Echiodon anchipterus: A Valid Western Pacific Species of the Pearlfish Family Carapidae with Comments on Eurypleuron

Jeffrey T. Williams¹ and Yoshihiko Machida²

 Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.
 Department of Biology, Faculty of Science, Kochi University, Akebono, Kochi 780, Japan

Abstract The collection of an adult specimen of *Echiodon* from Owase, Japan, enabled us to further evaluate one of the unresolved identification problems listed by Markle and Olney (1990). The recognition of *Echiodon anchipterus* Williams as a valid western Pacific species was questioned by Markle and Olney (1990), who tentatively synonymized it with the western Indian Ocean *E. coheni* Williams. The Japanese specimen had 15–16 pectoral fin-rays (vs. 18 in *Echiodon coheni*), 22 total nasal lamellae (vs. 24), and 21 precaudal vertebrae giving a range for *E. anchipterus* of 19–21 (vs. 18–19). These new data support the recognition of both *E. anchipterus* and *E. coheni* as valid, allopatrically distributed species. The phylogenetic relationships among the species of *Echiodon* are reexamined and a cladogram summarizing our hypothesis of their interrelationships is presented.

Eurypleuron owasianum (Matsubara) is considered to be endemic to the Japan zoogeographic region, where adults are known only from specimens taken off Owase, Japan. The South African, southeastern Australian, New Zealand, and Sala y Gomez Ridge specimens are collectively referred to Eurypleuron cinereum (Smith) pending a comprehensive revision of the group.

The genus Echiodon is a geographically widespread group of carapid fishes, including 11 nominal species. In a revision of the family Carapidae, Markle and Olney (1990) recognized ten named species of Echiodon and discussed an additional species, Ec. anchipterus, which they described as being of unresolved taxonomic status and tentatively considered it a junior synonym of Ec. coheni. Williams (1984a) discussed adult representatives of two populations of undetermined taxonomic status. Larval specimens of an additional unnamed species of Echiodon were reported by Markle and Olney (1990). Williams (1984a) placed Carapus owasianus (Japan) and Carapus cinereus (South Africa) in the genus Echiodon, but Markle and Olney (1990) reassigned these two species to their new genus, Eurypleuron.

An adult specimen of the Echiodon anchipterus-Ec. coheni species complex collected off Japan provided new information that allowed us to reevaluate the taxonomic status of Ec. anchipterus. These two species were described by Williams (1984a) based on one specimen of Ec. anchipterus from the Visayan Sea, Philippines, and two specimens of Ec. coheni

from Somalia. The characteristics of the Japanese specimen fit those of *Ec. anchipterus* and support the recognition of *Ec. anchipterus* as a species distinct from *Ec. coheni*.

We provide a complete description of the Japanese specimen, as it represents the second known adult of *Ec. anchipterus* and the first record of the genus *Echiodon* (sensu Markle and Olney, 1990) from Japan. Based on characters figured and described by Markle and Olney (1990), we reevaluate the relationships among the species of *Echiodon* and provide a more parsimonious cladistic hypothesis than that offered by Markle and Olney (1990). We also discuss the taxonomic status of the two nominal species of the genus *Eurypleuron*.

Methods for taking counts and measurements follow Williams (1984a). The illustrations of characters presented in Markle and Olney (1990) are not reproduced here. The specimen described herein has been placed in the Fisheries Research Laboratory, Mie University (FRLM). Analysis of phylogenetic characters was based on adult material listed in Williams (1983, 1984a, 1984b) and on data from larval and adult material presented in Markle and

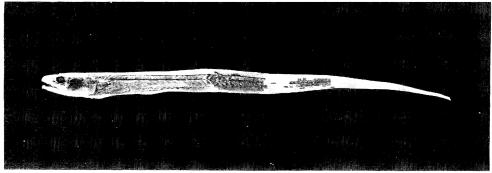


Fig. 1. Echiodon anchipterus, FRLM 10909, 172 + mm total length, from Owase, southern Japan.

Olney (1990).

Echiodon anchipterus Williams, 1984 (New Japanese name: Kumano-kakureuo) (Fig. 1)

Material examined. FRLM 10909, male, 172 + mm total length, off Owase, Pacific coast of southern Japan, bottom trawl, depth unknown, collected by Dr. Kiyoshi

Suzuki in 1952.

