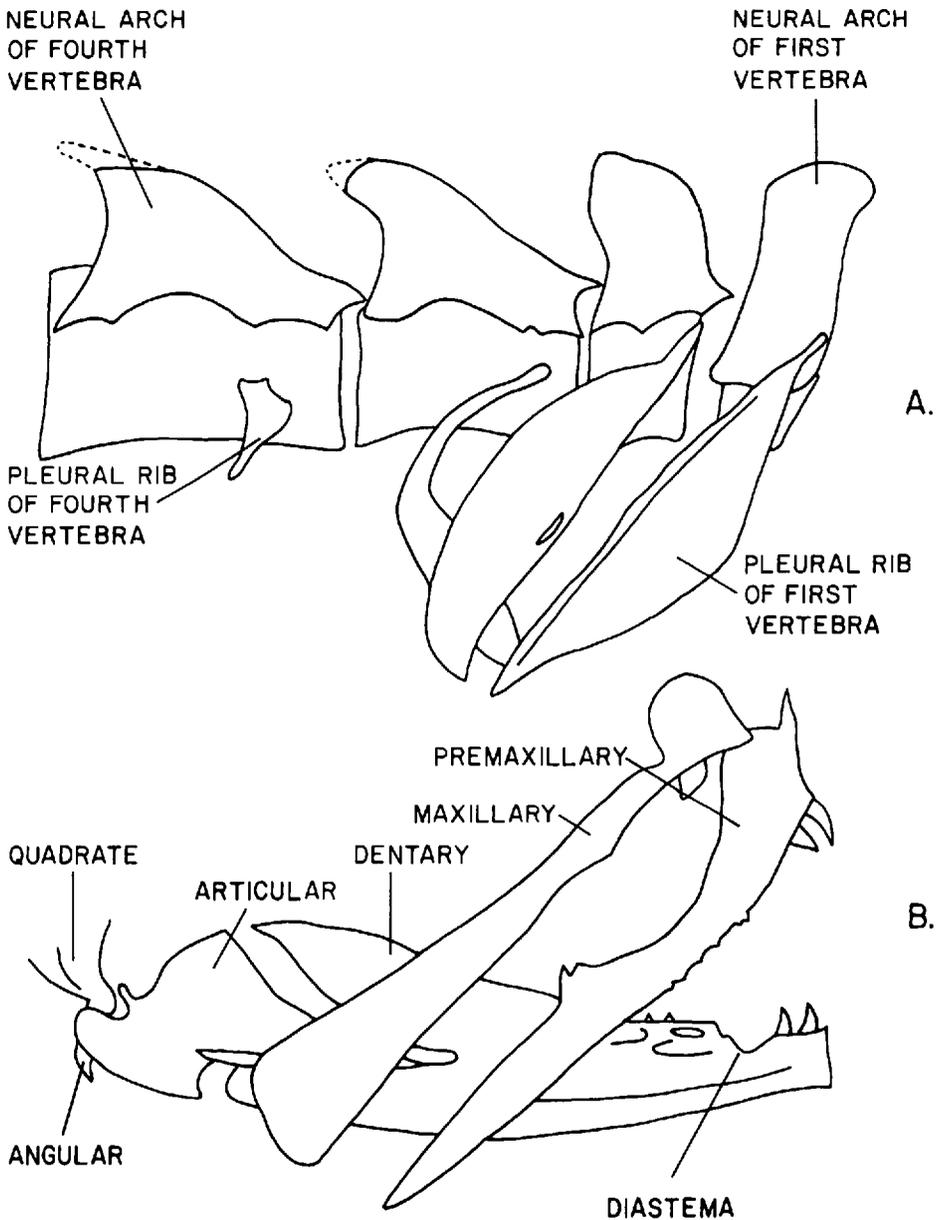


Figure 5. (A) Lateral view of the first four vertebrae of *Echiodon* sp. (USNM 216951, 3.5 mm HL). Dashed line indicates unstained cartilaginous tissue. (B) Lateral view of the upper and lower jaw and associated bones of *Echiodon* sp. (USNM 216951, 3.5 mm HL).

E. exsilium obtained from R. H. Rosenblatt (Scripps Institution of Oceanography) pectoral ray counts ranged from 19–22, with a mean count of 21. These counts are higher than those reported for any other carapine (Gosline, 1960; Robins and Nielson, 1970). The highest counts presently recorded in larvae may indicate that an ontogenetic loss of pectoral rays occurs in this species.

Carapus bermudensis.—Counts on two cleared and stained specimens (3.0, 4.1 mm HL) were: anal rays, 231, 229; dorsal rays, 207, 210; total vertebrae 141, 153;

branchiostegal rays, 7, 7. Pectoral-fin rays were damaged and missing on all cleared and stained vexillifers but one juvenile (7.3 mm HL) had 18 pectoral rays. Both cleared and stained vexillifers have developing caudal fins with hypural bones and 3–4 caudal rays visible.

