Journal of the
Ocean Science Foundation

2017, Volume 27

The status of *Enneanectes jordani* and a new species of triplefin blenny from the Greater Caribbean (Teleostei: Tripterygiidae)

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Abstract

A review of collections of triplefin blennies of the genus *Enneanectes* from the tropical western Atlantic Ocean reveals a new species, *Enneanectes quadra* n. sp., belonging to the scaled-belly subgroup. The species is distinguished by a lightly marked head, a mostly square dark bar on the caudal peduncle that is much darker than the other body bars, a short first dorsal fin, and no scales on the preopercle. The species is apparently uncommon and has been found to date in the Bahamas, St. Croix and Antigua in the Lesser Antilles, and in the western Caribbean Sea at Yucatán (Mexico), Honduras, Belize, and Providencia. The mtDNA barcode COI sequence is 12.1% divergent from its nearest relative. Some specimens of the new species in museums have been identified as "*E. jordani*", but a forensic-type reexamination of the status of *Enneanectes jordani* (Evermann & Marsh, 1899) reveals the type specimens to be the same species as the common *Enneanectes pectoralis* Fowler, 1941, and *Enneanectes jordani* now becomes the senior synonym for that widespread species. A phenetic NJ tree of mtDNA sequences and a revised key to the eight current species of *Enneanectes* in the Greater Caribbean region is presented.

Key words: taxonomy, ichthyology, systematics, coral-reef fishes, *E. pectoralis*, Squaretail Triplefin, Redbelly Triplefin, DNA barcoding.

Citation: Victor, B.C. (2017) The status of *Enneanectes jordani* and a new species of triplefin blenny from the Greater Caribbean (Teleostei: Tripterygiidae). *Journal of the Ocean Science Foundation*, 27, 48–73.
doi: https://doi.org/10.5281/zenodo.852637
urn:lsid:zoobank.org:pub:49AA87E8-864B-496C-B583-5E7D7B2A9F18
Date of publication of this version of record: 28 August 2017

Introduction

The triplefin blenny genus *Enneanectes* Jordan & Evermann, 1895 is a group of tiny blennioid fishes endemic to the New World tropics and includes all the known triplefin species (Family Tripterygiidae) in the western Atlantic Ocean. The number of species has recently increased, with three new species described from the eastern Pacific Ocean by Rosenblatt, Miller & Hastings (2013) and three more from the Caribbean Sea by Victor (2013), with a present total of 14 species (5 in the eastern Pacific and 9 in the western Atlantic [one from St. Paul's Rocks off Brazil only], including the new species described here).

The identity and placement of the type species for the genus *Enneanectes*, from the Mexican Pacific coast, has been controversial since Rosenblatt (1960) first characterized and reviewed the genus, noting that the type specimen was not actually of the species (or perhaps even the genus) described. Smith & Williams (2003) resolved the situation and fixed the type species as *Enneanectes carminalis* (Jordan & Gilbert, 1882), based on the neotype of Brock (1940).

In a curious parallel, the identity of the original representative species from the Atlantic Ocean is similarly confused. Evermann & Marsh described *Gillias jordani* in 1899 from Puerto Rico, but the species was not clearly distinguished from *Enneanectes pectoralis* Fowler, 1941 (from Florida) until Rosenblatt (1960) redescribed "*Enneanectes jordani*" based on a series of specimens from the Bahamas, which he united with the two type specimens from Puerto Rico, but with qualifications and a certain sense of reluctance. Subsequently, most ichthyologists have been quite tentative in identifying any fish as *E. jordani* (e.g. Greenfield & Johnson 1981, Robertson & Van Tassell 2015), and my examination of "*E. jordani*" specimens in museums indicates that most are misidentified *Enneanectes altivelis* Rosenblatt, 1960, which shares the diagnostic scaled-belly character (for example the record from Cayman Islands by Burgess *et al.* [1994]: ASNP 142569). These misidentifications are likely the result of inconsistent characters in Rosenblatt's (1960) key and the poor condition of older collections, where markings are faded and scales are lost. In this study, I conclude that the holotype and paratype of *E. jordani* are actually not members of the species reviewed by Rosenblatt from the Bahamas, but the same as the common *E. pectoralis* (and thus the senior synonym), leaving his Bahamian specimens as a new species, described here, with a distinct mtDNA COI lineage, 12.1% divergent from true *E. jordani* [ex-*pectoralis*].

Materials and Methods

Type specimens are deposited at the Florida Museum of Natural History, University of Florida, Gainesville (UF), the Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania (ANSP), and the National Museum of Natural History, Washington, D.C. (USNM).

A 652-bp segment (the "barcode" marker) was amplified from the 5′ region of the mitochondrial cytochrome c oxidase (COI) gene using a variety of primers (Ivanova *et al.* 2007). DNA extractions were performed with the NucleoSpin96 (Machery-Nagel) kit according to manufacturer specifications under automation with a Biomek NX liquid-handling station (Beckman-Coulter) equipped with a filtration manifold. PCR amplifications were performed in 12.5 µl volume including 6.25 µl of 10% trehalose, 2 µl of ultra pure water, 1.25 µl of 10× PCR buffer (10mM KCl, 10mM $(NH_4)_2SO_4$, 20mM Tris-HCl (pH8.8), 2mM $MgSO_4$, 0.1% Triton X-100), 0.625 µl of $MgCl_2$ (50mM), 0.125 µl of each primer (0.01mM), 0.0625 µl of each dNTP (10mM), 0.0625 µl of *Taq* DNA polymerase (New England Biolabs), and 2 µl of template DNA. The PCR conditions consisted of 94°C for 2 min., 35 cycles of 94°C for 30 sec., 52°C for 40 sec., and 72°C for 1 min., with a final extension at 72°C for 10 min. Specimen information and barcode sequence data from this study were compiled using the Barcode of Life Data Systems (Ratnasingham & Hebert 2007, Ward *et al.* 2009). The sequence data is publicly accessible on BOLD and GenBank (collection data and accession numbers are listed in Appendix 1). Sequence divergences were calculated using BOLD with the Kimura 2-parameter (K2P) model generating a mid-point rooted neighbor-joining (NJ) phenogram to provide a graphic representation of the species' sequence divergence.

Measurements were made by ocular micrometer and are presented as the range for the types, followed in parentheses by the holotype. Only adult specimens over 17 mm SL are included in the morphological measurements. Triplefins typically have the last dorsal and anal-fin ray split to the base: they are counted as one ray. Most

measurements of Rosenblatt (1960) are followed, although oblique measurements were avoided (except the length of the upper jaw and fin-element lengths); instead horizontal and vertical measurements were used for their greater consistency (as span). Lengths of specimens are mm standard length (mm SL), measured from the front of the upper lip to the base of the caudal fin (posterior end of the hypural plate); body depth is the vertical distance at the base of the first dorsal spine; body width is the maximum width side-to-side just posterior to the gill opening (unsqueezed); head length (HL) is the horizontal distance from the front of the upper lip to the most posterior end of the opercular flap (usually membranous in triplefins); head depth is the vertical distance at the midline of the orbit (closed-mouth specimens); snout length is the horizontal span (not angular distance) from the front of the upper lip to the anterior edge of the bony orbit (in closed-mouth specimens; note that Rosenblatt [1960] used the length from the front edge of the orbit, above the nostril, along an angle to the tip of the upper lip; however, this oblique measurement would not discriminate between fish with a deep head, blunt snout, and low-placed mouth from fish with a low forehead and long pointed snout, indeed an important species-level difference among triplefins); orbit diameter is the horizontal distance from edge to edge of the bony orbit; interorbital width is the least bony width; upper-jaw length is the full length (not a horizontal); caudal-peduncle depth is the least depth and caudal-peduncle length is the horizontal distance from the base of the last dorsal-fin ray to the caudal-fin base; lengths of fin spines and rays are measured to their junction with the body; caudal-fin length is the horizontal distance from the base of the fin to a vertical at the tip of the longest ray; pectoral-fin length is the length of the longest ray; pelvic-fin length is measured from the junction with the body to the stretched tip of the longest soft ray. Lateral-line pored (tubed) scales are counted from the scale above the end of the opercular flap (after the mostly fixed plate with serrations resembling ctenii) to the last tubed scale. Notched-scale counts are total scales in the line from the first notched scale to the last notched scale on the caudal-fin base, including unnotched scales which are sometimes found within the series. Total scale counts permit counts to be made when some scales are missing and their degree of notching is unknown.

Enneanectes jordani (Evermann & Marsh, 1899)

Redbelly Triplefin
Tres Aletas Panzaroja

Figures 1–7, 11, 12, 14 & 15; Table 1.

BOLD mtDNA barcode lineages BIN AAB9879 & AAB9881

Gillias jordani Evermann & Marsh, 1899: 357 (Cardona Lighthouse, Puerto Rico).
Gillias jordani Evermann & Marsh 1900: 307, fig. 95 (Cardona Lighthouse, Puerto Rico).
Enneapterygius jordani (Evermann & Marsh, 1899) Longley in Longley & Hildebrand 1941: 246–247 (Tortugas, Florida).
Enneapterygius pectoralis Fowler, 1941: 96–98, figs. 10–12 (Sanibel Island, Florida).
Tripterygion jordani (Evermann & Marsh, 1899) Schultz 1950: 268 (Puerto Rico)[as senior synonym for *E. pectoralis*].
Enneanectes pectoralis (Fowler, 1941) Rosenblatt 1960: 12–16, fig. 3 (Florida, Bahamas, U.S. Virgin Islands, Antigua [Antigua corrected to Aruba by Caldwell & Caldwell 1964], and Martinique).
Enneanectes jordani (Evermann & Marsh, 1899)(in part) Rosenblatt 1960: 16–19 (Puerto Rico types only).
Enneanectes pectoralis Caldwell & Caldwell 1964: 34 (Aruba).
Enneanectes pectoralis Cervigon 1966: 681 (Venezuela and Caribbean Sea).
Enneanectes pectoralis Birdsong & Emery 1968: 190 (Nicaragua, Belize, and Yucatán, Mexico).
Enneanectes pectoralis Böhlke & Chaplin 1968: 555, 1 fig. (Florida, Bahamas, and Lesser Antilles).
Enneanectes pectoralis Randall 1968: 243, fig. 276 (West Indies, photograph from Puerto Rico).