Description. Selected counts and measurements are given in Table 1. Body slender, compressed (Fig. 1); head length 24.0 mm; branchiostegal rays 7; snout rounded in lateral view, slightly projecting beyond upper jaw; mouth oblique, upper jaw extending posteriorly beyond posterior margin of eye; eye elliptical, its horizontal diameter equal to snout length; interorbital width equal to one-half horizon-

Table 1. Selected meristic and morphometric data for *Echiodon anchipterus* (based on 7 larvae (counts only) from Markle and Olney (1990) and the 2 known adults from Japan (the values in parentheses) and the Philippines) and *Ec. coheni* (based on the 2 known adults from Somalia). *Refers to the remnant vexillar radial persisting in adults.

	Ec. anchipterus	Ec. coheni
Number of specimens	9	2
Total length of adults (mm)	110 + -(172 +)	96 + -143 +
D_{30}	40-45 (41)	42-43
A_{30}	52-(55)	53-54
Precaudal vertebrae	19-(21)	18-19
Pectoral-fin rays	15-16 (16/15 right)	18
Total nasal lamellae	22	24
Dorsal-fin insertion	8-(10)	9
Anal-fin insertion	(3)-5	4
Preopercular pores	3	3
Upper lip flaps	2	2
Stomach color	tan	tan
Predorsal bone*	8	8
Lateral line developed	yes	yes
Measurements in % head length:		
Depth at nape	(43.3)-51.6	51.3- 53.5
Depth at 50 mm	(36.7)-40.4	22.7- 37.0
Predorsal length	147.2-(164.2)	138.0-150.0
Preanal length	107.5-(110.8)	96.0-102.0
Preanus length	(93.8)-96.9	91.5- 92.7
Maxillary length	(50.8)-50.9	51.3- 53.5
Snout length	(22.1)-24.2	19.3- 20.0
Horizontal eye diameter	19.9-(22.1)	21.5- 24.7
Interorbital width	(10.8)-11.8	11.0- 12.7

tal eye diameter; anterior nostril small, circular, positioned about halfway between snout tip and anterior margin of eye; posterior nostril circular, positioned near anterior margin of eye; short opercular spine exposed through an elliptical slit in skin; cephalic sensory pore system: IO 9, LT 6, MD 5, POP 3, SO 5, ST 3.

Villiform bands of teeth on both upper and lower jaws, 1 to 2 canine teeth present on each side of symphyses of both jaws. Teeth on vomer and palatines slightly larger than villiform teeth on jaws, arranged in about 6 rows on vomer, 3 to 4 rows on palatine. Gill rakers on first arch (1)0+1+2(6), longest raker nearly equal to interorbital width. Pseudobranchial filaments 2.

Dorsal-fin origin slightly posterior to a vertical from tip of pectoral fin. Anal-fin origin below pectoral-fin base. Pectoral fin shorter than postorbital length of head. Pelvic fins absent.

Head and body scaleless. Lateral line represented by a well-developed, continuous tube.

Color in alcohol: Head and body uniformly tan; top of skull behind middle of eye translucent, skin with many small melanophores. Mouth cavity pale. Peritoneum brown, stomach tan.

Remarks. The Japanese specimen described herein represents the fourth known adult specimen of Echiodon coheni-Ec. anchipterus species group. Both species were described by Williams (1984a), who recognized the Somalia and Philippine forms as distinct allopatric species. In a recent revision of the family Carapidae, Markle and Olney (1990: 274) included Ec. coheni and Ec. anchipterus among a group of "six cases of unresolved taxonomic status," which they summarized in their Table 3. They synonymized Ec. coheni and Ec. anchipterus as a result of "very small sample sizes" (Markle and Olney, 1990: 274) and suggested that their "larval data are crucial to the allocation of these two nominal forms" (Markle and Olney, 1990: 347). The later statement is surprising because the larval material does not resolve either of the crucial questions: 1) do the different pectoral-fin ray counts demonstrated by the Somalia and Philippine taxa warant recognition of two species; and 2) are larvae dispersing across the northern Indian Ocean thereby maintaining gene flow between the western Pacific and western Indian Ocean populations?

In regard to the first question, the larvae are uninformative in that the "pectoral rays are undeveloped or damaged in our larval material" (Markle and Olney, 1990: 347). As for the second question concerning gene flow, they noted that larvae of these taxa are not known from the Indian Ocean west of the Andaman Islands. Based on the available information the data do not support the idea that larvae of this species group disperse across the central Indian Ocean. It is worth noting that Markle and Olney (1990: Figs. 48, 87, 90, 96) reported central Indian Ocean collections of larval carapids of *Pyramodon*, *Onuxodon*, and Carapini. The absence of *Echiodon* from these collections does not prove the absence of *Echiodon coheni* or *Ec. anchipterus* from the central Indian Ocean, but neither should one accept that they are present simply because they have a pelagic larval stage.

