



Taxonomic revisions within Embiotocidae (Teleostei, Perciformes) based on molecular phylogenetics

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Abstract

Embiotocidae, a unique family within the Perciformes that has evolved a complex viviparous natural history, has lacked full resolution and strong support in several interspecific relationships until recently. Here we propose three taxonomic revisions within embiotocid surfperches based on recent molecular phylogenetic analyses that robustly resolve all interspecific relationship in the Eastern Pacific species: *Hypsurus caryi* (Agassiz, 1853) resurrected to its original name *Embiotoca caryi* Agassiz, 1853, *Rhacochilus vacca* (Girard, 1855) shifted into the genus *Phanerodon* Girard, 1854, and *Hyperprosopon anale* Agassiz, 1861 separated into the available genus *Hypocritichthys* Gill, 1862. The proposed changes would leave three previously paraphyletic groups monophyletic (*Embiotoca*, *Hyperprosopon*, and *Phanerodon*) and would maintain the current number of genera at 13.

Key words: viviparous fishes, surfperches

Introduction

The highly speciose teleost order Perciformes includes surfperches (Embiotocidae), a family of predominantly marine fishes endemic to the temperate coasts of the North Pacific. Over roughly the last 15 million years embiotocids have radiated into 23 valid species (Eschmeyer & Fong 2016) that occupy diverse ecological niches in two monophyletic subfamilies, Amphistichinae and Embiotocinae (Bernardi & Bucciarelli 1999; Longo & Bernardi 2015; Tarp 1952). Amphistichinae currently consists of six species in two genera, all of which prefer sandy habitat, while the more diverse Embiotocinae contains the remaining 17 species distributed across eleven genera and occupy a broad range of habitats including soft bottoms in deep water, kelp forest reefs, seagrasses, estuaries, and inland freshwater systems. A recent study using 523 genome-wide RADseq markers built a robust and well supported embiotocid phylogeny that clarified previously unresolved interspecific evolutionary relationships (Longo & Bernardi 2015). These findings corroborate previous calls for taxonomic revisions (Gill 1862; Tarp 1952; Bernardi 2009) and allow for a novel revision of the family suggested here. Specifically, we propose resurrecting *Embiotoca caryi* Agassiz, 1853 from *Hypsurus caryi* (Agassiz, 1853) as proposed by Bernardi (2009), moving *Rhacochilus vacca* (Girard, 1855), also called *Damalichthys vacca* Girard, 1855 by various researchers (Bernardi & Bucciarelli 1999; Page *et al.* 2013; Pietsch & Orr 2015), into the genus *Phanerodon* Girard, 1854, and separating *Hyperprosopon anale* Agassiz, 1861 into the available genus *Hypocritichthys* Gill, 1862, as proposed by Gill (1862). Additionally the minimal genetic differentiation observed by Longo and Bernardi (2015) between Guadalupe Island and mainland populations of *Brachyistius frenatus* Gill, 1862 supports the current synonymy of the Guadalupe Perch, *B. aletes* Tarp, 1952, with the Kelp Perch, *B. frenatus*.

Background. In 1852 Louis Agassiz received a letter from A.C. Jackson in which Mr. Jackson claimed that while fishing in Sausalito, CA (San Salita Bay in earlier correspondence) in San Francisco Bay he had caught a perch-like fish that remarkably was pregnant. Although Mr. Jackson described the fish and the state of its pregnancy in detail, he was not able to preserve the specimen as he was occupied at the time and lacked the necessary supplies. Upon Agassiz's request, both Mr. Jackson and Agassiz's brother-in-law who lived in San Francisco, T.G. Cary, sought out specimens to preserve and ship to Agassiz. Mr. Cary finally succeeded and sent multiple specimens to Agassiz, which in fact comprised two distinct species and Agassiz (1853) erected a new family, Embiotocidae or Holconoti, and genus, *Embiotoca* Agassiz, 1853. He commemorated the diligent work of Mr. Cary and Mr. Jackson by naming the two distinct species in their honor, *Embiotoca caryi* Agassiz, 1853 and *Embiotoca jacksoni* Agassiz, 1853. Unsure of whether the viviparous life history observed in *E. caryi* and *E. jacksoni* was characteristic of the family, Agassiz proposed either Holconoti or Embiotocidae with the latter proving appropriate as all surfperches indeed give birth to live young. Agassiz, however, confidently expressed that the discovery of the live bearing surfperches warranted some enthusiasm declaring that, "A country which furnishes such novelties in our days, bids fair to enrich science with many other unexpected facts, and what is emphatically true of California, is in some measure equally true of all our waters. This ought to stimulate to renewed exertions not only our naturalists, but all the lovers of nature and science in this country" (Agassiz 1853, p. 383).