Enneanectes pectoralis Starck 1968 (species list for Alligator Reef, Florida).
Enneanectes pectoralis Greenfield & Johnson 1981: 50–51 (Honduras and Belize).
Enneanectes pectoralis Randall 1983: 243, fig. 276 (West Indies, photograph from Puerto Rico).
Enneanectes pectoralis Robins & Ray 1986: 221–222, plate 44 (Florida to Bahamas, Yucatán to Venezuela).
Enneanectes pectoralis Greenfield & Johnson 1990: 441–442 (Honduras and Belize).
Enneanectes pectoralis Burgess, Smith & Lane 1994: 217 (Cayman Islands).
Enneanectes pectoralis Cervigon 1994: 68–69, fig. 46 (Los Roques, Venezuela and Caribbean Sea).
Enneanectes pectoralis Randall 1996: 300, fig. 375 (West Indies, photograph from Puerto Rico).
Enneanectes jordani Springer & Orrell 1996: 27 (USNM type catalog).
Enneanectes jordani (in part) Smith 1997: 588–589 (types).
Enneanectes pectoralis Smith 1997: 588 (Florida, Bahamas, Caribbean; not Fig. 329 which is *E. atrorus*).
Enneanectes pectoralis Smith-Vaniz *et al.* 1999: 377 (Bahamas and Florida).
Enneanectes pectoralis Burgess, Axelrod & Hunziker 2000: 507, 1 fig. (aquarium guide).
Enneanectes jordani Dennis 2000: 179 (Puerto Rico, types, list).
Enneanectes pectoralis Dennis 2000: 179 (Puerto Rico, list).
Enneanectes jordani (in part) Williams 2003: 1749 (types).
Enneanectes pectoralis Williams 2003: 1749 (Caribbean).
Enneanectes pectoralis Dennis *et al.* 2005: 730 & 732 (Mona Island, Puerto Rico, Tables 2 & 3).
Enneanectes jordani (in part) McEachran & Fechhelm 2005: 576 (types).
Enneanectes pectoralis McEachren & Fechhelm 2005: 577, 1 fig. (E. Gulf of Mexico, FL, Bahamas, and Antilles).
Enneanectes jordani (in part) Patzner *et al.* 2009: 444 (types, list).
Enneanectes pectoralis Patzner *et al.* 2009: 444 (list).
Enneanectes pectoralis Kells & Carpenter 2011: 326, 1 fig. (Florida, Bahamas, Antilles to Venezuela).
Enneanectes pectoralis Lin & Hastings 2013: DNA tree, fig. 2.
Enneanectes pectoralis Victor 2013: 47 (key), 68 (mtDNA sequences; Yucatán, Mexico & Bahamas).
Enneanectes pectoralis (in part) Smith-Vaniz & Jelks 2014: 66 (St. Croix, all except type of *E. quadra*).
?*Enneanectes pectoralis* Bolaños-Cubillos *et al.* 2015: 153 (list of fishes of San Andres area).
Enneanectes jordani (in part) Robertson & Van Tassell 2015: web guide, 1 drawing of holotype (types).
Enneanectes pectoralis Robertson & Van Tassell 2015: web guide, 4 photographs (Florida, Bahamas, and Caribbean).
Enneanectes pectoralis Miller, Lin & Hastings 2016: DNA tree, fig. 2.
Enneanectes pectoralis Snyder & Burgess 2016: 252–253 (Florida).

Figure 1. *Enneanectes jordani*, underwater photograph, Eleuthera, Bahamas (L. Johnson).

Figure 2. *Enneanectes jordani*, underwater photograph, Pompano Beach, Florida (A. Dimitris).

Holotype. USNM 49368, 28.4 mm SL, USA, Puerto Rico, Ponce, Cardona Lighthouse Reef, USFC *Fishhawk*, 1 February 1899.

Paratype. USNM 126096, 22.0 mm SL, USA, Puerto Rico, Ponce, Cardona Lighthouse Reef, USFC *Fishhawk*, 31 January 1899.

Diagnosis. Dorsal-fin rays III+XII+7; anal-fin rays II,15; pectoral-fin rays 15; first dorsal fin short, when adpressed not reaching second-spine base of second dorsal fin (often barely reaching fin origin); almost always 13 pored lateral-line scales and about 19 or 20 scales in notched midline row; scaled belly and pectoral-fin base and two scales above rear of pored lateral-line, upper scale much smaller [both characters of scaled-belly subgroup]; five body bars, last body bar on caudal peduncle much darker; anterior orbital flange with fine spines; [note all prior characters shared with *E. quadra*; following characters diagnostic for *E. jordani*]: orbital cirrus dark, relatively broad, ending in a broad flat end or one to several shallow points; a patch of 2–10 usually ctenoid scales on upper preopercle immediately behind eye, below sensory canal (in fish over 18 mm SL); a row of 4–9 intense dark, rounded spots along pored lateral-line, centered on dark body bars; iris with six wide, red, spoke-like bands

Figure 3. *Enneanectes jordani*, underwater photograph, Roatan, Honduras (M. Charteris).

with much narrower interspaces (when live or fresh), spoke at 2 o'clock notably narrower than others; snout short with a broad dark band from orbit across front half of upper and lower jaws; a prominent dark bar curving from lower rim of orbit usually past corner of jaws, followed behind by a broad light bar, often with a central dark patch; dorsal head, preopercle, and opercle dark; rear body bright red to red-orange, especially ventrally; anal fin usually uniformly pigmented, but sometimes barred with reddish or dusky bands slanting forward from base; caudal-peduncle dark bar typically ovoid (wider at center with corners rounded) and usually narrower in width than height, ending at base of caudal-fin rays and followed on caudal fin by a narrow "accent" bar, red and/or dark, and then, after a narrow pale (white in life) band, a broad dark tail band often interrupted with a pale circle top and bottom (lower is larger), then a narrow pale (white in life) band at rear margin.

Remarks. Rosenblatt (1960) pointed out that until 1960 the two species, *E. jordani* and *E. pectoralis*, were not considered different and Schultz (1950) listed *Tripterygion jordani* as the senior synonym for *E. pectoralis*. Rosenblatt (1960) reviewed the genus and distinguished his entity "*E. jordani*" from his "*E. pectoralis*" based on the absence of preopercular (cheek) scales (usually none, rarely 1 or 2 scales), a narrow pointed orbital cirrus, and some marking patterns, primarily a barred anal fin in "*E. jordani*". He also mentioned the absence of lateral-line spots as distinguishing "*E. jordani*" from "*E. pectoralis*" (p. 15). My suspicions of this distinction were raised by two observations: first, he reported that almost all of his "*E. jordani*" series had no preopercular scales (two specimens had one on one side), while the Puerto Rican holotype was an outlier with two; and, second, the available photograph of the *E. jordani* holotype had obvious dark lateral-line spots, clearly overlooked by Rosenblatt (USNM 49368: Fig. 6, upper middle).

Subsequent review and, in particular, a photograph of the paratype specimen (USNM 126096: collected at the same location and the day before the holotype), reveals an obvious cluster of at least 5 preopercular scales (see detail in Fig. 16); this specimen must not have been examined by Rosenblatt (1960). A further evaluation of characters shows that the features cited by Rosenblatt (1960) as separating the two species in his key are not consistent, i.e. the dividing line at three preopercular scales vs. two or fewer is not reliable; the orbital cirrus of *E. pectoralis* is not always broad with a rounded flat edge, but can be long, pointed, bifid or multifid; and some otherwise typical fresh *E. pectoralis* can also have barred anal fins (see Figs. 5 & 6 bottom, and detailed character comparisons below).

Figure 4. *Enneanectes jordani*, fresh photograph, UF 239080, Eleuthera, Bahamas; note prominent lateral-line dark spots (L. Johnson).

Figure 5. *Enneanectes jordani*, fresh photographs: AMNH 235927, Marathon Key, Florida (top); AMNH 240738, Exuma Cays, Bahamas (middle) (both J. Van Tassell & D.R. Robertson); USNM 414531, Berry Islands, Bahamas (bottom) (C.C. Baldwin *et al.*, Smithsonian Institution).

A review of many more specimens and photographs of fresh specimens from a wider geographic range confirms that there are indeed two entities in the Caribbean and Bahamas. The characters that most reliably separate these fishes into two groups are the presence vs. absence of preopercular scales, a row of lateral-line dark spots, the shape of the last body bar on the caudal peduncle, and the banding on the caudal fin. The two species correspond to two very divergent mtDNA COI lineages, 12.1% apart.