Markle and Olney (1990: 347) noted a difference in numbers of pectoral-fin rays (18 versus 15) between the Somalia and Philippine populations of the Ec. coheni-Ec. anchipterus complex, but discounted its taxonomic value because Ec. dawsoni has a pectoral fin-ray count (17-21) that varies by a difference of 4 rays (the count of 21 rays is found only in the disjunct Brazilian population, which may in fact be a distinct species) and stressed the need for additional material to resolve the problem. It is significant that Markle and Olney (1990: 350) reported a three-ray difference (18-21) in the pectoral-ray count demonstrated in a very small sample comprised of three adults from the disjunct Brazilian population of Ec. dawsoni. The range of three pectoral-fin rays (17-20) for the remaining Ec. dawsoni was also based on a small sample of only six specimens. In another case, Markle and Olney (1990: 362) observed a range of three pectoral-fin rays (14-17) in six specimens of Ec. rendahli. In contrast the seven specimens of Ec. exsilium exhibited a difference of only 1 ray (20-21). Thus it appears that in those species of Echiodon exhibiting highly variable pectoral fin-ray counts, the variation is discernible in a very small sample size. Accordingly, their statement (Markle and Olney, 1990: 274) concerning their taxonomically difficult decisions, where they say their intention is "to justify them on the basis of sample size...", does not appear to be a valid reason for their actions. The uniformity of the counts within each disjunct population of the Ec. coheni-Ec. anchipterus group clearly fit the pattern evident in taxa with almost constant counts.

The data for the Japanese specimen are significant. The pectoral fin-ray count is low (16 rays on the left side, 15 on the right) as expected. Additionally the

Japanese specimen has a precaudal vertebral count of The larvae identified by Markle and Olney (1990: 347) as Ec. coheni are referable to Ec. anchipterus based on geographic distribution and have a range of 19-20 precaudal vertebrae (Markle and Olney, 1990: Table 5). Thus the known range of number of precaudal vertebrae for Ec. anchipterus is 19-21. Echiodon coheni has 18-19 precaudal vertebrae (Markle and Olney noted that the holotype has 18; Williams (1984a) included centrum 19 as a precaudal vertebrae because the parapophyses overlap ventrally, but do not fuse into a distinct hemal spine). Both the Japanese and Philippine specimens of Ec. anchipterus have 22 nasal lamellae, whereas the Ec. coheni specimens have 24 lamellae. The low pectoral fin-ray counts, combined with higher average numbers of precaudal vertebrae and a low nasal lamellae count, support the recognition of Ec. anchipterus as a species distinct from its disjunct sister species, Ec. coheni.

Relationships. Markle and Olney (1990: Fig. 45) hypothesized that the Ec. coheni-Ec. anchipterus group (their Echiodon coheni) is associated in an unresolved trichotomy with Ec. exsilium and the Ec. dawsoni-Ec. unnamed sister group, supported by one character, a reversal in the number of precaudal vertebrae from more than 25 to 15-25 (these were arbitrary ranges established by Markle and Olney, 1990). The hypothesized sister species to this group is Ec. cryomargarites. The arbitrary assignment of 25 as the break in the ranges for precaudal vertebrae was inappropriately applied, as there are specimens of Ec. dawsoni, Ec. exsilium, and Ec. cryomargarites with 25 precaudal vertebrae. With vertebral number removed, the unresolved trichotomy collapses to the next node and becomes an unresolved polytomy with Ec. cryomargarites.

Reevaluation of a vexillar radial character discussed by Markle and Olney (1990: 307–308) supports an alternative hypothesis of interrelationships. In adults of some *Echiodon* and its two closest outgroups, *Eurypleuron* and *Onuxodon*, the vexillar radial is ossified (the "predorsal bone" of Williams, 1984a) and is distinct from the pterygiophore bearing the first dorsal-fin ray (Markle and Olney, 1990: Figs. 4A, 5). In the next outgroup, Carapini, the vexillar radial and the first dorsal pterygiophore are also separate and differ from those of all other carapids in that the dorsal-fin origin (as well as dorsal pterygiophores not bearing rays) is well posterior to the vexillar radial (Markle and Olney, 1990: 311). Most

Carapini lose the vexillar radial ontogenetically, a condition Markle and Olney (1990: 308) considered as synapomorphic for the tribe. Adults of *Encheliophis gracilis* and *En. vermicularis* have a small ossified vexillar radial anterior to or fused with the neural spine of vertebral centrum 4 (evident as a small anterior process in Markle and Olney's Fig. 6B).