Changes in Nomenclature. In the subfamily Embiotocinae we propose two revisions. The year after Agassiz erected the family, he described a third member of the genus, *Embiotoca lateralis* Agassiz, 1854. However in 1861 Alexander Agassiz, Louis's son, separated the genus *Embiotoca* based on unspecified skeletal characteristics proposing *Embiotoca lateralis* become *Taeniotoca lateralis* (Agassiz, 1854), a genus that was not retained, and *Embiotoca caryi* become *Hypsurus caryi* (Agassiz 1861). Subsequent DNA sequence analyses suggested *H. caryi* did indeed belong in *Embiotoca* (Bernardi 2009) and is in fact sister to *E. jacksoni*, the Black Perch (Longo & Bernardi 2015). Notably, the sister relationship of *E. jacksoni* and *H. caryi* is consistent with their shared ability to winnow (sort food within the mouth) while *E. lateralis* lacks this feeding specialization. Therefore, we propose resurrecting *Embiotoca caryi* as originally described by Agassiz (1853) based on the aforementioned molecular phylogenetic analyses.

In June of 1855, Girard erected a new genus in Embiotocidae when he described *Damalichthys vacca* (Girard 1855). Later Tarp (1952) would move *D. vacca* into *Rhacochilus* Agassiz, 1854 where it is currently recognized by some researchers, while others recognize *Damalichthys* (Girard, 1855). Subsequent phylogenetic work based on mtDNA sequences suggested *R. vacca* was more closely related to *Phanerodon furcatus* Girard, 1854 than to *Rhacochilus toxotes* Agassiz, 1854 (Bernardi & Bucciarelli 1999). Indeed, Longo and Bernardi (2015) found that *R. vacca* is sister to *P. furcatus* with *P. atripes* (Jordan & Gilbert, 1880) sister to that clade, rendering both *Rhacochilus* and *Phanerodon* paraphyletic (Fig. 1). Although most morphological characteristics prove uninformative, some traits corroborate these molecular findings. For instance, *R. vacca* possess a mandibular frenum, which is found in both *P. atripes* and *P. furcatus* but absent in *R. toxotes*. Also, *R. vacca* and *P. furcatus* exhibit a similar number of gill rakers on the first arch of the lower limb, 11–14 and 12–13, respectively, compared to 17–19 in *R. toxotes* (Tarp 1952). Additionally, *R. toxotes* has independently evolved the ability to winnow (*Embiotoca jacksoni* and *E. caryi* are the only other embiotocids known to winnow) while *R. vacca*, *P. atripes*, and *P. furcatus* lack this ability. With respect to the nomenclature, the genus *Rhacochilus* was first used with *R. toxotes* (Agassiz 1854), therefore *Phanerodon* is available for *R. vacca*. We propose placing *Rhacochilus vacca* into the genus *Phanerodon*, which would render the genus monophyletic and leave *Rhacochilus* monotypic with *R. toxotes*.

In his 1952 revision of surfperches Tarp recognized *Brachyistius* Gill, 1862 at the subgeneric level within *Micrometrus* Gibbons, 1854 in which he included four species, *aurora* and *minus* in the subgenus *Micrometrus* and *aletes* and *frenatus* in the subgenus *Brachyistius*. In this revision Tarp proposed that, *Brachyistius aletes* (Tarp, 1952), which is restricted to waters off Isla Guadalupe roughly 260 km off the coast of Baja California, Mexico (29 01'51"N, 118 16'48"W), constituted a valid species due to a slightly larger eye diameter and a tendency towards more pigmentation around the axilla than its mainland counterpart the Kelp Perch, *Brachyistius frenatus* Gill, 1862. However, the genetic distance between *B. frenatus*, and *B. aletes*, which are currently synonyms, is comparable to that observed between intraspecific individuals in *Zalembius rosaceus* (Jordan & Gilbert, 1880) and *Cymatogaster aggregata* Gibbons, 1854 (Longo & Bernardi 2015). Although *Brachyistius* on Guadalupe Island are isolated, prevailing currents and kelp rafts likely facilitate a sufficient amount of gene flow that has prevented significant

differentiation from mainland populations (Mitchell & Hunter 1970; Waples & Rosenblatt 1987). Considering that the viviparous reproductive strategy of surfperches results in very low dispersal relative to other marine fishes, populations tend to be genetically very different (Bernardi 2000) and further taxonomic subdivisions within species may come to light.

