

Convergent Evolution and the Red Sea Rover: *Emmelichthys marisrubri* (Teleostei: Emmelichthyidae) Is a Species of Fusilier (Lutjanidae: *Dipterygonotus*)

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Rovers, rubyfishes, and bonnetmouths (Emmelichthyidae) comprise a small family of fishes that can be distinguished from other perch-like fishes by their generally red, fusiform bodies, highly protrusible mouths, and large rostral cartilage. Their highly protrusible upper jaws have led ichthyologists to group morphologically similar but distantly related taxa within the Emmelichthyidae and is one of the stunning examples of morphological convergence within perch-like fishes. In 2014, the first and only emmelichthyid from the Red Sea, *Emmelichthys marisrubri*, was described. This species is diagnosed by 80–83 lateral-line scales, 8 dorsal-fin rays, and 4–5 isolated dorsal spines that are separated from membrane-bound dorsal-fin elements, among other features. While examining the osteology of *E. marisrubri*, I discovered several differences in the oral jaws, suspensorium, neurocranium, and dorsal fin when compared to other species of rovers. Based on these differences and the results of a phylogenetic analysis, I transfer this taxon to the genus *Dipterygonotus* within the Lutjanidae and among the fusiliers (formerly Caesionidae), an Indo-Pacific group of fishes that also have highly protrusible upper jaws.

ROVERS, rubyfishes, and bonnetmouths (Emmelichthyidae; Fig. 1) comprise a small family of fishes that are found in all temperate and tropical oceans at depths of 100–400 m. These fishes are predominantly planktivorous, with larvae and juveniles of some species feeding within and around pelagic tunicates (Pastana et al., 2022) and adults feeding on larger zooplankton (Heemstra and Randall, 1977). One of the most striking features of these fishes is their highly protrusible jaws, where the robust premaxilla, elongate lower jaw, and large rostral cartilage contribute to extensive jaw protrusion (Fig. 1E). While diagnostic for the family, this jaw morphology is one of the classic examples of morphological convergence in perch-like fishes and a major contributor to the turbulent taxonomic history of the Emmelichthyidae.

Early works by Jordan and Thompson (1912) and McCulloch (1914) considered the family to consist of three genera, noting the rover's protractile mouths were similar to those in *Dipterygonotus*, *Inermia*, and *Spicara*. Fowler (1933) went on to group six genera into his Emmelichthyidae (*Cypselichthys*, *Dipterygonotus*, *Emmelichthys*, *Erythrocles*, *Inermia*, and *Plagiogeneion*), noting all had a fusiform body, an oblique mouth with projecting jaw, a wide maxillary, and a toothless palate, among other features. Fowler (1933: 344) also highlighted behavioral and geographic similarities among these fishes, stating that they were “brilliant and active” and generally occurred in deep waters of the Indo-Pacific. In his description of *Emmelichthys atlanticus*, Schultz (1945) added five more genera to Fowler's (1933) Emmelichthyidae (*Centracanthus*, *Coleosmaris*, *Emmelichthyops*, *Merolepis*, and *Pterosmaris*), primarily grouping members of the Maenidae with emmelichthyids. Schultz (1945) defined the family by an oblong, fusiform, or compressed body, greatly protrusible jaws, and a premaxillary ascending process reaching to or beyond the anterior margin of the orbit, among other characters. This grouping was accepted by subsequent works on the classification of fishes (e.g., Greenwood et al., 1966) until

examinations of internal osteology were published by Heemstra and Randall (1977) and Johnson (1980). Heemstra and Randall (1977), with acknowledgments of personal communication from G. D. Johnson) separated Schultz's Emmelichthyidae into five families (*Dipterygonotus* to Caesionidae, *Centracanthus* and *Spicara* to Centracanthidae, *Emmelichthyops* and *Inermia* to Inermiidae, *Cypselichthys* = *Labracoglossa* to Labracoglossidae, and *Emmelichthys*, *Erythrocles*, and *Plagiogeneion* remaining in Emmelichthyidae), stating that all characters used by Schultz (1945), except for the greatly protrusible mouth, were common to many families of perch-like fishes and did not support the more-inclusive classification of the family. Heemstra and Randall (1977) also highlighted that detailed morphological comparisons among Schultz's emmelichthyids show the protrusibility of the upper jaw evolved independently across their five families. They restricted the Emmelichthyidae to three genera (*Emmelichthys*, *Erythrocles*, and *Plagiogeneion*; Fig. 1A–C), a similar classification to what Jordan and Thompson (1912) and McCulloch (1914) proposed. Heemstra and Randall defined the family by a maxilla not covered by the lachrymal, a distally scaled maxilla, a well-developed supramaxilla, a large rostral cartilage, a broad ascending process of the premaxilla, one postmaxillary process, and toothless or nearly toothless oral jaws. Throughout the remainder of this paper, usage of the Emmelichthyidae refers to the classification *sensu* Heemstra and Randall (1977). Johnson (1980: 65) later went on to characterize Heemstra and Randall's (1977) Emmelichthyidae, noting its “lack of close affinity with lutjanoids, sparoids, and haemuloids,” finding all emmelichthyids possess a scaley sheath surrounding dorsal and anal fins, the last 6–8 dorsal-fin pterygiophores trisegmental, the left and right pterospheneids joined at midline, and an endopterygoid with ventral flange that almost reaches the symplectic. Johnson (1980) grouped the Centracanthidae (former emmelichthyids) with the Lethrinidae, Nemipteridae, and Sparidae in his Sparoidea, the Inermiidae with the Haemulidae in his Haemuloidea, and the

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Fig. 1. Representative species of the Emmelichthyidae. (A) *Plagiogeneion rubiginosum* NMNZ P.061899. (B) *Erythrocles schlegelii* KAUM-I. 55963. (C) *Emmelichthys struhsakeri* KAUM-I. 106623. (D) *Dipterygonotus marisrubri* paratype HUJF 20199. (E) *Emmelichthys nitidus* NSMT 125978 with upper and lower jaws protruding. Scale bars = 1 cm.