Larvae of Echiodon dawsoni, Ec. exsilium, Ec. cryomargarites, and Ec. anchipterus (and probably Ec. rendahli, Ec. neotes, Ec. pukaki, Ec. pegasus, and Ec. coheni, whose larvae have not been collected or have not been cleared and stained) have a compound vexillar radial (their character 70) comprised of a fused first dorsal pterygiophore and vexillar radial (Markle and Olney, 1990: 308 and Fig. 38), whereas Echiodon dentatus, Ec. drummondii and all other larval carapids have a vexillar radial separate from the first dorsal pterygiophore (Markle and Olney, 1990: Fig. 39D-E). In adults of Ec. dawsoni, Ec. exsilium, Ec. cryomargarites, Ec. pukaki, and Ec. pegasus, most or all of the anterior portion of the larval compound radial is resorbed ontogenetically, leaving the posterior portion as an ossified first ptervgiophore in adults (Williams, 1984a; Markle and Olney, 1990: Table 4; J. E. Olney, in lit., indicates the possible presence of a reduced(?) "predorsal bone" in Ec. pukaki). In Ec. anchipterus, Ec. rendahli, Ec. neotes (the only known specimen may be a larva, but its hypothesized sister-group relationship with Ec. rendahli suggests its presence in adults), and all other Echiodontini, the anterior portion of the radial ossifies ontogenetically and is retained as a predorsal bone in adults. We consider the ontogenetic resorption of the anterior portion of the radial as synapomorphic within the Echiodontini.

The two characters Markle and Olney (1990) used to support the relationship between Ec. unnamed, Ec. dawsoni, Ec. exsilium, and Ec. cryomargarites are the posterior placement of the larval vexillum at a point above vertebrae 9–14 (their character 71) and the adult posterior dorsal-fin origin adjacent to the vexillum origin (their character 72). If character 72 concerns the proximity of the dorsal-fin origin to the vexillum origin, it is a plesiomorphic condition within Echiodon, as the two closest outgroups of Echiodon, Eurypleuron and Onuxodon (Markle and Olney, 1990: Fig. 39), and all Echiodon exhibit this condition. Markle and Olney (1990: 311) attempted to transform character 72 into a derived condition by linking it with the posterior position of the adult

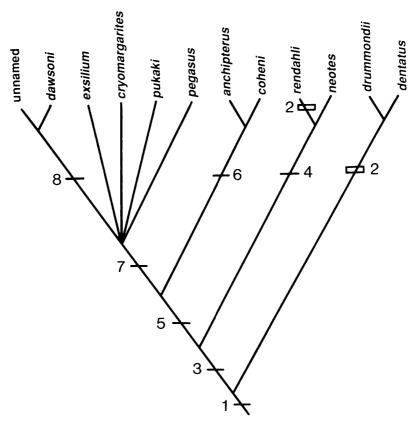


Fig. 2. Cladistic hypothesis of the relationships among the species of *Echiodon* (modified from Markle and Olney, 1990: Fig. 45). The following characters are used on the cladogram (synapomorphy numbers in parentheses following each character refer to numbers assigned by Markle and Olney, 1990): 1, parallel tunic ridges (synapomorphy 65); 2, swimbladder with an intrinsic constriction delimiting a small posterior chamber (synapomorphy 62); 3, compound vexillar radial supporting first dorsal-fin ray and vexillum (synapomorphy 70); 4, more than 32 precaudal vertebrae (synapomorphy 13); 5, larval vexillum situated above vertebral centra 9–14 (synapomorphy 71); 6, precocious fangs on vomer (synapomorphy 75); 7, resorption of anterior portion of vexillar radial (predorsal bone) during metamorphosis (character not used by Markle and Olney); 8, larvae with very large eyes (synapomorphy 76). Open rectangle represents homoplasy.

dorsal fin. This is invalid as the posterior position of the vexillum and the concomitant posterior shift of the dorsal-fin origin are the same condition described by character 71. The presence of character 71 cannot be confirmed for *Ec. pukaki* or *Ec. pegasus*, as their larvae have not been collected, but their dorsal-fin origin being over vertebrae 11–12 suggests that a larval vexillum would be positioned over vertebra 10, as all known larvae of the Echiodontini have the larval vexillum positioned immediately anterior to the dorsal-fin origin. If this assumption is correct, *Ec. pukaki* and *Ec. pegasus* also possess character 71.

Markle and Olney (1990: Fig. 45) incorrectly

placed Ec. pukaki and Ec. pegasus in an unresolved trichotomy with the Ec. rendahli-Ec. neotes sister group. They did not provide or discuss a synapomorphy for this trichotomy, which therefore collapses into an unresolved polytomy with the Ec. unnamed, Ec. dawsoni, Ec. exsilium, and Ec. cryomargarites group at the next lowest node.