In the Amphistichinae we propose one revision. In 1861, Alexander Agassiz also described a new species *Hyperprosopon analis* Agassiz, 1861 (correct spelling of species is *anale* when in *Hyperprosopon*), which is still recognized today. The next year, Gill (1862) suggested that the differences between *Hyperprosopon anale* and a typical *Hyperprosopon* Gibbons, 1854 were so great that it warranted its own generic recognition as *Hypocritichthys* Gill, 1862. Likewise, Tarp (1952) would later suggest that *Hype. anale* be placed in its own subgenus, *Hypocritichthys*, owing to its shallow body depth (0.387 of SL), small eye diameter (0.26 of head length), and low dorsal and anal ray counts (20–25 and 21–26, respectively) relative to *Hype. argenteum* (body depth 0.455 of SL, eye diameter 0.357 of head length, 25–29 dorsal rays, and 30–35 anal fin rays) and *Hype. ellipticum* (body depth 0.459 of SL, eye diameter 0.304 of head length, 25–29 dorsal rays, and 29–35 anal fin rays). Although Tarp believed *Hype. anale* to be a derived species of *Hyperprosopon*, subsequent phylogenetic analyses place *Hype. anale* sister to the rest of the Amphistichinae, with *Hype. ellipticum* and *Hype. argenteum* being more closely related to *Amphistichus* than to *Hype. anale*, rendering the genus paraphyletic (Longo & Bernardi 2015; Westphal *et al.* 2011). Here we suggest elevating *Hypocritichthys* from a subgenus to full generic status in *Hypocritichthys analis*, which would then leave *Hyperprosopon* monophyletic (Fig. 1). In conclusion, the proposed changes would keep the number of embiotocid genera at 13, comprising 23 species, and would render three paraphyletic groups (*Embiotoca*, *Hyperprosopon*, and *Phanerodon*) monophyletic. We present a comprehensive figure of the phylogenetic relationships with the proposed revisions (Fig. 1) and include a key to species for the Eastern Pacific embiotocid taxa.

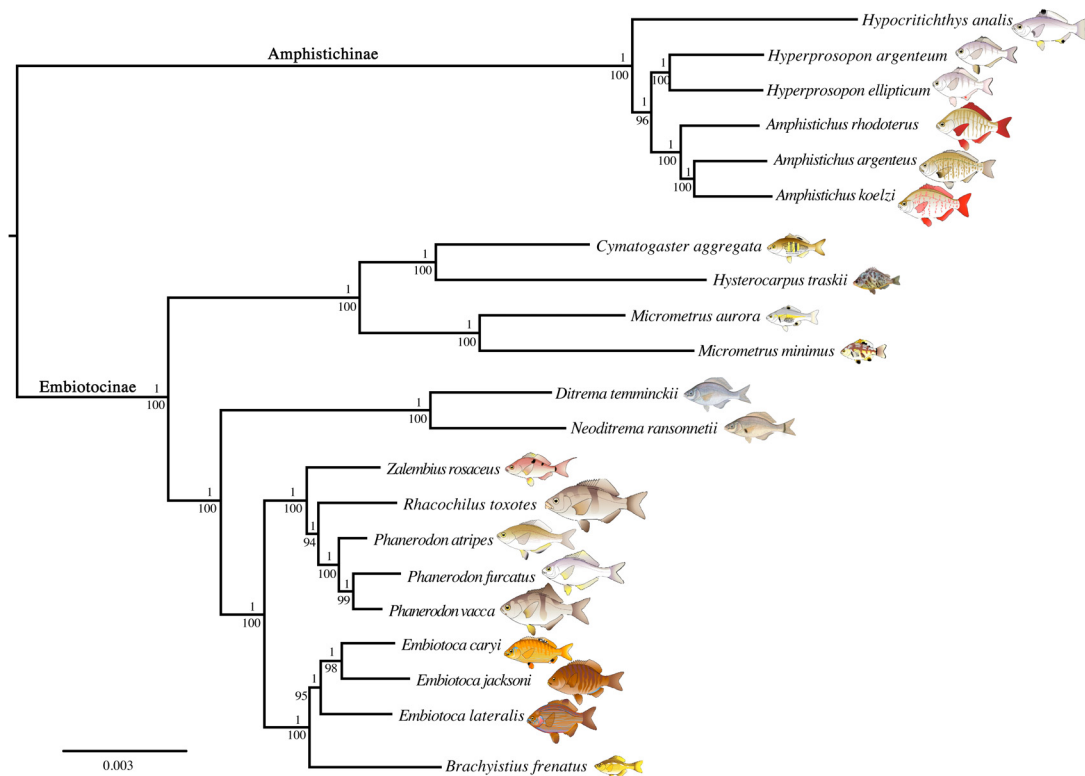
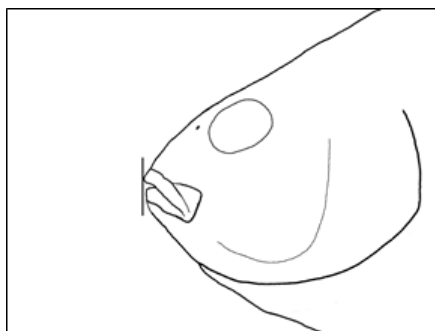


