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OBSERVATIONS ON STRUCTURE AND EVALUATION OF POSSIBLE FUNCTIONS OF THE VEXILLUM IN LARVAL CARAPIDAE (OPHIDIIFORMES)

John J. Govoni, John E. Olney, Douglas F. Markle and William R. Curtsinger

ABSTRACT

Elongate dorsal appendages adorn pelagic larvae of many fishes from disparate taxa, among them larvae of the family Carapidae, wherein the singular, elongate appendage is termed a vexillum. The vexillum is a complex larval specialization of the dorsal fin and is characteristic of all carapid genera. It is motile, well vascularized, and innervated by a branch of a cranial nerve with no apparent spinal innervation. Histological studies of *Echiodon dawsoni* and *Carapus bermudensis* vexilla show a two layered epidermis with mucous cells, an arteriole and venuole, two myelinated peripheral nerve fascicles, and two collagenous central shafts. No taste buds, free neuromasts or organized chemoreceptors were found on the vexillum, including its fleshy tabs; collateral branches of the nerve fascicles may end as free-nerve endings. In situ observations of living pearlfish larvae revealed a remarkably long and ornamented vexillum that assumed variable postures. The data suggest that carapid vexilla serve multiple functions, including predator deception, sensation, and hydrodynamic effects.

Elongate dorsal appendages adorn pelagic larvae of many fishes from disparate taxa (e.g., lophiiforms, bregmacerotids, carapids, carangids, trachipterids, regalecids, syngnathids, serranids, trichiurids and bothids), yet the function of these structures is largely speculative (Moser, 1981). These appendages may serve a common function, for some superficially similar structures have evolved independently among larvae that share a common habitat, the planktonic environment of the ocean's upper-mixed layer. Alternatively, these structures may not serve a common or even single function inasmuch as they are found on larvae of divergent shapes (deep-bodied bothids to elongate carapids), are variously stiff and serrated (as in some serranids) or are flexible and adorned with fleshy ornamentation (as in other serranids and carapids) and are retained in the adults of bregmacerotids and lophiiforms while lost, resorbed or allometrically reduced in size in others. Five hypotheses on the function of elongate dorsal appendages among larval teleosts are that they serve in sensory perception (Kyle, 1913; Moser, 1981), camouflage or predator deception (Moser, 1981), protection or predator deflection (Kyle, 1913; Moser, 1981), flotation (Amaoka, 1973; Hubbs and Chu, 1934; Yevseyenko, 1976; Dawson et al., 1979) and prey attraction (Moser, 1981). Among these hypothesized functions, flotation predominates.

Olney and Markle (1979) described the gross morphology of the larval carapid predorsal filament, the vexillum, but did not speculate on its function. Recently, material suitable for histological examination and in situ photographs of living pearlfish larvae have become available. This paper presents observations on the gross morphology and histology of the carapid vexillum in an attempt to further define this larval structure as a unique carapid specialization and to evaluate its possible function(s).

MATERIALS AND METHODS

We focused our studies on the vexillifer larvae of *Echiodon dawsoni* (Olney and Markle, 1979; Williams and Shipp, 1982) and *Carapus bermudensis,* which were collected on cruises on the Nova