Caesionidae with the Lutjanidae in his Lutjanoidea, bringing additional attention to the morphological convergence among these former allies. More recent studies using molecular characters (e.g., Rabosky et al., 2018) have supported Heemstra and Randall's (1977) and Johnson's (1980) separation of caesionids, centrarchids, and inermiids from emmelichthyids, further highlighting the convergent evolution now known to occur between emmelichthyids and other perch-like fishes.

In 1957, three small (69–75 mm standard length [SL]; Fig. 1D) fish specimens were captured in the southern Red Sea, near Eritrea. Initially identified as ariommatids (see Fricke et al., 2014), these fish have highly protrusible upper jaws, fusiform bodies, and 4–5 isolated spines between the membrane-bound spinous and soft dorsal fins. In 2014, these specimens were described as *Emmelichthys marisrubri*, the first and only emmelichthyid to be recorded from the Red Sea (Fricke et al., 2014; Golani and Fricke,

2018). Hereafter, taxonomic names in quotes refer to identifications that are revised in this study. Externally, "*E.*" *marisrubri* is similar to species of *Emmelichthys*, but several external characters differ from those that define the Emmelichthyidae (see above), including differences in upper-jaw morphology, squamation, and fin-ray counts. I examined the internal osteology of the types of the species using microcomputed tomography (μ CT) and discovered several additional differences between "*E.*" *marisrubri* and other species of rovers. Based on these findings, I provide osteological evidence that "*E.*" *marisrubri* is a fusilier in the Lutjanidae (*sensu* Fricke et al., 2023; formerly the Caesionidae [see Miller and Cribb, 2007]). With this taxon reasigned to the Lutjanidae, I analyze a morphological matrix to place "*E.*" *marisrubri* among fusilier genera.

MATERIALS AND METHODS

Morphological examination.—As specimens of "*E.*" *marisrubri* and emmelichthyids are rare in museum collections, internal osteology was examined via μ CT scanning. Specimens were scanned on a GE Phoenix v|tome|x M 240/180kV Dual Tube μ CT scanner at NMNH with the following settings: 90–110 kV, 120–150 μ A, 200–333 ms exposure time, and 20.0–34.0 μ m voxel size. The resulting x-ray projections were reconstructed into three-dimensional image stacks using the software package datos|x reconstruction vers. 2.4.0. The resulting three-dimensional image stacks were uploaded to MorphoSource (project ID 000553611), and media identification numbers for individual specimens can be found in the Material Examined section. Museum codes follow Sabaj (2020) except for NMNH referring to non-Fishes Division personnel and resources at the National Museum of Natural History, Smithsonian Institution. Image stacks were segmented and visualized using the SlicerMorph module (Rolfe et al., 2021) within 3D Slicer vers. 5.3.0 (Fedorov et al., 2012) and the protocol described in Girard et al. (2022). Additional specimens of emmelichthyids and lutjanids were cleared and stained following the protocol of Potthoff (1984), with the modifications listed in Girard et al. (2020). Catalog numbers for cleared-and-stained specimens can be found in the Material Examined section.

Taxon sampling, morphological characters, and phylogenetic analysis.—Taxa and characters sampled in this study are predominantly based upon those described and examined by Carpenter (1987, 1990). Carpenter (1990) sampled 20 species of fusiliers, including all genera, and rooted his analysis on a 'Lutjanidae' outgroup. In my modified matrix, eight species of *Caesio*, ten species of *Pterocaesio*, *Dipterygonotus balteatus*, and *Gymnocaesio gymnoptera* are included along with "*E.*" *marisrubri*, *Lutjanus griseus*, and *Pristipomoides aquilonaris*. I modified characters 1–34 from Carpenter (1990) based on character states listed in Carpenter (1987, 1990) and my own observations. These modified characters are listed in Appendix 1 and character states are presented as a matrix in Table 1. In total, the morphological matrix included 23 taxa and 45 characters (99.9% complete). The morphological matrix was analyzed in both a parsimony and a maximum-likelihood framework. The parsimony analysis was conducted using PAUP* vers. 4.0 (Swofford, 2003) using a branch and bound algorithm (see Supplemental Fig. 1; see Data Accessibility). Maximum-likelihood analyses were conducted using IQ-Tree vers. 2.2.0 (Chernomor et al., 2016; Kalyaanamoorthy et al., 2017; Minh et al.,