Notably, however, the holotype and paratype of *E. jordani* match the features of *E. pectoralis* in all characters, as detailed in the comparison of characters listed in a section below. Rosenblatt (1960) assigned the *E. jordani* holotype to a different species from common *E. pectoralis* mainly because he found it had two preopercular scales vs. 3 or more in *E. pectoralis*; curiously, he must have not examined the paratype he also assigned to the rare species, since it has an obvious patch of at least 5 ctenoid scales on the preopercle (Fig. 7, see detail in Fig. 16). Almost all the specimens of the non-*pectoralis* entity I (and Rosenblatt) examined have no preopercular scales (one individual I examined had a single scale on one side), and *E. pectoralis* can have as few as two scales on the preopercle. I thus conclude that the holotype and paratype of *E. jordani* is the same species and senior synonym of the common *E. pectoralis*.

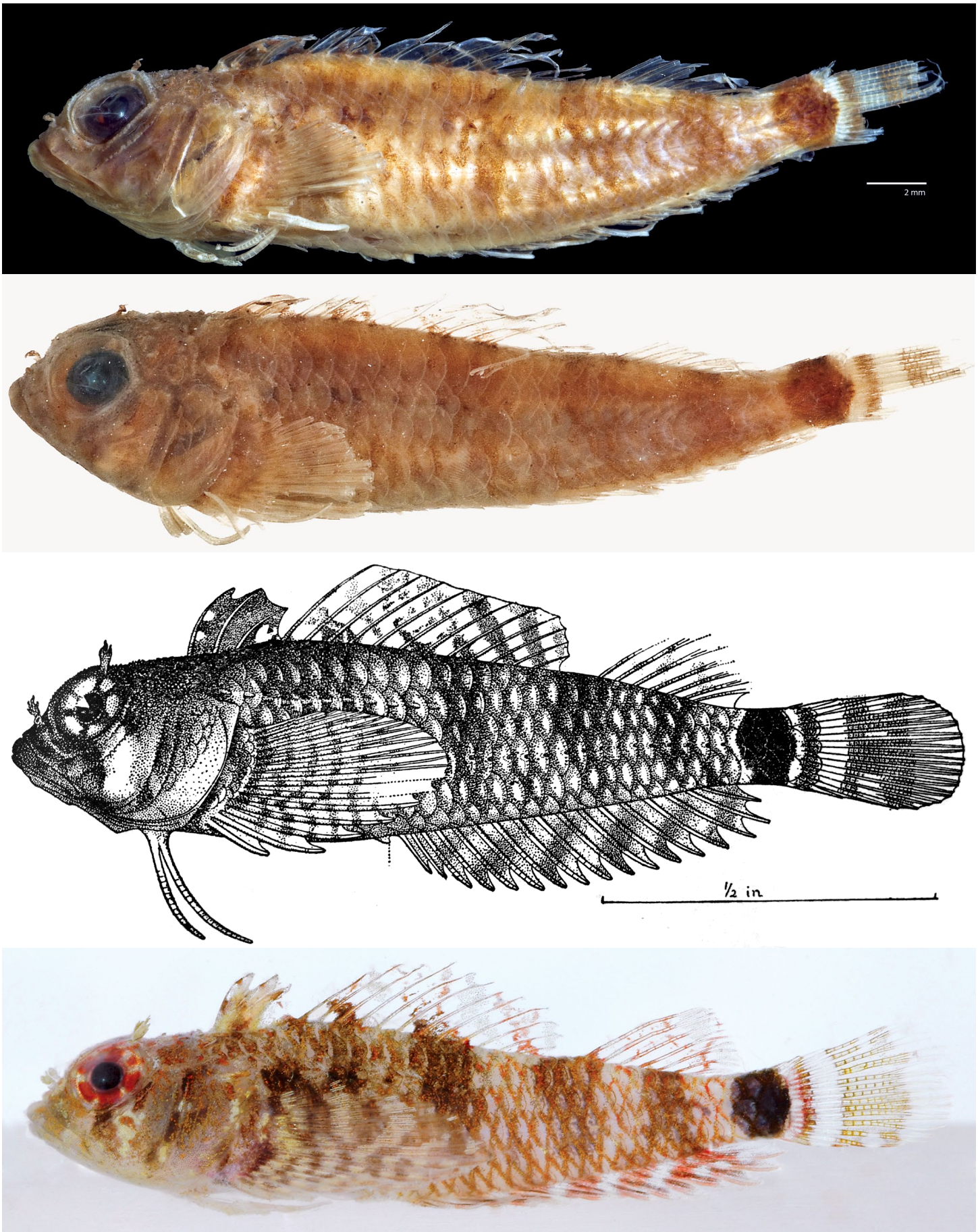

Figure 6. *Enneanectes jordani*, preserved holotype, USNM 49368, 28.4 mm SL, Puerto Rico, USA (both top & upper middle; Sandra Raredon, Smithsonian Institution Division of Fishes); drawing of holotype (lower middle; from Evermann & Marsh 1900); fresh photograph, AMNH 243492, Carabobo, Venezuela (bottom; J. Van Tassell & D.R. Robertson).

Figure 7. *Enneanectes jordani*, preserved paratype, USNM 126096, 22.0 mm SL, Puerto Rico, USA (courtesy Sandra Raredon, Smithsonian Institution Division of Fishes).

Rosenblatt (1960) noted that his "*E. jordani*" was relatively rare and he had few specimens– he then united the two Puerto Rican type specimens with a series from Bahamas, but with some hesitation and adding a paragraph explaining his justification, concluding that "the anal fin color and weak cheek squamation are, however, sufficient to establish that the Bahamas specimens reported here are indeed *jordani*" (p. 18). His text description then combines the specimens, but is mostly applicable to the Bahamas series, especially the description of markings which clearly apply more to the new species discussed below than to the *E. jordani* holotype. His description sometimes dramatically differs from the illustrated holotype by Evermann & Marsh (1900). For example, Rosenblatt (1960) lists for "*E. jordani*" a pale snout, lips, and lower jaw; an "evenly colored" caudal fin; and the caudal-peduncle bar the same width from top to bottom, all diagnostic features of the new species and directly contradicted by the illustration and specimen of the *E. jordani* holotype (Fig. 6).

Furthermore, the text descriptions of the holotype of *Gillias jordani* by Evermann & Marsh (1899, 1900) include characters that clearly do not conform with Rosenblatt's "*E. jordani*", but instead fit *E. pectoralis*. These include a "a broad bifid orbital tentacle" and a caudal fin with prominent alternating dark and light bands. They also note that the species is "well-marked" and point out that the "head and underparts [are] rusty", consistent with the red posterior and ventral aspect of *E. pectoralis*.

The common name Mimic Triplefin for "*E. jordani*" appears to have been applied first by Böhlke & Chaplin (1968), based on Bahamian specimens that now represent the new species, and named "mimic" to highlight the similarity to *E. pectoralis*. Since the question of similarity is now moot, the common name would not now correctly represent the holotype of *E. jordani*.

The common name Böhlke & Chaplin (1968) assigned to *E. pectoralis*, i.e. Redeye Triplefin, is non-specific and applies to most *Enneanectes* species. I therefore propose the common name Redbelly Triplefin for *E. jordani* (ex-*pectoralis*), since the species typically has a distinctive bright-red ventral and posterior body in life, often even in small individuals (Figs. 1–5).

The true *E. jordani* (ex-*pectoralis*) is relatively common in museum collections of triplefin blennies, most often collected in very shallow locations. It is likely found widespread on coral-reef areas in the Greater Caribbean, including South Florida and the Bahamas, and south to Venezuela, but collections from all localities have not been critically reviewed. Robertson & Van Tassell (2015) show the range throughout the region, absent only from the northern and central Gulf of Mexico and Panama/Colombia, but additional collecting could change the latter.

Interestingly, there are very few underwater photographs of the species; I am aware of only three instances (see Figs. 1–3). This dearth is likely the result of most underwater macrophotography being performed at scuba-diving depths and in less exposed conditions, combined with a very small adult size and especially elusive behavior by the fish.

Enneanectes quadra, n. sp.

Squaretail Triplefin
Tres Aletas Cola Cuadrada

urn:lsid:zoobank.org:act:FCFAFCDF-1F9E-4E42-856A-6256C4F25AAB

Figures 8–11, 13 & 16; Table 1.

BOLD mtDNA barcode lineage BIN AAB9880

Enneanectes jordani (Evermann & Marsh, 1899) (in part) Rosenblatt 1960: 16–19 (Bahamas series only).
Enneanectes jordani (in part) Böhlke & Chaplin 1968: 556, 1 fig. (Bahamas only [not Puerto Rican types]).
Enneanectes jordani Randall 1968: 243.
Enneanectes jordani (in part) Greenfield & Johnson 1981: 50 (Honduras and Belize).
Enneanectes jordani Randall 1983: 243.
Enneanectes jordani Randall 1996: 300.
Enneanectes jordani (in part) McEachran & Fechhelm 2005: 576, 1 fig. (Bahamas location only).
Enneanectes pectoralis (in part) Smith-Vaniz & Jelks 2014: 66 (St. Croix, USVI; only holotype of *E. quadra*).
Enneanectes (in part) Weigt *et al.* 2012: Table S1 (mtDNA sequences listed; Bahamas).
Enneanectes jordani? Victor 2013: 68 (mtDNA sequences; Quintana Roo, Yucatán, Mexico & Bahamas).
Enneanectes jordani Victor 2013: 47 (key), 69 (Providencia).
?*Enneanectes jordani* Bolaños-Cubillos *et al.* 2015: 152 (list of fishes of San Andres area).

Holotype. UF 149103, 20.2 mm SL, Virgin Islands (USA), St. Croix, off N. shore of Buck Island Reef National Monument, 17.78925° N, 64.61789° W, 1–3 m, location 140, field number BUIS2001-050, W. Smith-Vaniz & L. Rocha, 19 Aug. 2001.