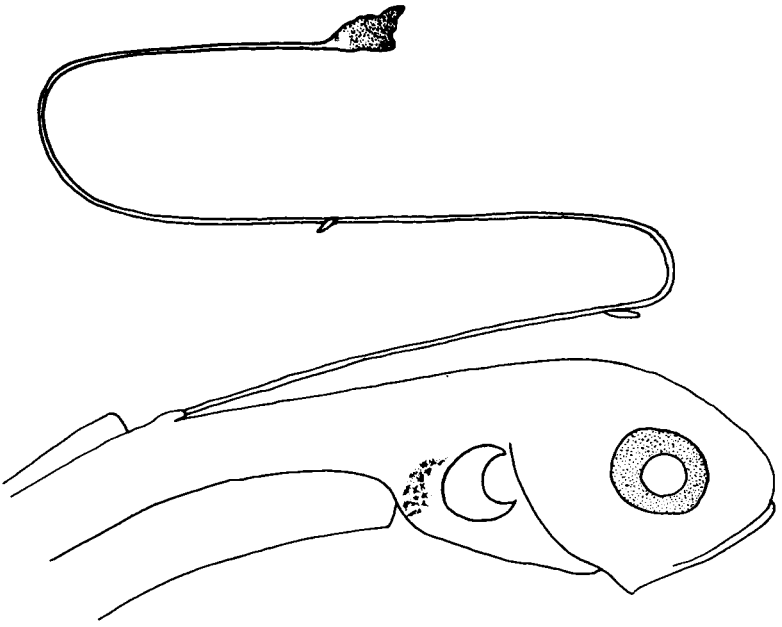

Figure 1. Line drawing of *Echiodon dawsoni* showing the complete vexillum with fleshy tabs and distal end.

Scotian shelf (Fisheries and Oceans Canada), the continental shelf, Bahamian banks, and abyssal plain of the western North Atlantic (Virginia Institute of Marine Science), and the northern Gulf of Mexico (NOAA-NMFS) from 1976 to 1981. Numerous other carapid vexillifers from Pacific localities were also examined as part of an ongoing systematic study.

Gross Morphology.—Skeletal elements were examined in specimens cleared and stained with alizarin red S and alcian blue 8 GS following the Taylor and Van Dyke (MS) modification of Dingerkus and Uhler (1977). In addition to larval carapids, specimens of *Bregmaceros* sp., *Trichiurus lepturus, Citharichthys cornutus,* and *Zu cristatus* were cleared and stained for comparison. Nerve tracings were accomplished by clearing and staining specimens following a modification of the Sihler technique (Freihofer, 1966; Fraser and Freihofer, 1971).

Histology.—*Echiodon dawsoni* and *Carapus bermudensis* vexillifers from formalin-fixed plankton collections were prepared by following standard paraffin procedures and were stained with hematoxylin–astra blue–eosin Y. Serial sagittal and cross sections, 7 μm thick, were made along the existing vexillum. The anterior body between the vexillar insertion and the snout of one *C. bermudensis* was serially sectioned in the sagittal plane along the dorsoventral axis.

Fresh specimens of *E. dawsoni* were fixed in chilled neutral buffered formalin and acrolein, dehydrated in methanol, and infiltrated and embedded in glycol methacrylate (plasticized with 2-ethyl-1 butyl alcohol and polymerized with N,N-dimethanaline, a modification of Ruddell, 1971). The blocks were then serially sectioned at 2 and 4 μm in the sagittal and cross sectional plane and stained with acid fuchsin–toluidine blue, alkali blue 6 B–neutral red, or alizarin fast blue G. This procedure was used in preference to standard paraffin techniques because it facilitated the handling of delicate structures (vexilla) and revealed finer cytological detail.

RESULTS

Gross Morphology.—In preserved material, the vexillum of larval pearlfishes varies from a highly ornamented and pigmented structure to a simple filament (Padoa, 1937; Olney and Markle, 1979). Apparently, the carapid vexillum is subject to mechanical damage by plankton nets during collection, which often results in abrasion of apical epithelial tissue and loss of fleshy tabs. This loss can vary