FIGURE 1. Molecular phylogeny of Embiotocidae inferred using genome wide RADseq markers with maximum likelihood and Bayesian methods (Longo & Bernardi 2015) with the following proposed taxonomic revisions; resurrecting *Hypsurus caryi* (Agassiz 1853) to its original name *Embiotoca caryi*, moving *Rhacochilus vacca* (Girard 1855) into the genus *Phanerodon*, and separating *Hyperprosopon anale* Agassiz 1861 into the available genus *Hypocritichthys*. Note: The Western Pacific genus *Ditrema* includes two other valid species not present in this figure, *D. viride* and *D. jordani*; see Katafuchi *et al.* (2010) for proposed interspecific relationships in this genus. Top and bottom node values represent posterior probability and bootstrap support, respectively.

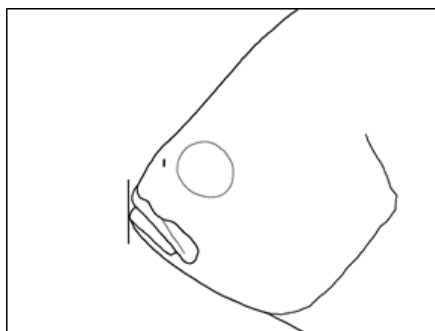
Key to species of the Embiotocidae

Note: coloration descriptions refer to live or freshly caught specimens.

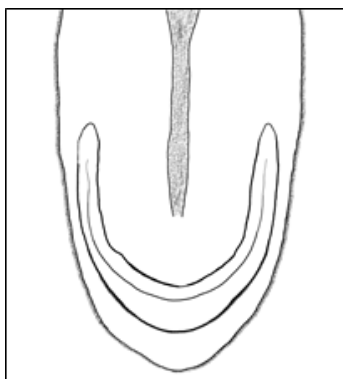
- 1A Species occurring in East Asia [the western North Pacific; Korea, Japan, China, Sea of Japan, Yellow Sea]. Four species are known from this area: *Neoditrema ransonnetii*, *Ditrema jordani*, *D. temminckii*, and *D. viride*. The genus *Ditrema* was revised by Katafuchi and Nakabo (2007) and included a key to species. *Neoditrema* is distinguished from *Ditrema* by number of dorsal spines; *Neoditrema* VI–VIII vs. *Ditrema* IX–XI.
- 1B Species occurring in the eastern North Pacific; Alaska to Baja California and Gulf of California 2
- 2A Dorsal spines XV – XVIII; occurrence in freshwater, rarely brackish water *Hysteroecarpus traskii*
- 2B Dorsal spines XII or less; marine, some species estuarine 3
- 3A Lips thick and fleshy; center of lower lip with 2 ventral lobes *Rhacochilus toxotes*
- 3B Lips not especially thick and only moderately fleshy; lower lip lacking ventral lobes 4
- 4A Patch of enlarged scales in area posterior to pectoral fins *Embiotoca jacksoni*
- 4B No patch of enlarged scales posterior to pectoral fins. 5
- 5A Anal fin without a row of scales extending onto the base of anal fin 8
- 5B Anal fin with a row of scales extending onto the base of anal fin 6
- 6A Upper lip extending slightly beyond mandible; fins typically dusky, not reddish *Amphistichus argenteus*