Paratypes. UF 24974, 16.9 & 17.4 mm SL, Colombia, Isla Providencia, Crab Cay, C. Gilbert, W. Clerke & I. Stevens, 20 Aug. 1970. ANSP 72608, 21.1 mm SL, Bahamas, Hog Island, N. shore, Men's Beach behind Paradise Beach, 25.08° N, 77.32° W, C.C.G. Chaplin & H.R. Roberts, 28 March 1952. ANSP 74439, 17.6 mm SL, Bahamas, Green Cay, N. of Rose Island, 25.12° N, 77.19° W, Böhlke, J.E., C.C.G. Chaplin *et al.*, 7 May 1956. ANSP 188858, 21.4 mm SL, Bahamas, New Providence Island, Delaport Pt., 25.07639° N, 77.44389° W, G. Chaplin & L. Kellogg, 12 Nov. 2006. ANSP 188859, 21.0 & 21.5 mm SL, Bahamas, Great Bahama Bank, North Cay/Long Cay, 25.09306° N, 77.39833° W, G. Chaplin & L. Kellogg, 14 July 2006. AMNH 34713, 3 specimens (22.3–23.5 mm SL), Bahamas, Berry Islands, Frazer's hog cay, southeast point, C.L. Smith & J.C. Tyler, 4 Feb. 1968.

Figure 8. *Enneanectes quadra*, n. sp., preserved holotype, UF 149103, 20.2 mm SL, St. Croix, Virgin Islands, USA (B.C. Victor).

Figure 9. *Enneanectes quadra*, n. sp., fresh photographs of mtDNA-ID specimens in tree: USNM 414530, 17.0 mm SL, Berry Islands, Bahamas (upper); USNM 414532, 19.5 mm SL, Berry Islands, Bahamas (lower)(C.C. Baldwin *et al.*).

Non-type Material. ANSP 191595, 3 specimens (17.0–18.6 mm SL), tissue samples B1905, B1908, B1910 (sequences pending), Bahamas, New Providence Island, Delaporte Point, K.L. Ilves, M.W. Westneat, R.I. Eytan, G.W. Chaplin, R. Ilves, & H. Hertler, 17 Nov. 2010. AMNH 34135, 18.7 & 18.8 mm SL, Bahamas, East Plana Cay, N. side, room and pillar Reef, C.L. Smith & J.C. Tyler, 26 January 1968. USNM 414530, 17.0 mm SL, Bahamas, Berry Islands, Hoffman Cay, 25.7515° N, 77.6681° W, 6–9 m, field number BAH08-02, C.C. Baldwin *et al.*, 16 June 2008. USNM 414532, 19.5 mm SL, Bahamas, Berry Islands, Hoffman Cay, 25.7515° N, 77.6681° W, 6–9 m, field number BAH08-02, C.C. Baldwin *et al.*, 16 June 2008. UF 11949, 12.2 & 21.4 mm SL, Green Island, Antigua, 17.07000° N, 61.66574° W, 0–5 m, field number CRG64-8, C. Gilbert *et al.*, 23 April 1964. UF 99160, 17.6 & 19.7 mm SL, Bahamas, San Salvador, Cat-O-Cay, near White Cay, 24.14094° N, 74.47195° W, 2–3 m, field number XII68-2, M. Hancock & A. Gillespie, 6 June 1968. UF 25332, 19.4 mm SL, Colombia, Isla Providencia, Santa Catalina Island, J. Tyler *et al.*, 22 Aug. 1968. UF 25394, 4 specimens (17.0–19.9 mm SL), Colombia, Isla Providencia, Three Brothers, J. Tyler *et al.*, 24 Aug. 1968. ECO-CH LP 3788 (tissue MFL812), 8.0 mm SL, Mexico, Yucatán, Quintana Roo, Othon P. Blanco, Xcalak region, 18.265° N, 87.827° W, S. Morales Gutierrez & D. Acevedo Reyes, 12 July 2007. FMNH 84517, 1 specimen, Honduras, southwest side of Little Hog Island, 1–5 m, R.K. Johnson, D.W. Greenfield, T.A. Greenfield & G.S. Glodek, 19 May 1975. FMNH 86129, 5 specimens, Belize, Glover's Reef, wreck of *Alps*, 5 m, D.W. Greenfield & T.A. Greenfield, 2 Aug. 1973. FMNH 89363, 1 specimen, Belize, Carrie Bow Cay, S. end, 1 m, D.W. Greenfield, T.A. Greenfield & C. Rakocinski, 2 Jan. 1978. FMNH 96767, 2 specimens, Honduras, Roatan, east of Halfmoon Bay, 0–4 m, R.K. Johnson & D.W. Greenfield, 20 Feb. 1984.

Diagnosis. Dorsal-fin rays III+XII+7; anal-fin rays II,15; pectoral-fin rays 15; first dorsal fin short, when adpressed not reaching second-spine base of second dorsal fin (often not reaching fin origin); 13 modal pored lateral-line scales and about 19 or 20 scales in notched midline row; scaled belly and pectoral-fin base and two scales above rear of pored lateral-line, upper scale much smaller [both characters of scaled-belly subgroup]; five body bars, last body bar on caudal peduncle much darker; anterior orbital flange with fine spines; [note all prior characters shared with *E. jordani*; following characters diagnostic for *E. quadra*]: orbital cirrus dark and narrow, more than twice longer than wide, ending in a single point (rarely bifid); no scales on upper preopercle immediately behind eye, below sensory canal (one individual with one on one side); no dark spots along pored

lateral-line; iris with three red, spoke-like bands at about 8, 10, and 1 o'clock with wide interspaces (as wide or wider than red spokes) and a red rear lower quadrant (when fresh); snout short with reddish band from orbit across front half of upper and lower jaws, pale in preserved fish with only patches (not a complete band) of fine melanophores; a short reddish bar extending from lower rim of orbit, when preserved only a short dark bar, not reaching past corner of jaw; often a white patch immediately behind suborbital bar, when preserved only a scattering of fine melanophores; preopercle and opercle pale, except for reddish and dark patch at orbital rim at 5 o'clock and a bar along posterior margin of preopercle; rear body not red; anal fin barred, with 6 to 8 dark patches corresponding to each body bar and mid-interspace; caudal-peduncle dark bar typically about square (same width throughout with corners squared) or slightly wider than high, extending onto caudal-fin ray insertions; caudal fin mostly unmarked, almost clear on preserved specimens, with faint melanin outlining ray shafts.

Description. Body somewhat stout and elongate, body depth 22–23 (22)% SL, body width 18–21 (20)% SL; predorsal span short, 24–27 (26)% SL; prepelvic span shorter, 17–21 (19)% SL; preanal distance 48–50 (48)% SL; caudal-peduncle length 12–15 (15)% SL, caudal-peduncle depth 8–10 (9)% SL. Head short, large, and relatively deep, head length 28–31 (34)% SL; head depth (at midpoint of orbit) 17–19 (19)% SL or 55–62 (55)% HL; snout short and blunt, sloping sharply downward in front of eye, snout span 14–20 (19)% HL; eye large, orbit diameter 31–34 (33)% HL; single narrow, short, single-pointed orbital cirrus, more than twice longer than wide, heavily pigmented black (rarely bifid); interorbital narrow, mostly flat, minimum width 8–11 (12)% HL; bony orbital rim spiny, including anterior orbital flange, sparing only anterior inferior quadrant; nasal surface barely spiny, cranial surface spiny; anterior nostril a low tube with a speckled fingerlike cirrus about three times nostril diameter, posterior nostril an elliptical opening adjacent to upper orbital rim; head pores in two rows along preopercular canal, two large pores at ends of radial canals behind upper orbital rim, variably present one or a pair of small anterior interorbital pores; in two rows on each side of posterior infraorbital canal, two or three along anterior infraorbital canal, and a row of mandibular pores; mouth large, upper-jaw extending back past vertical through midpoint of eye, oblique length 37–42 (41)% HL; upper and lower jaws with variable-sized caniniform teeth, in multiple irregular rows with outermost largest; preopercle a tilted-back L-shape, rounded angle, edge mostly smooth with small irregularities; bony opercular margin with broad indentation above level of pectoral-fin base (underlying membranous flap not indented), lower portion rounded with mostly smooth edge. Gill rakers few, stubby with multiple spinules, two on the upper limb of the first arch, six or seven additional on the lower limb (Fig. 10).