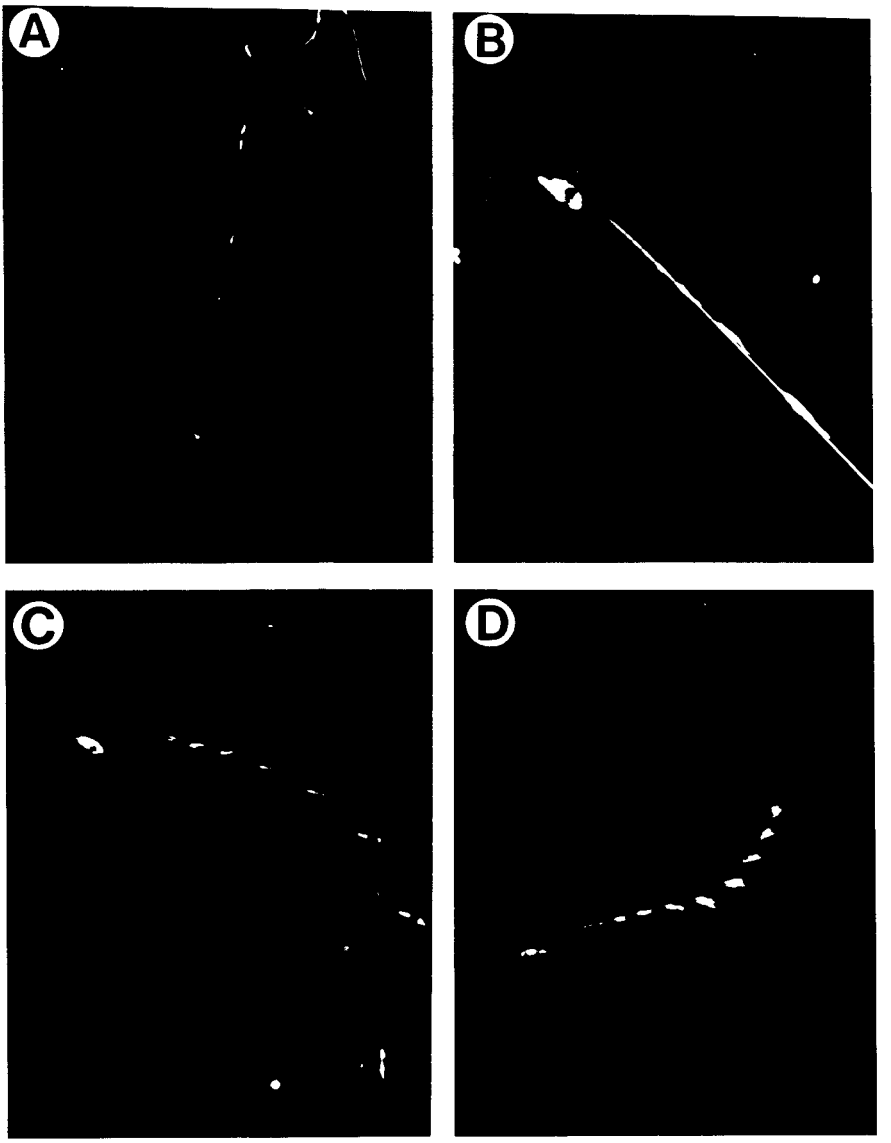

Figure 2. In situ photographs of Hawaiian pearlfish larvae illustrating variable vexillum postures. A, perpendicular to the body; B, directed forward; C, extended downward; D, trailing behind the head. Photographs A and C are of the same specimen.

dramatically between species as well as within species, thus obviating vexillum ornamentation as a useful taxonomic character. For example, Olney and Markle (1979), who examined 522 larval *Echiodon dawsoni,* concluded that the vexillum was unornamented and illustrated skeletal shafts exiting through the distal end. Examination of additional material in the present study indicates that the undamaged vexillum of *E. dawsoni* is indeed ornamented with fleshy tabs and has skeletal shafts supporting the proximal third of the vexillum with an unsupported