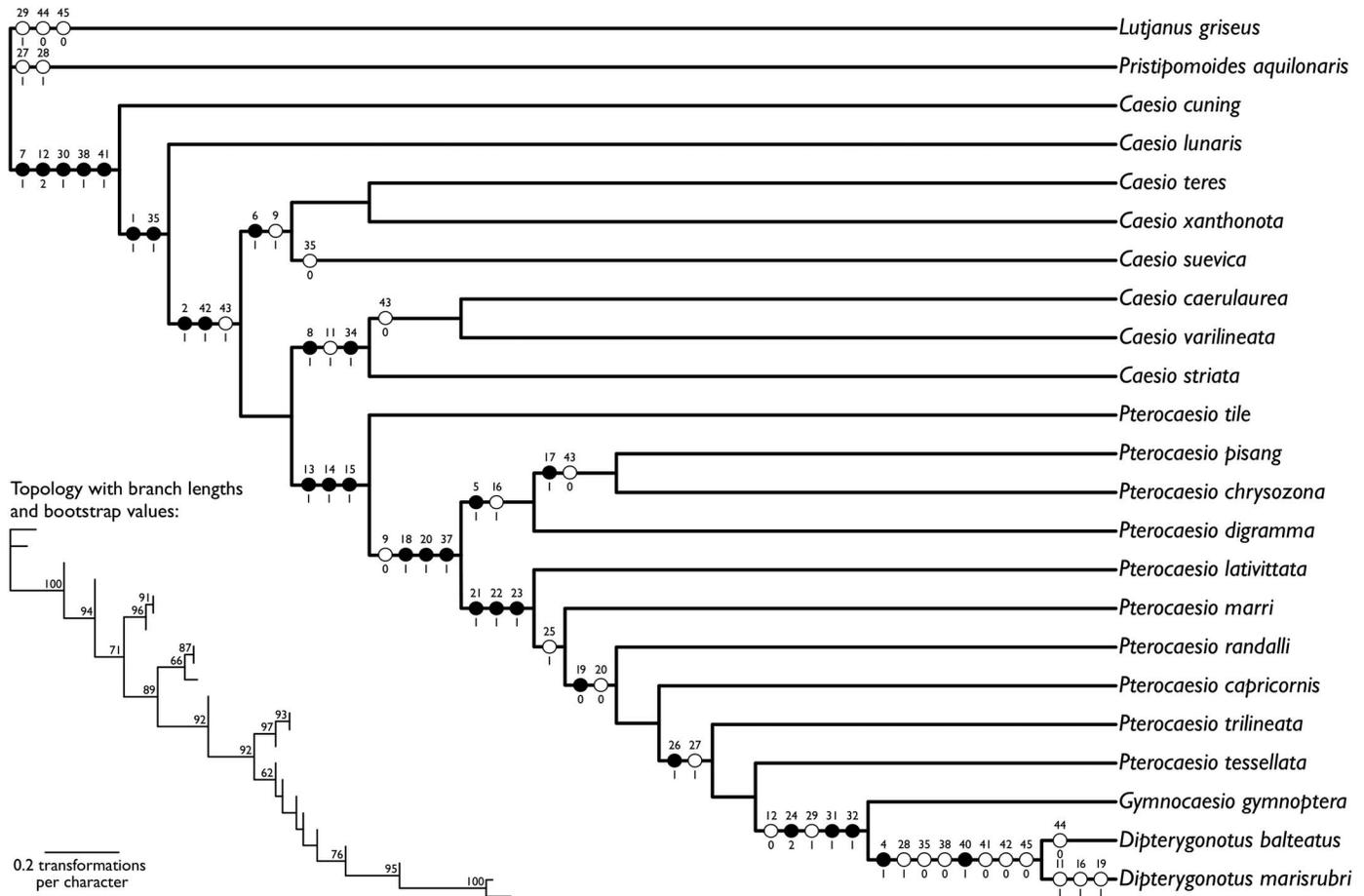


Fig. 2. Hypothesis of relationships from likelihood analysis of fusiliers based on morphological dataset. Morphological characters optimized unambiguously onto each branch are represented by a circle with the corresponding character number listed above and character state below. Circles with black fill are unique and unreversed character states. Circles with white fill are states that optimized multiple times in the phylogeny. Branch lengths and bootstrap support values for phylogeny are in the lower left-hand corner. See Data Accessibility for tree file.

2020) under the MK+FQ+ASC model of evolution. Support for the resulting topology was assessed using 100 standard nonparametric bootstrap replicates. The resulting tree topologies from both analyses and morphological matrix (Table 1) were used to view morphological transformations across the phylogeny using WinClada vers. 1.00.08 (Nixon, 2002). The characters were mapped using a parsimony optimization and the WinClada option that allows for unambiguous changes only (Fig. 2, Supplemental Fig. 1; see Data Accessibility). All analyses were rooted on *L. griseus*.