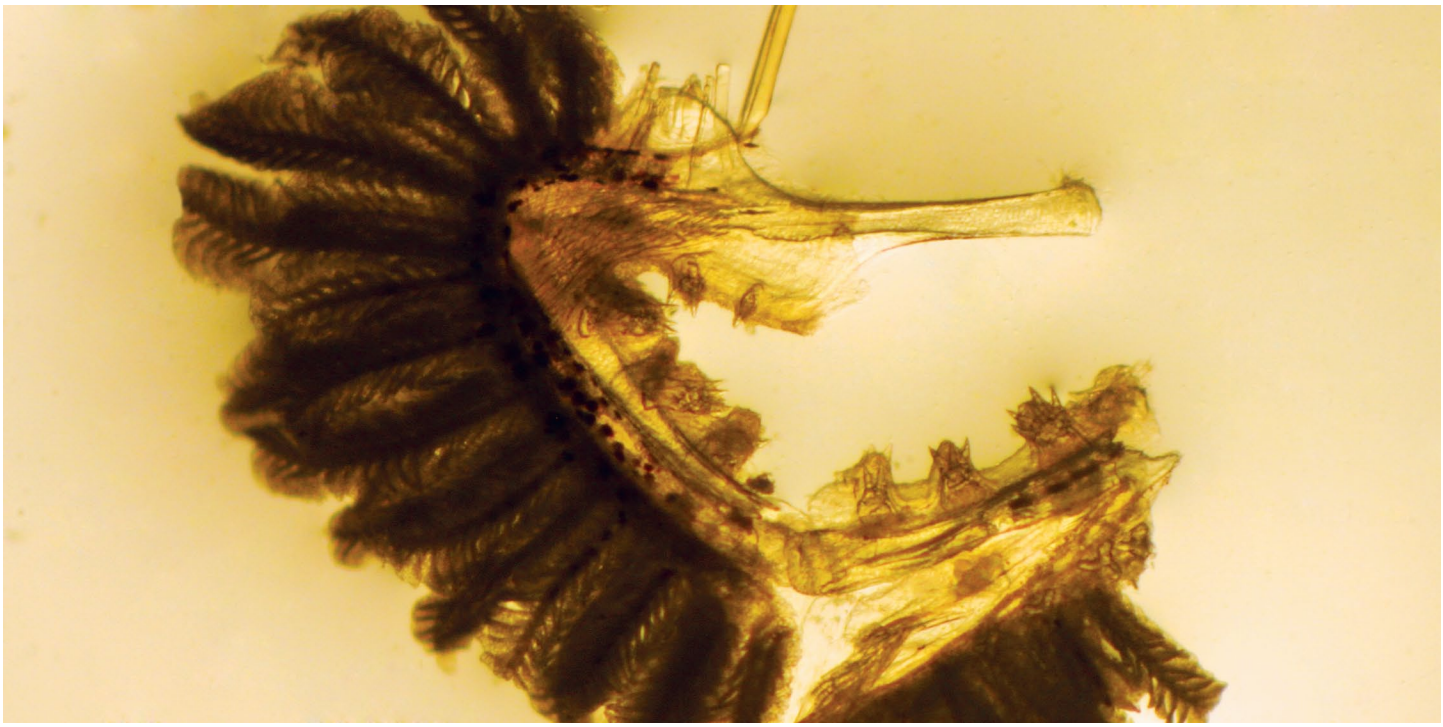

Figure 10. *Enneanectes quadra*, n. sp., first branchial arch from right side of preserved holotype, UF 149103, 20.2 mm SL, St. Croix, Virgin Islands, USA (B.C. Victor).

Three dorsal fins, first two spinous, dorsal-fin rays III+XII+7 (III+XI–XII+7–8); anal-fin rays II,15 (II,15–16); pectoral-fin rays 15 (14–15); two pelvic-fin rays; combined dorsal-fin base long, 60–64 (60)% SL, first dorsal fin short, when adpressed most extended spine (third) not reaching base of second spine of second dorsal fin (often not reaching fin origin); first dorsal-fin spine 8–10 (9)% SL, second spine 7–10 (7)% SL, third spine 7–8 (7)% SL; third spine of second dorsal fin 13–15 (13)% SL; third dorsal fin with soft rays barely branching, last split to base, usually second ray longest, 15–16 (18)% SL; anal-fin base long, 38–41 (42)% SL, with two short spindly spines rooted close together, second slightly longer than first and about half length of first ray, soft rays unbranched, antepenultimate ray longest 12–14 (14)% SL; pectoral fin long, longest ray 7th from bottom, 32–36 (31)% SL, uppermost 2–3 rays unbranched, middle about 6 branched, lower rays unbranched; two pelvic-fin rays unbranched, inner longest, 24–28 (28)% SL; caudal fin truncate, length 21–24 (22)% SL, 14–15 segmented caudal-fin rays, one or two uppermost and two or three lowermost unbranched, 4–6 upper and 3–5 visible lower procurrent rays.

Body covered with large ctenoid scales, becoming cycloid on scaled belly and on outer pectoral-fin base; head mostly unscaled, except for a patch of scales on upper operculum; no scales on preopercular area immediately behind eye and below sensory canal (occasional individual with one on one side); fins bare except for about three large, flat, cycloid scales covering lower caudal-fin rays. Scales between rear of pored lateral-line and second dorsal-fin base in two rows, upper row much smaller. Lateral-line made up of anterior segment of 13 (13–14) tubed scales, above and partially overlying discontinuous posterior segment, lying along lateral midline, comprising about 19 or 20 mostly notched scales in a series extending to caudal-fin base.

Genital papilla of males a short wide cone; urogenital opening of females with edges scalloped with many fleshy processes.

Color in life. (Fig. 9) Body pale to translucent; head pale with mostly reddish markings; fins mostly translucent, except first dorsal fin black, and six to eight dark bars along anal fin. Body with five dark bars, first broad and indistinct, below anterior portion of second dorsal fin; second and third more distinct, narrowing ventrally, centered below posterior half of second dorsal fin and gap to front of third dorsal fin, respectively; fourth narrower and more complete top to bottom, beneath rear half of third dorsal fin; fifth on caudal peduncle much darker and about square. An indistinct dark bar on pectoral-fin base and a more distinct dark bar on thorax adjacent to pectoral-fin insertion. Scales on body prominently outlined in thin dark as well as golden and orange lines. Iris with broad red spokes. Head mostly pale with a dusky cranium, reddish snout band, a short reddish suborbital bar, often a white patch immediately behind suborbital bar, and a reddish dark patch at about 4 o'clock on orbital rim; a thin dark bar along preopercular rim. Orbital cirrus black.

Color in preservative. (Fig. 8) Head and body pale yellowish with dark markings; body with network of thin dark lines outlining scales in a prominent cross-hatch pattern, overlain by five dark bars, first broad and indistinct, below anterior portion of second dorsal fin; second and third more distinct, narrowing ventrally, centered below posterior half of second dorsal fin and gap to front of third dorsal fin, respectively; fourth narrower and more complete top to bottom, beneath rear half of third dorsal fin; fifth on caudal peduncle much darker and about square with squared-off corners, ending at caudal-fin ray insertions with some melanin deposits around insertion, especially centrally. An indistinct dark bar running full-length of pectoral-fin base and a more distinct dark bar just anterior on thorax. First dorsal fin black, remaining fins mostly translucent, except a series of six to eight dark bars spaced along anal fin one beneath each body bar and each interspace. Head with a dark cranium and pale all over elsewhere, except for a short dark bar below eye, often a scattering of fine melanophores where a white patch was immediately behind suborbital bar, a dark patch at about 4 o'clock on orbital rim, and a streak along preopercular margin; a scattering of fine melanophores present in a band across snout from orbital rim to upper jaw.

Etymology. The specific epithet (Latin for "square") is based on the characteristic squared shape of the dark caudal-peduncle bar. It is treated as a noun in apposition.

Distribution. Type specimens and additional material have been collected from the Bahamas, the Virgin Islands (USA), and Antigua, as well as in the western Caribbean: at Yucatán, Mexico (as a larva), Honduras and Belize, as well as the offshore islands of Providencia. It appears that the species has never been photographed underwater.

Comparison of characters of *E. jordani* (= ex-"*E. pectoralis*") vs. *E. quadra*, n. sp.

Note: "*E. jordani*" in quotes in this discussion represents the Rosenblatt (1960) entity now named *E. quadra*; *E. jordani* without quotes is the true *E. jordani* which previously was called *E. pectoralis*.

Snout band and suborbital bar: (Fig. 11) *Enneanectes quadra* is differentiated from *E. jordani* by a particularly lightly marked snout. The broad dark band that extends from the lower anterior quadrant of the orbit across the lips to the front of the jaws and chin is found on specimens of *E. jordani* and is illustrated in the drawing of the holotype (Figs. 1–6). In contrast, in fresh *E. quadra* the equivalent band is reddish, speckled with a few melanophores, mostly on the upper lip (Figs. 9 & 11), and, after preservation, only a scattering of melanophores remain in the area, primarily on the orbital rim, the upper lip, and near the tip of the lower jaw (Fig. 8), on a few darker specimens the area is more speckled, but the band is broken above the upper lip. Rosenblatt (1960) singled out this character as diagnostic of his (preserved) Bahamian "*E. jordani*" (=*E. quadra*), i.e. "the head is much lighter. Only the median parts of the snout and lips are pigmented, and the chin is immaculate."

Similarly, *E. jordani* has a prominent dark suborbital bar, often curving, usually extending past the corner of the jaw (Fig. 11), sometimes as a broad black patch (Fig. 5 bottom); this bar is illustrated in the drawing of the holotype (Fig. 11). In contrast, *E. quadra* has a short red bar below the eye with some underlying melanophores, usually ending before the corner of the jaw (Fig. 11). Rosenblatt (1960) describes his "*E. jordani*" (=*E. quadra*) as having only a few melanophores where the dark suborbital bar is found in *E. pectoralis* (see Fig. 10).

Iris spokes: (Fig. 11) Fresh and live specimens of *E. jordani* have a prominent pattern of six broad red spokes covering the iris, with much narrower interspaces that are white in fresh specimens and bluish in underwater photographs. Notably, the illustration of the *E. jordani* holotype shows this characteristic arrangement of spokes, including the spoke at 1 to 2 o'clock being smaller than the others. Fresh *E. quadra* have a different pattern of three broad red spokes, plus one covering the entire rear lower quadrant of the iris, and the interspaces are as wide or wider than the anterior spokes. None of these markings are apparent in preserved specimens.