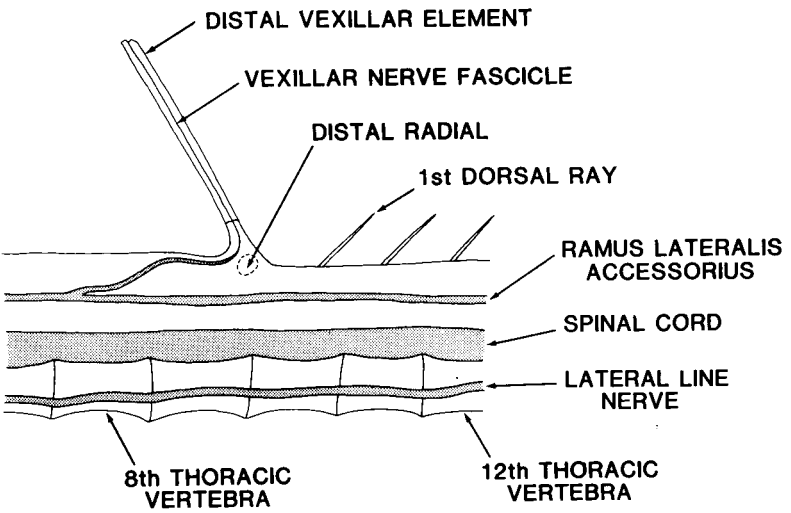

Figure 3. Camera lucida drawing (lateral view) of the nerves (stippled) in the area of vexillum insertion in *Echiodon dawsoni.*

fleshy extension constituting the distal two thirds (Fig. 1). The conclusion that the vexillum is fragile is further supported by diver observations of living pearlfish larvae[1] off Hawaii (Fig. 2). In situ photographs reveal a vexillum equal in length to body length and ornamented with numerous petaline fleshy tabs, a condition not yet seen in preserved material.

A stout branch of a peripheral cranial nerve innervates two nerve fascicles of the carapid vexillum (Fig. 3). The dorsal peripheral course of this nerve and its parietal entrance into the cranium suggests that the nerve is the parietal-dorsal branch of the ramus lateralis accessorius (RLA) of cranial nerve VII; we were unable to trace the origin of nerve fibers back to cell bodies in the geniculate ganglion or observe terminal taste buds (Freihofer, 1963). In *Echiodon dawsoni* the branch leaves the main trunk of the ramus above the eighth vertebra and courses closely parallel to its bilateral counterpart before diverging around the proximal radial above the ninth vertebra (Fig. 3). It then passes obliquely dorsal to the distal radial, regains but does merge with its counterpart, and passes into the vexillum. In *Carapus bermudensis* the branch leaves the trunk above the second vertebra. Our preparations did not reveal dorsal spinal rami or branches of the RLA leading to the dorsal fin of carapid larvae. The pectoral branch of the RLA (Freihofer, 1970) conjoined the RLA after its exit from the cranium, but there was no evidence of junctions with other nerves (for example the vagus or lateral line nerve) outside of the cranium.

Although the most conspicuous and universal appendage characterizing carapid larvae is the vexillum (Markle and Olney, 1980), it is not the only extended, banner-like structure on some species. In the most highly ornamented genus, *Carapus,* we have some examples of *C. bermudensis* and an undescribed Pacific species in which the basic vexillum ornamentation is repeated in the caudal

[1] These larvae are tentatively identified as *Onuxodon margaritiferae* on the basis of vexillum and first dorsal ray position, gross morphology and distributional data.