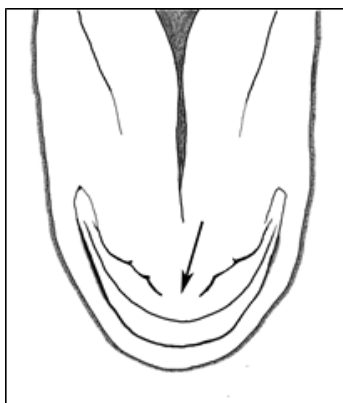


- 6B Jaws typically subequal or lower lip slightly projecting; fins reddish including caudal. 7



- 7A Dorsal fin spines and soft-rays approximately equal in length; rakers on lower limb of first gill arch 14–18. *Amphistichus koelzi*
- 7B Longest dorsal fin spines noticeably longer than soft-rays; rakers on lower limb of first gill arch 10–14 *Amphistichus rhodoterus*
- 8A Lower lip without a frenum. 9





- 9A Conspicuous black spot on spinous part of dorsal fin and anterior portion of anal fin. *Hypocritichthys analis*
- 9B No conspicuous spot on dorsal or anal fin 10
- 10A Body elongate; total length 3 times greatest body depth; body tinged with yellow, scales with black flecking
..... *Cymatogaster aggregata*
- 10B Body ovoid; total length less than 3 times body depth; body silvery, scales without black flecking 11
- 11A Pelvic fins with black tips; 20–23 rakers on lower limb or first gill arch *Hyperprosopon argenteum*
- 11B Pelvic fins without black tips; 15–19 rakers on lower limb of gill arch *Hyperprosopon ellipticum*
- 12A Body uniformly pinkish; last anal soft-ray thread-like *Zalembius rosaceus*
- 12B Body coloration not as above; last anal soft ray normal, not elongated 13
- 13A Body without stripes 15
- 13B Body with blue, red, and/or yellow stripes 14
- 14A Profile of abdomen essentially straight; snout extending beyond lower jaw; anal fin base shorter than distance from pelvic base to anal fin origin *Embiotoca caryi*
- 14B Profile of abdomen convex; jaws subequal, terminal; anal fin base longer than distance from pelvic base to anal fin origin. . . .
..... *Embiotoca lateralis*
- 15A Anal fin base longer than distance from base of last anal soft-ray to end of scales on midcaudal ray; caudal fin deeply forked .
..... 18
- 15B Anal fin base shorter than distance from base of last anal soft-ray to end of scales on midcaudal ray; caudal fin only slightly
forked 16
- 16A Lower jaw slightly projecting; axilla of pectoral fin with no black marking *Brachyistius frenatus*
- 16B Jaws subequal; axilla of pectoral fin with a jet-black blotch 17
- 17A Ventral portion of body with a series of continuous stripes; dorsal soft-rays 12–16; body depth 2.0–2.4 into standard length . .
..... *Micrometrus minimus*
- 17B Ventral portion of body with a series of half rings on scales; dorsal soft-rays 15–19; body depth 2.4–2.8 into standard length. .
..... *Micrometrus aurora*
- 18A Longest dorsal soft-ray approximately twice as long (1.6–3.0) as longest dorsal spine; 8–9 scales between first dorsal spine and
lateral line *Phanerodon vacca*
- 18B Longest dorsal soft-ray only slightly longer (1.0–1.4) than longest dorsal spine; 4–7 scales between first dorsal spine and lat-
eral line 19
- 19A Pelvic fins white (rarely with faint dusky speckling at tips); no reddish speckling on scales on upper body
..... *Phanerodon furcatus*
- 19B Pelvic fins with black tips; scales on upper part of body with reddish speckling. *Phanerodon atripes*

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