Orbital cirrus: Rosenblatt (1960) described the orbital cirrus of *E. pectoralis* as "broader than long, its tip flat or broadly rounded" and elevated that feature to the key, distinguishing it from the narrow pointed cirrus of his "*E. jordani*" (=*E. quadra*) . However, the 1899 text description of *E. jordani* mentions a bifid cirrus that is broad, not narrow, i.e. a "broad bifid orbital tentacle", which is clearly shown in the holotype illustration (Fig. 11). Rosenblatt (1960) overlooked that text and illustration, which do not conform with the narrow single-pointed cirrus of his "*E. jordani*" (=*E. quadra*) description, and he indicated the holotype he examined had a ragged and shrunken cirrus and thus he could not determine the shape exactly (p. 18). In fact, the broad bifid cirrus is consistent with *E. jordani* (ex-*pectoralis*), which has a variety of shapes of the orbital cirrus; some specimens have the cirrus somewhat longer than broad and with ragged edges, bifid, or with single or multiple points (e.g. Fig. 12). Some

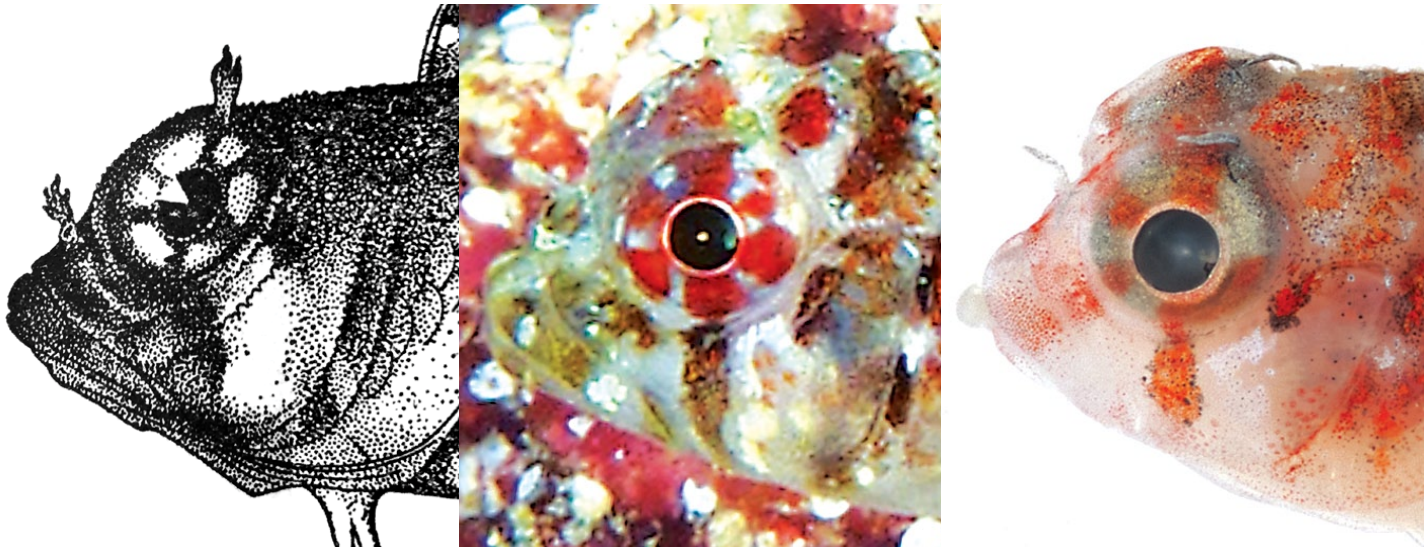

Figure 11. *Enneanectes jordani* vs. *E. quadra* n. sp., fresh eye markings (iris spokes): *E. jordani* holotype (left); *E. jordani*, Bahamas (middle)(L. Johnson); *E. quadra*, Bahamas (right)(C.C. Baldwin *et al.*).

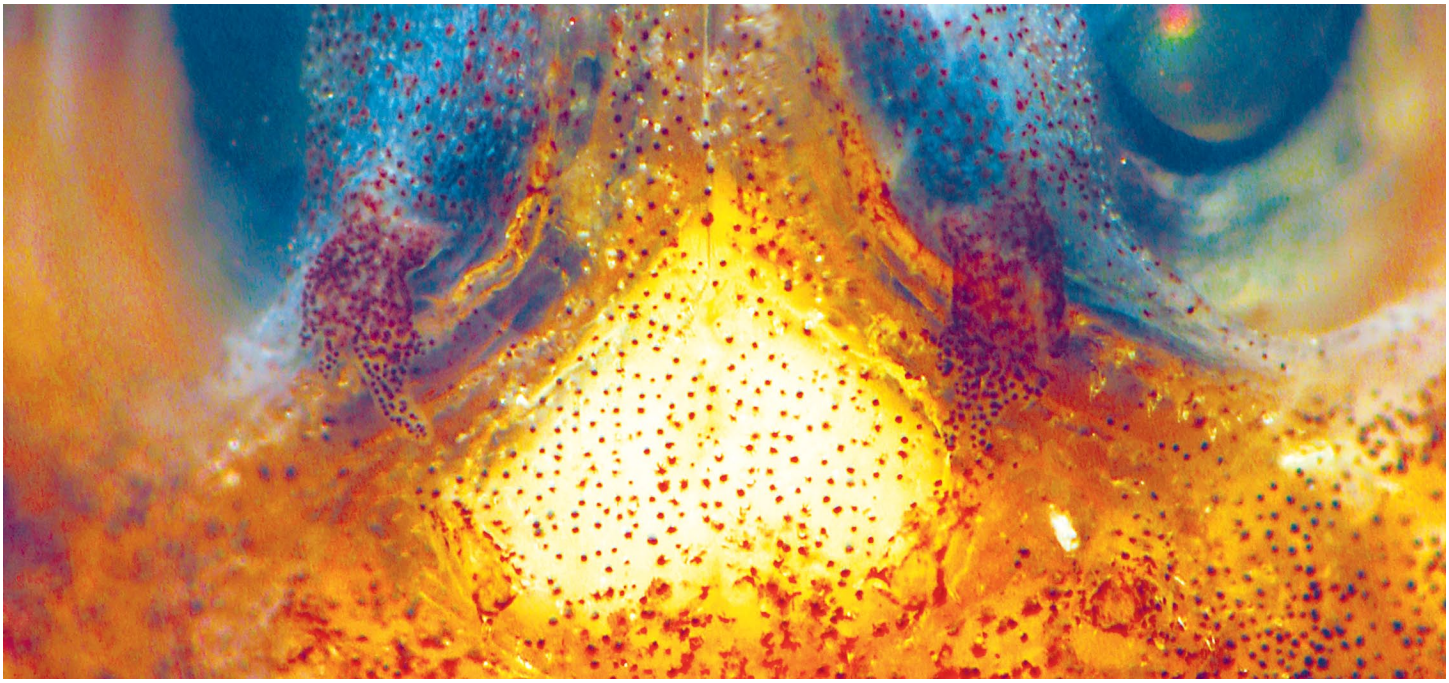

Figure 12. *Enneanectes jordani*, multifid orbital cirri (head pointing up), preserved specimen, 23.1 mm SL, UF 239077, St. Croix, Virgin Islands, USA (B.C. Victor).