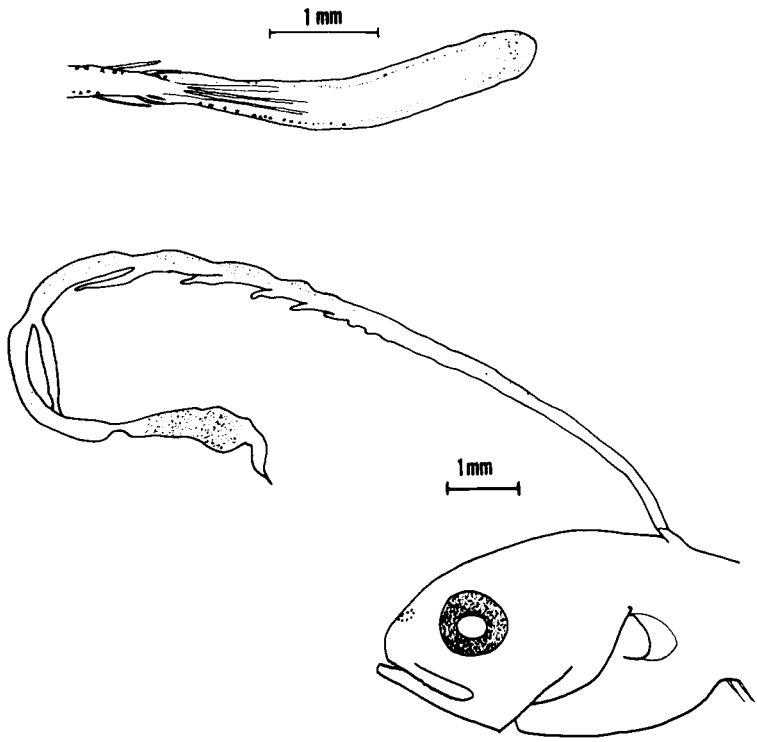

Figure 4. Line drawing of a larval *Carapus* sp. showing caudal filament (upper) and vexillar ornamentation (lower).

filament (Fig. 4). The caudal filament of these larvae is similar to that observed in larval and adolescent stages of eutaeniophorid fishes (Bertelsen and Marshall, 1956). In many specimens the caudal filament appears damaged or lost, so that the frequency of caudal filament and vexillum concomitance may be higher than our observations indicate. The structure of these caudal filaments differs from that of the vexillum in that they are supported by three cartilagenous shafts (modified caudal rays) and are laterally flattened. The trailing gut of Robertson's (1975) as yet unidentified "exterilium" larva provides another gross structural analog to the vexillum.

Histology.—Vexilla are sheathed by an epidermal layer composed of two stratified, cuboidal, epithelial cells (Fig. 5). Nuclei are visible and the cytoplasm is basophilic. The epidermis surrounding the vexillar core lies on a collagenous basal lamina. Mucous cells with acid mucopolysaccharides are dispersed within the epidermis. Epithelial and mucous cells along with scattered melanophores constitute the fleshy tabs as well as the apical end of the vexillum. Capillary blood vesicles are also evident in the apical end. We did not observe taste buds, free neuromasts, or specialized chemoreceptors (Whitear, 1971a) on the surface of the vexillar shaft, its fleshy tabs, or apical tip (Fig. 6).

The core of the vexillar shaft is bilateral with two acellular collagenous shafts, two nerve fascicles, and two blood vesicles: an arteriole and a venuole (Fig. 5). Melanophores are occasionally visible within the core. There is no true cartilage or bone in the vexillum, though Olney and Markle (1979) described the supporting

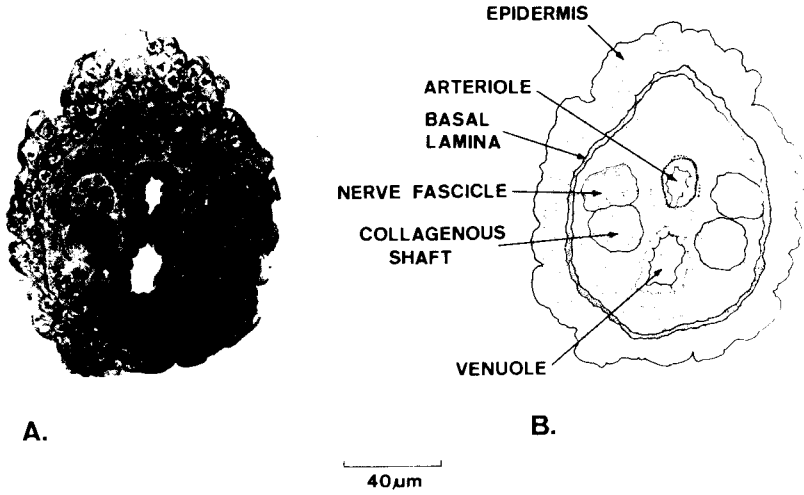

Figure 5. Cross section of the vexillum of *Echiodon dawsoni*: A, photomicrograph (alkali blue 6B–neutral red); B, line drawing of section illustrating tissue structure.