Based on the above discussion, the most parsimonious cladistic hypothesis (Fig. 2) for the relationships among the species of *Echiodon* places the *Ec.* unnamed-*Ec. dawsoni* group in an unresolved polytomy with *Ec. exsilium*, *Ec. cryomargarites*, *Ec. pukaki*, and *Ec. pegasus*, all of which share in having

resorbed most or all of the anterior portion of the larval vexillar radial (i.e., lost the adult predorsal bone; character 7). The Ec. coheni-Ec. anchipterus group is the sister group of the previous group of species based on their common possession of a compound vexillar radial (character 5). The Ec. rendahli-Ec. neotes sister group is the next sequential branch on the cladogram, sharing with the preceding taxa, a compound vexillar radial (character 3) as discussed by Markle and Olney (1990: 308). The relationship of the Ec. dentatus-Ec. drummondii group as the next sequential group on the cladogram is unchanged from its placement by Markle and Olney (1990: Fig. 45). Our hypothesis of the relationships among the species of Echiodon is tentative because the nodes are weakly supported and the addition of a few characters could dramatically alter the branching sequence.

Eurypleuron Markle and Olney, 1990

Markle and Olney (1990: 338) considered the southern African Carapus cinereus Smith as a junior synonym of Eurypleuron owasianum and presented limited information on South Pacific specimens they identify as this species. Although they noted differences in D₃₀ counts, precaudal vertebral numbers, and stomach color among the disjunct populations (Markle and Olney, 1990: 338–340), they concluded, based on two contradictory statements, that the different geographic forms are conspecific. Their first statement attributed the distinctive différences in characters among disjunct populations to "geographic" variation. Their second statement supported the concept of a single widespread taxon "because of their teleplanktonic larvae." The reason these two statements are contradictory is that widely dispersing larvae should maintain gene flow between the disjunct adult populations, thereby maintaining homogeneity in characters across populations. A constant swamping of the gene pool by dispersing larvae should eliminate "geographic" differences in the characters. The fact that in spite of a pelagic larval stage there exists a suite of characters diagnosing the isolated adult populations can only lead to the conclusion that the isolated populations are taxonomically distinct. As Markle and Olney (1990) provided only lumped data for the complex, a thorough geographic analysis of the group will have to be undertaken before the taxonomic status of the allopatric southern hemisphere populations can be resolved.

Pending a comprehensive study of the group, we follow Williams (1984a) in restricting the name Eurypleuron owasianum (Matsubara) to the Japanese form. We tentatively refer all of the disjunct southern populations to Eurypleuron cinereum (Smith), the only species name available for the complex.

Eurypleuron demonstrates a typical antitropical distribution pattern in that the adults of E. owasianum occur north of 20° north latitude and E. cinereum is known only from south of 20° south latitude. The single collection of a larva off the northwestern end of New Guinea (Markle and Olney, 1990: Fig. 62) is probably anomalous as it has not been collected in any of the numerous other larval samples taken throughout the Indo-Malayan Archipelago.

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クマノカクレウオ(新称)の有効性とソコカクレウオに関する知見

Jeffrey T. Williams·町田吉彦

カクレウオ科の Echiodon anchipterus はフィリピン産の 1 個体に、 Ec. coheni はソマリア産の 2 個体に基づき、1984 年に Williams により記載されたが、Markle and Olney (1990) は暫定的に前者を後者のシノニムとした。本研究で、従来未報告の熊野灘産の本属標本 1 個体を Ec. anchipterus と同定した。 Ec. anchipterus は Ec. coheni とは胸鳍鳍条数が 15-16 (後者では 18)、嗅板数と2 (24)、腹椎骨数が 19-21 (18-19) と異なり、さらに、浮遊性の幼魚期を経る両者の分布域は大きく隔っており、両者はそれぞれ独立種と判断される。 Ec. anchipterus に新和名を与え、本標本

を詳細に報告するとともに、Markle and Olney (1990) が扱ったカクレウオ科のいくつかの形質を吟味し、本属内の新たな分岐図を提示した。Williams (1984a) は Carapus owasianus (ソコカクレウオ)と C. cinereus を Echiodon に含めたが、Markle and Olney (1990) は Echiodon から分離させた新属 Eurypleuron を創設し、C. cinereus は Eu. owasianum のシノニムとした。しかし、ソコカクレウオは日本固有種と思われ、南緯 20 度以南に分布する本属は Eu. cinereum とするのが妥当であろう。

(Williams: アメリカ合衆国 スミソニアン研究所; 町田: 780 高知市曙町 2-5-1 高知大学理学部生物学教室)