RESULTS

Morphological characters of “Emmelichthys” marisrubri and taxonomic implications.—Morphology of “*E.*” *marisrubri* is compared to the type species of *Emmelichthys* (*E. nitidus*) and *Dipterygonotus* (*D. balteatus*) in Table 2 and Figures 3–5. The absence of a supramaxilla (Fig. 3), absence of a ventral expansion of the endopterygoid separating the metapterygoid from the quadrate (Fig. 3), absence of medial contact between the left and right pterosphenioids (Fig. 4), presence of posterior extension of the lateral ethmoid (Fig. 4), and presence of two supraneurals (Fig. 5) do not support the placement of “*E.*” *marisrubri* within *Emmelichthys* or the Emmelichthyidae (see Table 2). The separation of the ascending process from the articular process of the premaxilla

(Fig. 3), presence of two postmaxillary processes (Fig. 3), presence of a robust apophysis on the ventral margin of the parasphenoid (Fig. 4), and ventral extension of the prootic covering *pars jugularis* (Fig. 4) support “*E.*” *marisrubri* being placed among the fusiliers in the Lutjanidae (see Table 2).

Phylogenetic analysis and reassignment of “Emmelichthys” marisrubri to Dipterygonotus.—Parsimony analyses resulted in seven optimal trees of 86 steps. Out of 20 nodes, 11 (55%) were supported by a bootstrap value ≥ 70 and 3 (15%) were supported by a bootstrap value ≥ 95 . In all trees, “*E.*” *marisrubri* was recovered sister to *D. balteatus*. All likelihood analyses resulted in a single optimal tree with a $\ln L = -456.198$ (Fig. 2). Out of 20 nodes, 14 (~70%) were supported by a bootstrap value ≥ 70 and 5 (25%) were supported by a bootstrap value ≥ 95 . The resulting topology recovered “*E.*” *marisrubri* sister to *D. balteatus*. To identify synapomorphies, morphological characters were optimized onto the resulting likelihood topology. Of the character transformations, 30 of 58 (~51%) are unique and unreversed (Fig. 2). The relationship between “*E.*” *marisrubri* and *D. balteatus* is supported by eight morphological characters, including the presence of a horn-like ventral process on the basioccipital and presence of two supraneurals (see Table 2, Fig. 2). As a result of my analysis and the characters listed above (see Table 2) and discussed below, I reassign “*E.*”

Table 2. Comparison of significant characteristics among *Emmelichthys nitidus*, *Dipterygonotus marisrubri*, and *D. balteatus*.

Character	<i>Emmelichthys nitidus</i>	<i>Dipterygonotus marisrubri</i>	<i>Dipterygonotus balteatus</i>
Relationship of ascending process to articular process of premaxilla	Fused along entire anterior length of articular process	Separate elements	Separate elements
Relationship of left and right premaxillary ascending processes	Separate elements	Fused along majority of length	Fused along majority of length
Number of postmaxillary processes	1	2	2
Supramaxilla	Present	Absent	Absent
Posterior expansion of lateral ethmoid	Absent	Present	Present
Ventral extension of prootic covering <i>pars jugularis</i>	Absent	Present	Present
Contact of pterosphenoïds medially	Present	Absent	Absent
Apophysis on ventral margin of parasphenoid	Rudimentary	Robust	Robust
Ventrolateral process of basioccipital for insertion of Baudelot's ligament	Absent	Present	Present
Posteriorly expanded tubule of pterotic that interacts with ventral arm of posttemporal	Absent	Present	Present
Indentation in posterior margin of supraoccipital	Absent	Present	Present
Ventral expansion of endopterygoid separating metapterygoid from quadrate	Present	Absent	Absent
Number of supraneurals	3	2	2
Isolated dorsal-fin spines separating membrane-bound spinous and soft dorsal fins	Present	Present	Present
Number of dorsal-fin trisegmental pterygiophores	8	3	2–3

marisrubri to the genus *Dipterygonotus*. Hereafter, the taxon will be referred to as *Dipterygonotus marisrubri* (Fricke, Golani, and Appelbaum-Golani 2014).

DISCUSSION

***Dipterygonotus marisrubri* and differences from the *Emmelichthyidae*.**—Based on the morphological assessments by Heemstra and Randall (1977) and Johnson (1980), emmelichthyids have diagnostic features in their oral jaws, suspensorium, neurocranium, and medial fins (see above). All emmelichthyids have a broad ascending process on the premaxilla that extends slightly above the dorsal margin of the articular process (Fig. 3A characters 1 and 2). The articular process is robust and fused to the ascending process throughout its rostral margin. Additionally, all emmelichthyids have a single postmaxillary process on the premaxilla (Fig. 3A character 3) and a well-developed supramaxilla (Fig. 3A character 4), although these two characters are found in other fishes (e.g., some haemulids, lutjanids, and sparids; see Johnson, 1980). In *D. marisrubri*, I find an elongate and narrow ascending process that is a separate element from the articular process, with the left and right parts of the ascending process fused together at the midline (Fig. 3B characters 1* and 2*). The articular process extends about half the length of the ascending process and the supramaxilla is absent. Differences between *D. marisrubri* and members of the *Emmelichthyidae* are also seen in the suspensorium, as all emmelichthyids have a ventral flange that extends from the endopterygoid (Fig. 3A character 5) and separates the metapterygoid from the quadrate. This flange is not present in any other group of fishes, and it is absent from the endopterygoid of *D. marisrubri* (Fig. 3B character 5*). In the neurocranium, emmelichthyids lack a posterior extension of the lateral ethmoid (Fig. 4A character 1), and the left and right pterosphenoïds contact each other at the midline, behind the orbit (Fig. 4A character 2). In *D. marisrubri*, a pronounced