shafts on the basis of alcian blue and alizarin red S reactions as cartilaginous with marginal ossification. Alizarin fast G did not show the presence of elastin fibers. The inner bilateral components are surrounded by mesenchymal cells with basophilic cytoplasm and acidophilic nuclei. The nerve fascicles comprise several myelinated peripheral nerve fibers held together by collagenous perineurium. Cross sections of nerve fascicles often showed collateral branches oriented toward the epidermis or along the collagenous shafts, where they probably terminate as free nerve endings (Whitear, 1971b). The arteriole is composed of a single layer of endothelium sheathed by smooth muscle cells. The venuole is also lined with a single layer of endothelial cells, but no muscle cells were visible. There is no intrinsic striated musculature present within the vexillum. At the insertion of the vexillum, the core shafts laterally diverge around the distal cartilagenous radials

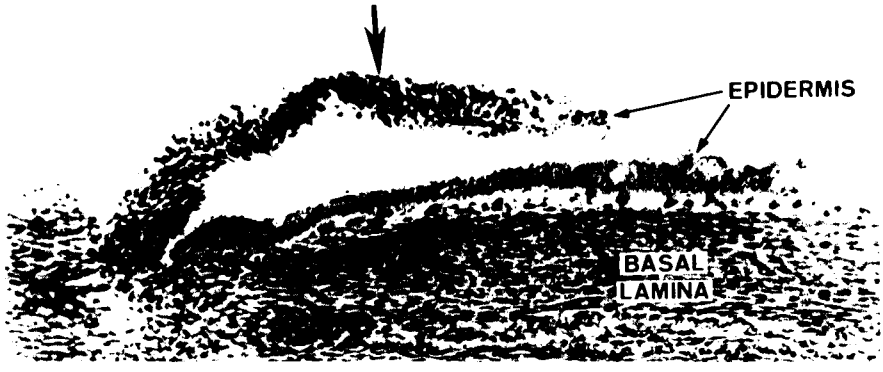

Figure 6. Sagittal section of the vexillum and a fleshy tab (arrow) of *Carapus bermudensis* (hematoxylin–astra blue–eosin Y).

(Olney and Markle, 1979). Two muscles on each side, a superficial and a deep slip, originate on the fascia covering the lateral axial musculature, pass around the distal and proximal radials, and insert on the proximal lateral flanges of the core shafts. This pattern resembles the typical dorsal fin ray musculature described by Greene and Greene (1913) and thus provides the proximal vexillum with movement in the anterior-posterior and lateral dimensions.

Behavior, Vexillum Posture and Food Habits.—With the exception of brief shipboard aquaria observations of living *Echiodon dawsoni* (present study) that agree with reports of head-down swimming behavior in newly-hatched vexillifers of *E. drummondi* (Kennedy and Champ, 1971), little is known of swimming and vexillum postures of carapid larvae. During a series of nighttime underwater encounters with larval pearlfish in December 1980 off Hawaii (depth of observation, surface to 40 m; approx. location, 19°30′N, 156°03′W), one of us (WRC) recorded a number of remarkable behavioral patterns (Fig. 2). Except during periods of active swimming (undulating, anguilliform movement), pearlfish larvae were observed to maintain a head-up, oblique posture while drifting motionless in prevailing currents. Vexillum postures were variable: extending perpendicular to the body and reaching a height approximately equal to total body length above the head (Fig. 2A); directed immediately forward of the head and in the body plane (Fig. 2B); extended downward in a long arc (Fig. 2C); and trailing behind the head along the body plane (Fig. 2D). Avoidance response was observed when larvae were cued to the proximity of photographic gear. Larvae swam rapidly forward away from the camera with the extended filament (vexillum) trailing behind the head. During these dashes, the vexillum was observed to decrease in length to approximately ⅓–½ original total length. This apparent change in the size of the vexillum could be accomplished by the engorgement and disengorgement of capillaries in the apical end of the vexillum. Larvae were not observed to feed, although surrounding waters were sometimes densely inhabited with invertebrate zooplankters. During seven separate encounters in varying locations over a 3-week period, pearlfish larvae were not observed to be in association with flotsam or living organisms.