Dentition

In *Echiodon* sp., premaxillary dentition on specimens greater than 3.2 mm HL consisted of prominent recurved canines at the jaw tips followed by a small toothless gap or diastema and smaller, less developed teeth (Fig. 5B). On the dentary, the paired canines were separated from the remaining smaller teeth by a more prominent diastema (Arnold, 1956, Fig. 3). Below 2.5 mm HL, the canines and diastema were not apparent in either jaw and only small premaxillary teeth are visible. On a large cleared and stained specimen (USNM 216950, 3.9 mm HL) small palatine and vomerine teeth were apparent. These were detectable in a 3.5 mm HL specimen (USNM 216951) only as 3–5 minute swellings on the palatine.

In vexillifers of *C. bermudensis* there were no enlarged canines on the dentary or premaxillary. Dentition consisted of a single row of small, well developed teeth along the dentary and premaxillary without diastemas. Both palatine and vomerine teeth were detectable in specimens larger than 4.0 mm HL.

DISTRIBUTION, ABUNDANCE AND TIME OF SPAWNING

Echiodon sp.—Over 97% of the *Echiodon* sp. vexillifers examined in this study were taken at three stations in the eastern Gulf of Mexico and Caribbean Sea. Most of these vexillifers were less than 1.0 mm HL and were taken in oblique plankton tows in depths of 130–195 m. The remaining specimens were larger (1.7–4.2 mm HL) and taken north of Cape Hatteras, North Carolina. Most of these were taken in plankton tows in surface waters (0–150 m) over bottom depths ranging from 350–1,500 m in the area of the Norfolk Submarine Canyon off Virginia. In addition, four vexillifers (2.8–4.0 mm HL) were taken in the Sargasso Sea off Bermuda during Ocean Acre cruises (Gibbs et al. 1971). The most northerly capture was on the Scotian Shelf from a neuston net towed over a bottom depth of 481 m.

Relative abundance of *Echiodon* sp. vexillifers was greatest at two Gulf of Mexico stations which were sampled over a 24 h period. In hauls containing carapids, abundances varied from 21–126 vexillifers/100 m² (\bar{x} = 48/100 m²) at one station and from 13–1,180 vexillifers/100 m² (\bar{x} = 321/100 m²) at the other. No significant differences in night-day abundances were noted. At the Caribbean station (No. 31), an estimate of 105 vexillifers/100 m² was noted. Although abundance estimates were unavailable for most collections north of Cape Hatteras, two stations had abundances of 22 and 28 vexillifers per 100 m² sea surface area.

Information on spawning of *Echiodon* sp. is quite limited. September collections in the Gulf of Mexico contained both recently hatched larvae (although no yolk sac vexillifers were found) as well as large size classes up to 3.4 mm HL suggesting either a protracted spawning season or a long larval period. In support of the latter possibility, all specimens from the Sargasso Sea, Middle Atlantic Bight and Scotian Shelf were relatively large (1.7–4.2 mm HL). Additional records of the occurrence of this carapid are necessary before an accurate description of its spawning period and distribution is possible.

Carapus bermudensis.—In addition to two vexillifers reported from the northern Gulf of Mexico (Dawson, 1971), we examined 34 *C. bermudensis* vexillifers taken in the Sargasso Sea off Bermuda in Ocean Acre cruises (Gibbs et al. 1971). These

specimens ranged in size from 2.1–4.1 mm HL and were taken in collections during all seasons. The majority of *C. bermudensis* vexillifers were taken by 3 m IKMT in surface waters (0–400 m) during summer cruises in 1968, 1969 and 1971.

Although *C. bermudensis* ranges to Bermuda (Böhlke and Chaplin, 1968) and the majority of our specimens were taken off the island (Gibbs et al. 1971), there is no indication that the present vexillifers are products of a Bermudian insular spawning population. All vexillifers examined were in excess of 2.1 mm HL and 40 mm TL. Spawning times and distributions of this carapid cannot be delimited until smaller size classes become available.

FEEDING NOTES

Although stomach contents of all *Echiodon* sp. vexillifers were not examined, several cleared and stained specimens had recently fed. The guts contained the exoskeletons of unidentified calanoid copepods as well as many smaller crustacean remains, probably those of calanoid copepodites.

UNIDENTIFIED CARAPIDAE

Two small vexillifers (1.85 mm HL/9.4 mm NL and 2.15 mm HL/11.3 mm NL) taken in the mid-Caribbean (Station 165) could not be referred to *Echiodon* since the vexillum inserted over the fifth or sixth myomere, and the snout to vexillum length was equal to that of the snout to anus. On the other hand, the specimens could not be assigned to *Snyderidia* or *Carapus* since pectoral rays and total myomeres were not apparent and dentary dentition was undeveloped. The largest specimen was cleared and stained following the method of Dingerkus and Uhler (1977). Vertebral centra and pectoral rays were unstained and only a few rays in the mid-portions of the anal and dorsal fins were visible. Head length as a percent of notochord length in the two unidentified specimens (19.02–19.68%) greatly exceeded that value for vexillifers of *Carapus bermudensis* (3.05–5.68%) of comparable head lengths, but more closely approached that reported by Strasburg (1965) for *Snyderidia canina* (11.9 mm HL/104 mm TL $\times 100 = 11.44\%$). Clearly, additional larval material of *Carapus* and *Snyderidia* in a smaller size range is necessary before we can accurately identify these specimens.