posterior extension of the lateral ethmoids is present (Fig. 4B character 1*), and the pterosphenoïds are distinctly separate (Fig. 4B character 2*). A well-defined apophysis is present on the ventral margin of the parasphenoid of *D. marisrubri* (Fig. 4B character 3*), which is rudimentary in species of *Emmelichthys* (Fig. 4A character 3), and only well-defined in species of *Plagiogeneion* within the *Emmelichthyidae*. Finally, *D. marisrubri* has fewer supraneurals (2; Fig. 5B character 1*) and trisegmental pterygiophores (3; Fig. 5B character 2*) than any species of emmelichthyid (Fig. 5A characters 1 and 2). All emmelichthyids have three supraneurals (Fig. 5A character 1), and the last 6–8 dorsal pterygiophores are trisegmental (Fig. 5A character 2). Based on this suite of characters, *D. marisrubri* should not be considered a member of *Emmelichthys* or the *Emmelichthyidae* (see Table 2). These characters are indicative of fusiliers and are discussed within the context of the Lutjanidae below.

***Placement of Dipterygonotus marisrubri* among the fusiliers.**—Fusiliers are a tropical Indo-Pacific group of fishes that have highly protrusible upper jaws and a similar life history to emmelichthyids, feeding predominantly on zooplankton. The Caesionidae was described by Bonaparte (1831) and later considered a member of the *Emmelichthyidae* (see Fowler, 1933; Schultz, 1945). Later, Johnson considered the family the sister group of the Lutjanidae within his Lutjanoidae. Caesionids have subsequently been included within the Lutjanidae (see Miller and Cribb, 2007; Rincon-Sandoval et al., 2020; Fricke et al., 2023) based on analyses of DNA data. Fusiliers are diagnosed by having the ascending process as a separate element from the articular process of the premaxilla (Fig. 3C characters 1* and 2*; Johnson, 1980) and a ventral extension of the prootic covering *pars jugularis* (Carpenter, 1987; see Table 2, Fig. 4C character 4*). Several features indicate *D. marisrubri* is a species of fusilier, including the diagnostic separate ascending process of the premaxilla (compare Fig. 3B characters 1* and 2* with 3C characters 1*



Fig. 3. Comparison of oral-jaw and suspensorial characters among (A) *Emmelichthys nitidus* NSMT 125987, (B) *Dipterygonotus marisrubri* paratype USNM 410584, and (C) *D. balteatus* USNM 388679. Arrows and numbers highlight characters being compared. (1) Ascending processes separate from each other. (1*) Ascending processes fused at midline. (2) Articular process fused to ascending process along majority of length. (2*) Articular and ascending processes as separate elements. (3) One postmaxillary process. (3*) Two postmaxillary processes. (4) Supramaxilla present. (4*) Supramaxilla absent. (5) Endopterygoid with ventral flange separating metapterygoid from quadrate. (5*) Endopterygoid without ventral flange. Scale bars = 1 mm.

and 2*), ventral extension of the prootic covering *pars jugularis* (compare Fig. 4B character 4* with 4C character 4*), and two postmaxillary processes on the premaxilla (compare Fig. 3B character 3* with 3C character 3*; present in all species of *Dipterygonotus*, *Gymnocaesio*, and *Pterocaesio*). Once considered a

member of the Emmelichthyidae (see Schultz, 1945), the monospecific *Dipterygonotus* was placed among the fusiliers by Heemstra and Randall (1977) based on it having an ascending process as a separate element from the articular process of the premaxilla (see Table 2). Later, Johnson (1980) corroborated the revised



Fig. 4. Comparison of neurocranial characters among (A) *Emmelichthys nitidus* NSMT 125987, (B) *Dipterygonotus marisubri* paratype USNM 410584, and (C) *D. balteatus* USNM 388679. Arrows and numbers highlight characters being compared. (1) Lateral ethmoid without posterior expansion. (1*) Lateral ethmoid with posterior expansion. (2) Pterosphenoids contact each other at midline. (2*) Pterosphenoids separate throughout length. (3) Apophysis of parasphenoid rudimentary. (3*) Apophysis of parasphenoid robust. (4) Prootic not ventrally expanded. (4*) Prootic with ventral extension covering *pars jugularis*. (5) Posterior margin of supraoccipital without indentation. (5*) Posterior margin of supraoccipital with indentation. (6) Basioccipital without ventral expansion. (6*) Basioccipital with horn-like ventral expansion. (7) Pterotic with flange that interacts with ventral arm of posttemporal. (7*) Pterotic with tube-like process that interacts with ventral arm of posttemporal. Scale bars = 1 mm.