Although no live observations have been made on feeding behavior in larval Carapidae, vexillifers are planktivorous, as are most other pelagic marine fish larvae. Olney and Markle (1979) reported that guts of cleared and stained specimens of *Echiodon dawsoni* larvae contained exoskeletons of unidentified calanoid copepods. In the present material, guts of both *E. dawsoni* and *Carapus bermudensis* contained only copepods. For example, one *E. dawsoni* vexillifer (3.1 mm HL) caught off Nova Scotia on 15 August 1978 contained 30 copepods: *Oithona* sp.—10; *O. atlantica*—4; *O. helgolandica*—1; *Microcalanus pusillus*—4; *Mecynocera clausi*—1; *Clausocalanus arcuicornis*—1; *Paracalanus parvus*—1; calanoid nauplii and unidentified copepods—8.

Discussion

Olney and Markle (1979) described the vexillum as an elongate, singular, deciduous or resorbed, dorsal fin ray. Present evidence supports the conclusion that the vexillum is a dorsal fin derivative since the distal vexillar core shafts resemble actinotrichia in the fin anlagen of other embryonic and larval teleosts (Goodrich, 1904; Francois, 1956; Geraudie, 1977). Resemblance is based in part on the collagenous composition, median position, and lack of multiple segmentation and branching of the core shafts, as well as on the supposition that the carapid vexillum

is resorbed at metamorphosis. Lepidotrichia were not observed in the present material, though Strasburg (1965) referred to the vexillar core shafts as such. Arnold (1956) speculated that the vexillum is resorbed during metamorphosis and subsequently Courtney and McKittrick (1970) and Olney and Markle (1979) reported resorption of the vexillar axial supports in *Carapus bermudensis*. If so, the resorption must occur quickly since all of the larger vexillifers we have seen either have an apparently complete vexillum or have only the short proximal segment. The deciduous loss of the vexillum, thus, remains a possibility.

The vexillum appears to be a unique carapid specialization and thus the term can be restricted to the Carapidae as indicated by Olney and Markle (1979) and Markle and Olney (1980). Although the vexillum grossly resembles some elongate rays of other taxa, its structure differs. A cross section of the elongate dorsal ray of the larval serranid *Liopropoma* (=*Flagelloserranus*; Kotthaus, 1970) as well as cleared and stained larvae of *Trichiurus lepturus* (Trichiuridae) and *Bregmaceros* sp. (Bregmacerotidae) show single skeletal supports that lack the joint separating proximal and distal elements as in the carapids. In the bothid *Arnoglossus* (Kyle, 1913), elongate dorsal rays are supported by singular, serially jointed skeletal elements whereas in *Citharichthys* (Bothidae) and *Zu* (Trachipteridae) by paired elements that lack joints.

In ophidiiform fishes the dorsal fin is innervated by serial branches of the RLA and sequential spinal rami (Freihofer, 1970). We did not observe either spinal rami leading to the vexillum or joint innervation of the vexillifer dorsal fin by the RLA and spinal rami. These sources of innervation may not be developed in the carapid vexillifer, or our Sihler's preparations may not have revealed these nerves. In either case, the RLA branch that innervates the vexillum is noticeably stout (Fig. 3). Nerves supplying other median fin derivatives, for example, gonopodia (Riehl et al., 1978), are also stout in comparison to their serial homologues.