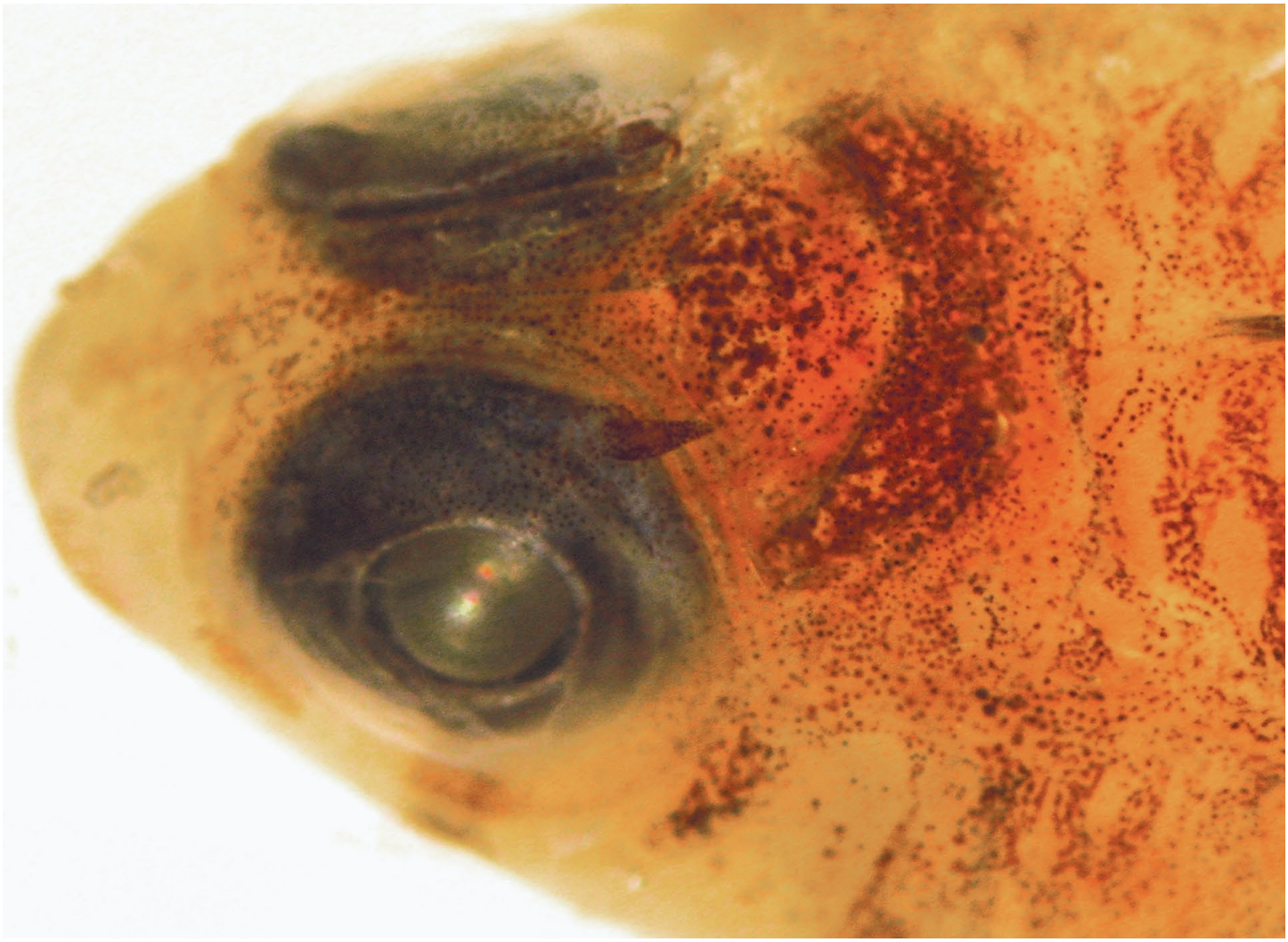

Figure 13. *Enneanectes quadra* n. sp., narrow orbital cirrus with a single point, preserved holotype, UF 149103, 20.2 mm SL, St. Croix, Virgin Islands, USA (B.C. Victor).

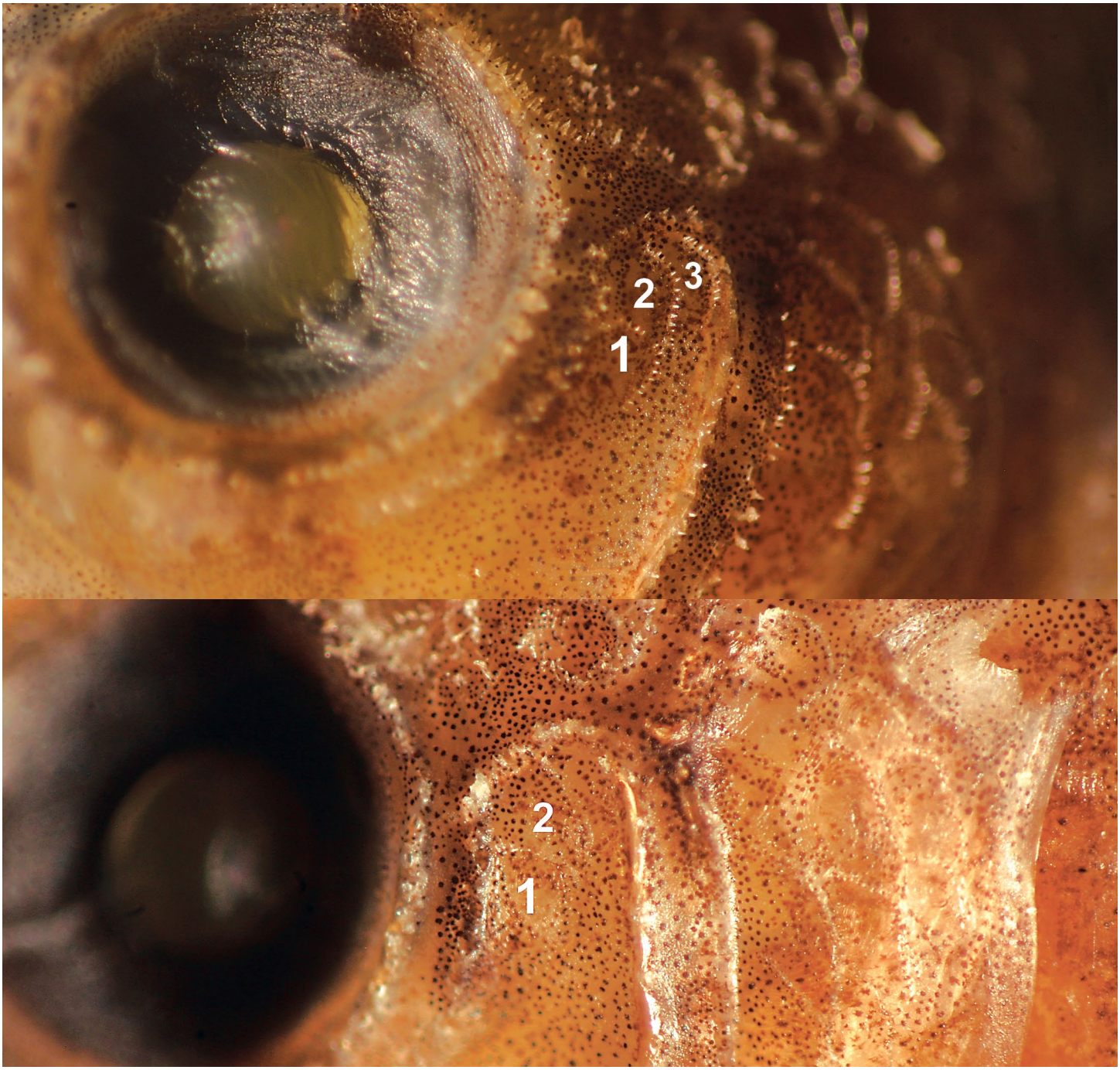

Figure 14. *Enneanectes jordani*, preopercular scale patch with 3 ctenoid scales on the left side (above) and 2 scales on the right side (image reversed), preserved specimen, UF 239077, 20.7 mm SL, St. Croix, Virgin Islands, USA (B.C. Victor).

specimens examined from St. Croix have bifid or trifid orbital cirri. The shape in the species clearly varies: indeed some individuals have single points (e.g. Fig. 3) and others have a wide tab. In contrast, *E. quadra* has a narrow orbital cirrus, more than twice as long as broad, almost always with a single point (see Figs. 11 & 13), consistent with the cirrus of Rosenblatt's Bahamian "*E. jordani*" (=*E. quadra*), which he described as narrow and pointed.

Preopercular scales: Almost all *E. quadra* examined lacked scales on the preopercle (the area immediately behind the eye below the sensory canal); one individual had one scale on one side. All *E. jordani* specimens examined did have a patch of scales in this area (2 to 10 ctenoid scales), but sometimes embedded, and depending on preservation, variably apparent. A similar-sized *E. jordani* specimen (UF 239077) in the St. Croix collection containing the holotype of *E. quadra* has two scales on one side and three on the other (Fig. 14), indicating that the dividing line of three or more in Rosenblatt's *E. pectoralis* was not as diagnostic as presumed. Furthermore, the ctenoid edges of the scales are not always grossly apparent, even in a relatively dried state.

Rosenblatt (1960) concluded that while almost all of his "*E. jordani*" (=*E. quadra*) had no preopercular scales, the holotype of *E. jordani* from Puerto Rico must also be a member of that species since it had only two, apparently cycloid, scales, instead of the 3 or more ctenoid scales in his description of *E. pectoralis*. However, the paratype from Puerto Rico (USNM 126096), which was listed in his material examined, has an obvious patch of more than 5 ctenoid scales on the preopercle (Fig. 15), confirming the distinction between the type specimens of *E. jordani* from Puerto Rico and the series of *E. quadra* from Bahamas examined by Rosenblatt (1960).

Lateral-line spots: A series of dark spots underlying the pored scales along the lateral line is apparent on lightly marked *E. jordani* (Figs. 1, 2, 4, & 5), and clear on the preserved holotype of *E. jordani* (Fig. 6). In contrast, on fresh or preserved *E. quadra*, there are typically no prominent spots and, when spots of melanin are present beneath those particular scales, they are of the same relative intensity as pigment around other scales.

Anal-fin pattern: The markings on the anal fin were considered diagnostic by Rosenblatt (1960) and were used in his and subsequent identification keys as a prime character: i.e. uniform in *E. pectoralis* and bars in "*E. jordani*" (=*E. quadra*). The faint oblique bars on the anal fin of the illustration of the *E. jordani* holotype (Fig. 6) was one of the primary criteria used by Rosenblatt (1960) to distinguish the holotype from other *E. pectoralis* and used by subsequent authors to single out specimens as "*E. jordani*". However, fresh photographs of *E. jordani* show some specimens with exactly these bars (see Figs. 5 & 6); perhaps the fact that the bars are mostly reddish

Figure 15. *Enneanectes jordani*, head detail of preserved paratype, USNM 126096, 28.4 mm SL, Puerto Rico, USA; white circle surrounds patch of preopercular ctenoid scales (courtesy Sandra Raredon, Smithsonian Institution Division of Fishes).

Figure 16. *Enneanectes quadra* n. sp., preserved specimen, ANSP 115050, 18.8 mm SL, note squared-off dark bar on caudal peduncle and unmarked caudal fin, specimen illustrated in Böhlke & Chaplin (1968), New Providence Island, Bahamas (courtesy M. Sabaj Pérez, ANSP).

and/or dusky and less likely to show on preserved specimens promoted the utility of the character for preserved fishes. These bars are consistently present and darker on *E. quadra*, and useful for distinguishing preserved specimens: the number is usually 7, but ranges from 6 to 8.