Fig. 5. Comparison of dorsal-fin characters among (A) *Emmelichthys nitidus* NSMT 125987, (B) *Dipterygonotus marisrubri* paratype HUJF 20199, and (C) *D. balteatus* USNM 388679. Arrows and numbers highlight characters being compared. (1) First of three rod-like supraneurals. (1*) First of two supraneurals, the first being "T"-shaped. (2) First of eight trisegmental pterygiophores. (2*) First of three trisegmental pterygiophores. (2**) First of two trisegmental pterygiophores. Comparison of vertebral characters between (D) *Dipterygonotus marisrubri* paratype HUJF 20199 and (E) *D. balteatus* USNM 388679. (3) First neural-arch prezygopophysis large and robust, extending far forward over the exoccipitals. (3*) First neural-arch prezygopophysis flat or strut-like, extending slightly over the exoccipitals. (4) First epipleural rib broad proximally, tapering distally. (4*) First epipleural rib uniform throughout length. Scale bars = 1 mm.

placement of *D. balteatus* based on additional characters from the pelvic girdle and facial musculature. Since then, molecular phylogenies have also recovered *Dipterygonotus* allied within fusiliers and within the Lutjanidae (see Miller and Cribb, 2007; Rincon-Sandoval et al., 2020). Carpenter (1990) found several characters that support a sister-group relationship between *D. balteatus* and *G. gymnoptera*, including the supraoccipital crest not extending anteriorly and fusion of the left and right premaxillary ascending processes at the midline (Fig. 3C character 1*). Although not coded in Carpenter's matrix, the posterior margin of the supraoccipital is indented in both *Dipterygonotus* and *Gymnocaesio*, a character not seen in other fusiliers (this study; Fig. 4C character 5*). Carpenter (1987, 1990) also found several autapomorphic characters in *Dipterygonotus*, including a horn-like process that extends ventrally from the basioccipital (Fig. 4C character 6*), two supraneurals (Fig. 5C character 1*), and a deeply notched dorsal fin, with the posterior three spines isolated from the membrane-bound dorsal-fin spines and rays. My analysis recovered a sister-group relationship between *D. balteatus* and *D. marisrubri*, supported by eight morphological characters (two unique and unreversed; see Fig. 2). Both species have a horn-like process on the basioccipital (compare Fig. 4B character 6* with Fig. 4C character 6*), two supraneurals (compare Fig. 5B character 1* with Fig. 5C character 1*), and the last few spines of the dorsal fin isolated from membrane-bound dorsal-fin spines and rays, among other shared character states (see Fig. 2). Although not mentioned in previous studies, the two species of *Dipterygonotus* also share a tube-like posterior extension of the pterotic where the ventral arm of the posttemporal inserts (Fig. 4C character 7*). This pterotic morphology is not found in any other fusiliers examined. Based on this analysis, *D. marisrubri* is a fusilier (Lutjanidae) in the genus *Dipterygonotus*.

Characters differentiating *Dipterygonotus marisrubri* from *Dipterygonotus balteatus*.—Prior to the inclusion of *D. marisrubri*, *Dipterygonotus* had been recognized as a monospecific genus (*sensu* Carpenter, 1987). Both Bleeker (1849) and Chabanaud (1924) described additional species in the genus, but these nominal taxa were placed in synonymy under *D. balteatus* by Carpenter (1987). *Dipterygonotus balteatus* occurs in the Indian and western Pacific Oceans and has recently been recorded as a possible Lessepsian migrant in the Mediterranean Sea (Bariche and Fricke, 2018). The taxon has not been reported from the Arabian Gulf or Red Sea (Golani and Fricke, 2018) but given this Lessepsian invasion, *D. balteatus* is likely also present in the Red Sea. *Dipterygonotus balteatus* has the following external counts and characters: dorsal fin XII–XV, 8–11, with last few spines isolated; anal fin III, 9–11; pectoral-fin rays 16–19; 28–30 gill rakers, lateral-line scales 68–80; circumpeduncular scales 26–32; scales above lateral line to origin of dorsal fin 9–11; scales below lateral line to origin of anal fin 15–18; dorsal and anal fins without scales. *Dipterygonotus marisrubri* overlaps with *D. balteatus* in number of dorsal-fin spines (XII–XIII), anal-fin spines and rays (III, 10–11), pectoral-fin rays (18–20), gill rakers (26–31), scales above and below lateral line to origin of dorsal and anal fins (8–9 and 16–18, respectively), and circumpeduncular scales (30–32). The two species also have the last few dorsal-fin spines isolated from the membrane-bound spinous and soft dorsal-fin elements and overlap in the number of trisegmental pterygiophores, with *D. balteatus* typically having between two and three and *D. marisrubri* having three. However, *D. marisrubri* has fewer dorsal-fin rays (8) and more lateral-line scales (80–83) than *D. balteatus* (Carpenter, 1987). Further, the first neural-arch

prezygopophysis of *D. marisrubri* is similar to Carpenter's (1990 fig. 7c) description for *Pterocaesio digramma*, *P. chrysozona*, and *P. pisang*, where the process is large and robust, extending far forward over the exoccipitals (Fig. 5D character 3). Carpenter (1990) described the first neural-arch prezygopophysis of *D. balteatus* as flat or strut-like, extending slightly over the exoccipitals (Fig. 5E character 3*). There are also differences between the two species in the morphology of the first epipleural rib, with *D. marisrubri* having a proximally broadened first epipleural that tapers distally (vs. uniform width in *D. balteatus*; compare Fig. 5D character 4 with 5E character 4*). Based on these differences in counts and internal morphology in a limited number of specimens, I consider *D. marisrubri* to be a valid second species of *Dipterygonotus*, but additional specimens are needed to further test the validity of this taxon.