The vexillum clearly has a sensory capacity, although the exact sensory function is unknown. The RLA is ascribed to somatic taste sensibility (Freihofer, 1963). In cyprinoids and siluroids (Herrick, 1901; 1903; 1905) and percoids (Freihofer, 1978), its fibers have been shown to originate in the geniculate ganglion and to carry fasciculus communis fibers which terminate in somatic taste buds. Could the nerve identified herein as the RLA also carry fibers associated with tactile and proprio-reception or were taste buds missed in our examinations? Cutaneous taste buds are quite numerous and concentrated on modified fin rays and barbels (Bardach and Case, 1965), but abrasion of apical epithelial tissue and loss of fleshy tabs due to mechanical damage of preserved specimens may have biased our histological results. Other nerves arising from cranial nerve VII can innervate free nerve endings that serve as tactile (Hoagland, 1933) and proprio-reception (Ono, 1979). Moreover, in many fishes, including ophidiids, a vagal (cranial nerve X) ramus joins the RLA before it exits the cranium (Freihofer, 1963). Herrick (1900) included vagal communis fibers and possibly general cutaneous fibers from the jugular ganglion with the RLA in *Gadus morhua*. Thus, rami associated with certain cranial nerves often originate in more than one ganglion and consequently vary in the type of sensory components that they carry (Whitear, 1971a).

The wide range of vexillum postures and the remarkable extensions of vexillar distal portions (Fig. 2) are suggestive of a remote sensory function. Free nerve endings, if present either in the epidermis or on the collagenous shafts, could serve as tactile (Bardach and Loewenthal, 1961) or proprio-receptors (Ono, 1979). Tactile or proprio-reception in the carapid vexillum would provide sensory information on the positional state of the appendage and monitor turbulence fields

of ambient water including turbulence created by copepods (Kerfoot et al., 1980). The posture of the vexillum could cue the vexillifer by tactile or proprioreceptive stimuli to the presence of food or forewarn the larva of impending danger.

The observation that vexillar length decreases during fright response and that the vexillum assumes a trailing posture during avoidance swimming activity implies that predator deflection is not afforded physically by the structure. The vexillum is supported by collagenous shafts which are strong but flexible. Thus, it is unlikely that the vexillum offers protection as suggested for the elongate dorsal rays of bothids (Kyle, 1913), or in the same manner as the spinous, serrated, dorsal rays of some serranid larvae.

The superficial similarity of the vexillum and the elongate dorsal rays of some larvae of other taxa as well as its repetition by caudal filaments in some species of *Carapus* and exterilial guts in other carapid vexillifers are suggestive that the vexillum, the caudal filament, and exterilial guts might serve in predator deception. Carapid larvae are usually sparsely pigmented while the vexillum and caudal filaments have more pigment per surface area and presumably could function as a will-of-the-wisp to distract the attention of predators. The vexillum would be more expendable than other body parts. The vexillum also increases the apparent size of the vexillifer and thus may deceive a predator as suggested by Moser (1981). The serial fleshy tabs and pigment aggregations of pearlfish larvae (Padoa, 1937; Fig. 2) resemble those of *Zu cristatus* (Sparta, 1937), *Liopropoma* (Kotthaus, 1970), and *Arnoglossus* (Amaoka, 1973). The vexillum might serve a function in common with the elongate rays of these larvae by mimicking siphonophores, hydromedusae, or salps. Fraser and Smith (1974) suggested a similar function for the exterilial guts of a brotulid larva.

A hydrodynamic effect of an appendage such as the vexillum is no doubt present. Vexillifer larvae are long and serpentine with large gas bladders, thus the increase in surface area accomplished by the vexillum would not appear necessary to provide flotation. The vexillum may function as a stabilizer that aids in the maintenance of the body posture of resting vexillifers.

Moser (1981) suggested that fleshy tabs on elongate dorsal appendages might attract food organisms. Inasmuch as the vexillum is often directed anteriorly one might suspect a similar function. Copepods, however, constitute the diet of vexillifers and are known to avoid objects of similar or larger size (Strickler, 1975). The fleshy tabs of the carapid vexillum are equal to or larger than the copepods in their diets.

The carapid vexillum is anatomically unique and, of the five hypothesized functions, appears to play a role in sensory perception, predator deception, and hydrodynamics. Flotation by itself does not seem to be a major function. Because it bears superficial resemblance to elongate dorsal fin rays of planktonic larvae of other families, comparative studies are clearly needed to answer questions of functional analogy.

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