DISCUSSION

Morphology

Elongate dorsal fin rays or spines are found in larvae of numerous unrelated families of fishes including bothids, trachipterids, regalecids, trichiurids, carangids and serranids. Obviously, these structures are serially homologous. The so-called pelvic "vexillum" of *Kasidoron* (= *Gibberichthys*) (Robins and de Sylva, 1965; Robins, 1966; Courtenay and McKittrick, 1970) is clearly not homologous with carapid vexilla. The term "vexillum" has little use when it refers broadly to any elongate dorsal-fin ray. It is also misleading in statements such as "These bones (predorsal bones in lower percoids) may possibly represent the persistent supporting elements of larval vexilli" (Courtenay and McKittrick, 1970). The statement, made in a phylogenetic rather than an ontogenetic context, could be misinterpreted as suggesting that carapids are closely related to the lower percoid ancestor.

We have chosen to continue use of the term vexillum in its restricted sense (applicable to carapids only) until more detailed studies on elongate larval fin rays

are available. In the meantime, the following may be useful in delimiting other serially homologous dorsal-fin rays. The carapid vexillum can be characterized as an elongate, singular, deciduous or resorbed, larval, dorsal-fin ray located in front of the first adult dorsal-fin ray and composed of bilaterally-paired, segmented components, each of which contains a proximal and distal element. It is covered by a fleshy, sometimes ornate sheath and supported by an expanded proximal radial which may fuse with the proximal radial of the first adult dorsal-fin ray, and which may be resorbed at metamorphosis.

In *C. bermudensis*, the modified proximal radial (Fig. 2) which supports the larval vexillum may be resorbed at metamorphosis since a predorsal bone is not apparent in adult material (Courtenay and McKittrick, 1970, Fig. 1). This may also be the case in adults of *Echiodon* sp. as suggested by Courtenay and McKittrick (1970). In some carapids (as in *Onuxodon*, Courtenay and McKittrick, 1970, Fig. 3), the ontogenetic loss of the vexillum creates a predorsal bone which is clearly derived from a dorsal fin radial. In general, however, it is not possible to determine if particular predorsal bones evolved from dorsal fin radials or supraneurals (Kendall, 1976). In the percoid grammistids and serranids, it remains to be shown whether predorsal bones evolved through ontogenetic loss of a larval dorsal-fin spine (Courtenay and McKittrick, 1970) or a phylogenetic backward shift of the dorsal fin (Smith and Bailey, 1961).

Throughout the size range of our vexillifers of *Echiodon* sp., we could find no indication of an "exterilium" or detached and trailing gut condition (Fraser and Smith, 1974). In contrast, Robertson (1975) has figured an exterilium larva of *Echiodon rendahli* from New Zealand waters. Since the configuration of the gut in larval fishes is sometimes considered useful in separating larval fishes at the ordinal or subordinal level (Ahlstrom and Moser, 1976), we find this discrepancy confusing. It is possible that an exterilium represents a unique larval specialization in *E. rendahli*. On the other hand, this extreme departure from the gut morphology as found in the present specimens as well as the inconsistent placement of the vexillum and first rays of the dorsal and anal fins suggest the possibility that Robertson's (1975) vexillifer may be referable to another carapid genus.

Distribution

Since larval stages are an important dispersal phase in many fishes, their occurrence outside the normal geographic boundaries of adults should not be considered unusual under certain circumstances. The larval *Echiodon* sp. reported herein from areas north of the Gulf of Mexico and Caribbean Sea fit a Gulf Stream dispersal pattern that has been repeatedly observed in subtropical western North Atlantic fishes (Colton, 1961; Smith et al. 1975; Evseenko, 1976; Futch, 1977). Larval *Callionymus* spp., *Gobionellus* sp., *Hemipteronotus novacula*, *Bothus ocellatus*, *Syacium* sp., *Elops saurus*, *Coryphaena* spp. certain myctophidae, trachipteridae, gerridae, and many others (pers. observ.) are all encountered in the ichthyoplankton north of Cape Hatteras, while adults are unknown or only occasionally found north of the Cape. The presence of larvae of *Echiodon* sp. from 0.43–3.35 mm HL in September 1970 collections (SEFC) in the Gulf of Mexico and the absence of larvae under 1.7 mm HL north of the Gulf support the conclusion that spawning of this carapid occurs in the Gulf of Mexico and Caribbean Sea. In addition, the few adults that have been collected are from the Gulf of Mexico (Shipp, pers. comm.).

The scarcity of vexillifers of *C. bermudensis* in the present collections is puzzling. The most obvious explanation is lack of sufficient sampling. However, one

ethological difference between *Carapus* and *Echiodon* may relate to the differences noted in larval abundances. Adult *Carapus* are all known to be inquiline in invertebrate hosts while no *Echiodon* adult has been collected from a host and the genus is suspected of being free-living (Arnold, 1956; Trott, 1970). Perhaps the inquiline adult behavior has selected for a shorter larval life or some change in larval behavior which decreases its availability to plankton nets.

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