Through detailed morphological investigations, ichthyologists continue to uncover the extent of convergence in perch-like fishes (e.g., Heemstra and Randall, 1977; Johnson, 1980, 1984; Smith et al., 2016, 2022; Girard et al., 2020). Despite the remarkably similar external appearance of *D. marisrubri* to species in the Emmelichthyidae, evidence from the oral jaws, suspensorium, neurocranium, and dorsal fin and my analysis of morphological characters demonstrates this taxon is a member of the Lutjanidae and in the genus *Dipterygonotus*. Differences in lateral-line-scale count, dorsal-fin rays, and morphology of the first vertebral prezygopophysis also suggest *D. balteatus* and *D. marisrubri* are different species. However, additional specimens and genetic data from both species of *Dipterygonotus* are needed from the region to test if the variation in counts and osteology are indicative of a separate and second species of *Dipterygonotus*.

MATERIAL EXAMINED

Specimen preparation type is listed after the count of specimens: CS—cleared and stained; ET—whole ethanol specimens. “*” indicates an ethanol specimen from the lot was scanned using μ CT. Image stacks of μ CT scans were uploaded to MorphoSource, with associated media identification numbers listed in brackets following the preparation type.

Caesio varilineata: USNM 264347, 8 ET* [553617]; USNM 466568, 1 CS.

Dipterygonotus balteatus: USNM 388679, 5 ET* [553624]; USNM 466569, 1 CS.

Dipterygonotus marisrubri: HUJF 20199 paratype, 1 ET* [553631]; USNM 410584 paratype, 1 ET* [553638].

Emmelichthys nitidus: NSMT 125978, 1 CS, 15 ET* [553651].

Emmelichthys struhsakeri: KAUM-I. 106623, 1 ET; USNM 214690 holotype, 1 ET* [553667].

Erythrocles schlegelii: KAUM-I. 55963, 1 ET; NSMT 102427, 1 CS, 9 ET; NSMT 105302, 1 ET* [553656].

Gymnocaesio gymnoptera: USNM 290488, 3 CS.

Lutjanus griseus: USNM 144173, 3 ET* [553645]; USNM 466570, 1 CS.

Plagiogeneion rubiginosum: NMNZ P.061845, 1 ET; NMNZ P.061847, 1 ET* [553662]; NMNZ P.061899, 1 ET; NMNZ P.061982, 1 ET.

Pristipomoides aquilonaris: USNM 185204, 1 CS.

Pterocaesio tile: UW 15681 [73120].

DATA ACCESSIBILITY

Supplemental material is available at <https://www.ichthyologyandherpetology.org/i2023048>. Unless an alternative copyright or statement noting that a figure is reprinted from a previous source is noted in a figure caption, the published images and illustrations in this article are licensed by the American Society of Ichthyologists and Herpetologists for use if the use includes a citation to the original source (American Society of Ichthyologists and Herpetologists, the DOI of the *Ichthyology & Herpetology* article, and any individual image credits listed in the figure caption) in accordance with the Creative Commons Attribution CC BY License.

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- characters 2 and 3 based on table 3 in Carpenter, 1987): 0, no distinct process; 1, process of various prominence present.
3. Process size on basioccipital (Carpenter, 1990 character 2 modified based on table 3 in Carpenter, 1987; coded as inapplicable for taxa with no distinct process [character 2, state 0]): 0, small, indistinct process; 1, large, distinct process.
 4. Process shape on basioccipital (Carpenter, 1990 character 2 modified based on table 3 in Carpenter, 1987; coded as inapplicable for taxa with no distinct process [character 2, state 0]): 0, broad process; 1, horn-like process.
 5. Basioccipital process relative to condyle (Carpenter, 1990 character 2 modified based on table 3 in Carpenter, 1987; coded as inapplicable for taxa with no distinct process [character 2, state 0]): 0, separated from condyle by concavity on ventral surface of basioccipital; 1, directly adjacent to condyle.
 6. Openings in lateral wall of *pars jugularis* (Carpenter, 1990 character 4 modified based on table 3 in Carpenter, 1987): 0, two; 1, three to four; 2, five; 3, one.
 7. Ventral extension of prootic covering *pars jugularis* to varying degrees (modified from Carpenter, 1990 character 4): 0, absent; 1, present.
 8. Shape of ventral extension of prootic (modified from Carpenter, 1990 character 4; coded as inapplicable for taxa with ventral extension of prootic absent [character 7, state 0]): 0, plate-like; 1, strut-like.
 9. Ventral extension of contact arm of prootic (modified from Carpenter, 1990 character 4; coded as inapplicable for taxa with ventral extension of prootic absent [character 7, state 0]): 0, absent; 1, present.
 10. Number of epipleural ribs (Carpenter, 1990 character 5): 0, fewer than 10; 1, 10–11; 2, 12; 3, 13; 4, 14.
 11. Number of dorsal-fin trisegmental pterygiophores (Carpenter, 1990 character 6): 0, three or more; 1, two or fewer.
 12. Anterior extension of supraoccipital crest (Carpenter, 1990 character 7): 0, crest does not extend to middle of orbit; 1, crest extends to middle of orbit; 2, crest extends forward to the anterior portion of the orbit.
 13. Number of postmaxillary processes (Carpenter, 1990 character 8): 0, one; 1, two.
 14. Shape of posterior tip of maxilla (Carpenter, 1990 character 9): 0, blunt, deepest posterior to the posterior tip of the premaxilla; 1, tapered, deepest anterior to posterior tip of premaxilla.
 15. Shape of parasphenoid apophysis (Carpenter, 1990 character 10): 0, V-shaped; 1, nearly straight to slightly U-shaped.
 16. Shape of first epipleural rib (Carpenter, 1990 character 11): 0, simple rod-shaped rib; 1, flattened rib with lateral extensions along about two-thirds of its length.
 17. Process on second epipleural rib (Carpenter, 1990 character 12): 0, simple rod-shaped rib; 1, flattened rib with strut-like process about one-fourth of the distance from the proximal tip.
 18. Size of first neural arch prezygopophysis (modified from Carpenter, 1990 characters 13 and 14): 0, small; 1, large.
 19. Shape of first neural arch prezygopophysis (modified from Carpenter, 1990 characters 13 and 14; coded as inapplicable for taxa with small neural arch prezygopophysis [character 18, state 0]): 0, conical; 1, broad and robust.
 20. Anterior extension of first neural arch prezygopophysis (modified from Carpenter, 1990 characters 13 and 14):

APPENDIX 1

Descriptions and states for the characters analyzed. All multistate characters are unordered.

1. Tooth plate on third epibranchial (Carpenter, 1990 character 1): 0, present; 1, absent.
2. Ventrolateral process on basioccipital for insertion of Baudelot's ligament (modified from Carpenter, 1990

- 0, extends slightly beyond vertical plane of centrum, towards exoccipitals; 1, extends well beyond vertical plane to exoccipitals.
21. Palatine teeth (Carpenter, 1990 character 15): 0, present; 1, absent.
 22. Dentary teeth (Carpenter, 1990 character 16): 0, teeth along entire biting surface; 1, teeth scarce and feeble in the middle biting surface; 2, teeth restricted to the apex of the jaw.
 23. Premaxillary teeth (modified from Carpenter, 1990 character 17): 0, teeth along entire biting surface; 1, teeth restricted on premaxilla.
 24. Shape of first anal-fin pterygiophore (Carpenter, 1990 character 18): 0, distal end wide with convex profile; 1, extended but not pronounced distal anterior profile; 2, slender profile with no pronounced extension of distal anterior side.
 25. Vomerine teeth (Carpenter, 1990 character 19 [coding for *D. balteatus* was changed to state 1]): 0, present; 1, absent.
 26. Supraneural between neurocranium and first neural arch (modified from Carpenter, 1990 character 20): 0, present; 1, absent.
 27. Number of supraneurals between first and second neural arch (modified from Carpenter, 1990 character 20): 0, one; 1, two.
 28. Supraneural between second and third neural arch (modified from Carpenter, 1990 character 20): 0, present; 1, absent.
 29. Procurent caudal-fin rays (Carpenter, 1990 character 21): 0, more than eight; 1, eight or fewer.
 30. Ascending process of premaxilla relationship to premaxilla: 0, ascending process and premaxilla as one element; 1, ascending process separate as median ascending process from premaxilla.
 31. Median ascending processes (Carpenter, 1990 character 22; coded as inapplicable for taxa with ascending process and premaxilla as one element [character 30, state 0]): 0, left and right processes separated, abutting at midline; 1, left and right processes fused at midline.
 32. Scales associated with dorsal and anal fins (modified from Carpenter, 1990 character 23): 0, present; 1, absent.
 33. Percent of scale coverage on dorsal and anal fins (modified from Carpenter, 1990 character 23): 0, scales cover 75% of fin height; 1, scales cover 90% of fin height; 2, scales cover 50% of fin height.
 34. Orientation of scale coverage on dorsal and anal fins (modified from Carpenter, 1990 character 23): 0, obliquely oriented; 1, horizontally oriented.
 35. Dark pigmentation on caudal fin (modified from Carpenter, 1990 character 24): 0, absent; 1, present.
 36. Shape of dark pigmentation on caudal fin (modified from Carpenter, 1990 character 24; coded as inapplicable for taxa without dark pigmentation on caudal fin [character 35, state 0]): 0, prominent black blotch on tips of caudal lobes; 1, prominent black median streak along caudal lobes.
 37. Pigmentation on outer base of pectoral fin (Carpenter, 1990 character 25): 0, present; 1, absent.
 38. Supratemporal scale band (modified from Carpenter, 1990 character 26): 0, indistinct; 1, distinct.
 39. Supratemporal scale-band pattern (modified from Carpenter, 1990 character 26; coded as inapplicable for taxa with indistinct supratemporal scale band [character 38, state 0]): 0, posterior to ascending premaxillary process and confluent at dorsal midline; 1, posterior to ascending premaxillary process and interrupted at dorsal midline by scaleless zone.
 40. Dorsal spines (modified from Carpenter, 1990 character 29): 0, 11 or fewer; 1, 12 or more.
 41. Dorsal rays (modified from Carpenter, 1990 character 30): 0, 14 or fewer; 1, 15 or more.
 42. Anal rays (modified from Carpenter, 1990 character 31): 0, 11 or fewer; 1, 12 or more.
 43. Pectoral rays (modified from Carpenter, 1990 character 32): 0, 20 or fewer; 1, 21 or more.
 44. Upper gill rakers (modified from Carpenter, 1990 character 33): 0, seven or fewer; 1, eight or more.
 45. Lower gill rakers (modified from Carpenter, 1990 character 34): 0, 23 or fewer; 1, 24 or more.