Caudal-peduncle bar: One of the more constant features identifying *E. quadra* is the squared-off, relatively wide, dark bar on the caudal peduncle (the fifth body bar), for which the new species is named. The bar typically ends with deposits of melanin around the insertion of the central caudal-fin rays. The width of the bar is about the same or wider than the height of the bar and the anterior margin of the bar is usually well squared-off at the top and bottom ends, resulting in a dark square that is immediately apparent. In contrast, *E. jordani* has a typically narrower bar, almost always narrower than tall, with rounded corners, usually approximating an oval (see Figs. 1–7). Other species of *Enneanectes* have a variety of dark caudal-peduncle bars, either with the anterior margin of the bar slanting down and rearward, e.g. in *E. atrorus* and some *E. boehlkei* and *E. deloachorum*, or noticeably narrower than tall, as in *E. altivelis*, *E. matador*, and *E. wilki* (Victor 2013).

Note that the illustration of "*E. jordani*" (=*E. quadra*) in Böhlke & Chaplin (1968; p. 556), and copied in McEachran & Fechhelm (2005; p. 576), shows a fish with most of the attributes of the new species, except for a relatively narrow caudal-peduncle bar. However, the actual specimen the drawing is based on (ANSP 115050), despite being faded (Fig. 16), has the characteristic relatively wide squared-off bar, with the typical concentration of melanin along the bases of the central caudal-fin rays that is evident in fresh specimens (see Figs. 7 & 8). Apparently the drawing was somewhat distorted and not representative– in all likelihood remodeled to conform with the illustration of the holotype in Evermann & Marsh (1900). Additional evidence for that conclusion of a "hybrid" drawing is that the body bars are drawn as uniform width, but are wedge-shaped in the specimen, and two preopercular scales are added to the drawing, but not apparent on the specimen.

"Accent" caudal bar: One of the more obvious differences between fresh *E. quadra* and *E. jordani* is in the markings on the caudal fin. On both the holotype specimen and on the drawing of the holotype of *E. jordani*, and on fresh photographs of *E. jordani*, there is a prominent thin, dark or reddish band following shortly after the caudal-peduncle bar (Figs. 1–7). There is no equivalent on fresh or preserved *E. quadra*. This accent bar is centered on the first part of the shaft of the caudal-fin rays, clearly beyond the insertion of the rays where some pigment is concentrated in *E. quadra*. On *E. jordani* individuals with a reddish accent bar, as in the fresh photographs, the upper and lower ends are typically dark, and often only the ends show dark in preserved specimens.

Caudal-fin bands: The caudal fin of *E. jordani* is usually well-marked with a conspicuous wide central dark band, in live and fresh fish, as well as most preserved specimens. This dark band is illustrated in the drawing of the holotype and is prominent on the remaining piece of caudal fin on the holotype (Fig. 6). The band is typically interrupted by two pale circles midway out, on the upper and lower margins, with the lower circle larger and more obvious; that pattern is illustrated in the engraving of the *E. jordani* holotype. In contrast, the caudal fin of *E. quadra* is pale and mostly unmarked in both fresh and preserved specimens, often with only thin streaks of melanin outlining the shafts of the rays, visible under the microscope.

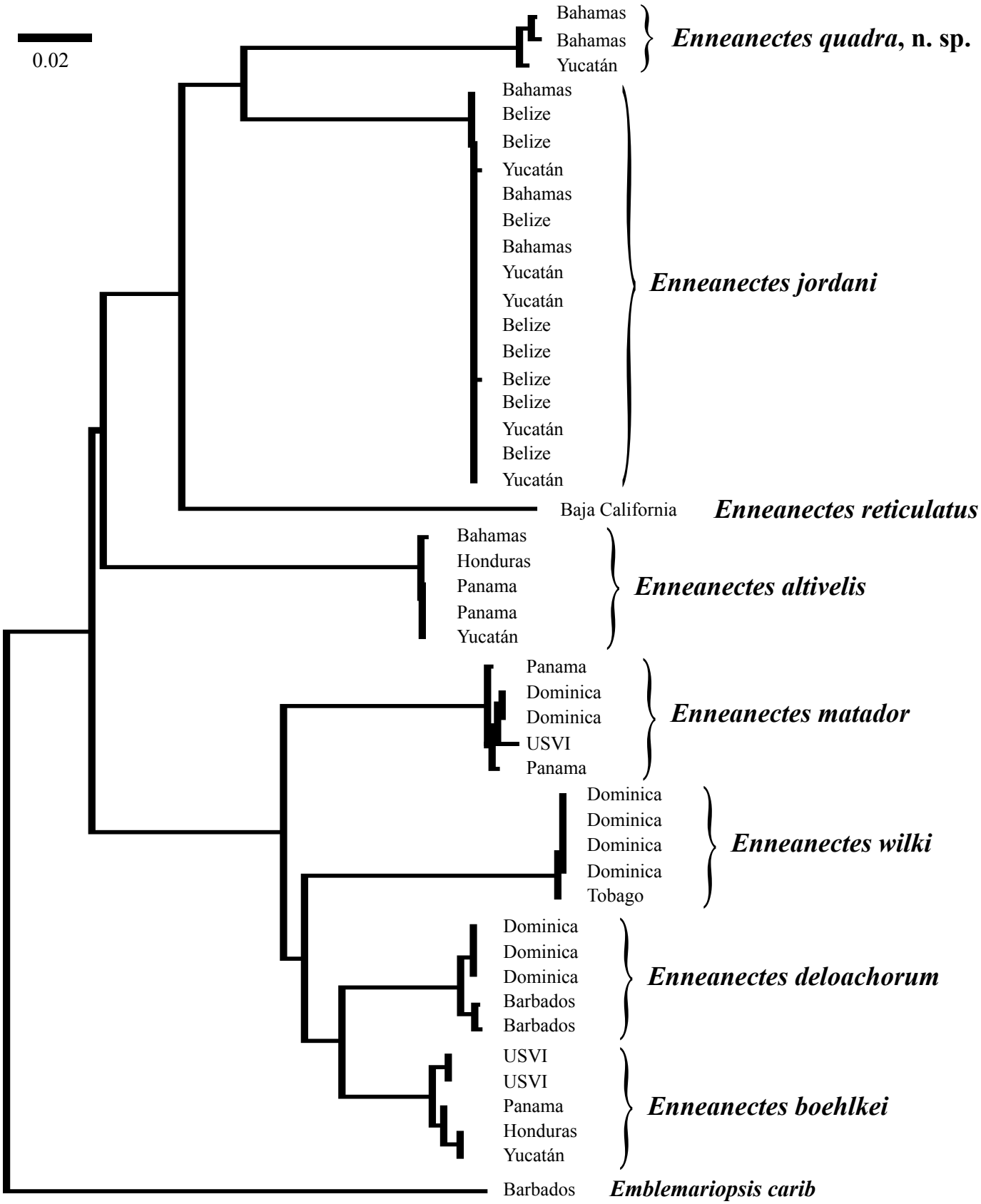

Figure 17. The neighbor-joining phenetic tree of the triplefin genus *Enneanectes* based on mtDNA COI sequences, following the Kimura two-parameter model (K2P) generated by BOLD (Barcode of Life Database); http://boldsystems.org/. The scale bar at left represents a 2% sequence difference. Collection locations for specimens are indicated. GenBank accession numbers and collection data for the sequences in the tree are listed in Appendix 1. The blennioid chaenopsid *Emblemariopsis carib* is used an outgroup.

Genetic Analysis

Mitochondrial DNA sequences have been useful in delineating new species in the genus *Enneanectes*, which has relatively deep divergences between lineages (Fig. 17). Victor (2013) described three new species coexisting on the reefs of Dominica that formed three distinct mtDNA COI lineages, each more than 10% divergent from the other. Despite the genetic divergence, related species are morphologically very similar and DNA identification assisted in confirming diagnostic differences in marking patterns.

The new species *E. quadra* is similarly divergent from its nearest relative, *E. jordani* (ex-*pectoralis*); the two mtDNA COI lineages differ by 12.1% (minimum interspecific distance by K2P; 12.2% pairwise). Intraspecific divergences are low within lineages, however there are some cryptic lineages within nominal species that raise the intraspecific variation to varying degrees. In many cases, these cryptic lineages may prove to have no diagnostic morphological or marking differences and therefore would represent genovariant populations of the same species; in others they show phenotypic differences and represent undescribed species. These close sets of lineages are typically allopatric and represent regional populations, and are commonly found among Caribbean gobioid and blennioid fishes (Victor 2015).

Revised Key to Species of *Enneanectes* from the Greater Caribbean region

This new key is updated from Victor (2013). The meristic values for the 8 species are presented in Table 1. The revised key includes the new species from this paper and adjusts some imprecise characters from the prior key. Typical habitat is also included, because it can be very helpful in ambiguous cases; the two species found

TABLE 1

Meristic values for the *Enneanectes* species of the Greater Caribbean Region

	2nd dorsal-fin spines				Dorsal-fin soft rays			Anal-fin soft rays				Pectoral-fin rays (both)			
	X	XI	XII	XIII	7	8	9	14	15	16	17	13	14	15	16
E. matador		1	17			8	10			9	9		1	35	
E. wilki		2	9	1	1	9	2		1	9	2			23	1
E. deloachorum			3	2		1	4			3	2			9	1
E. boehlkei		2	21	1	4	17	3		1	23				46	2
E. atrorus			13			2	11			12	1			25	1
E. altivelis	2	15	3		4	15	1	1	19			2	39		
E. jordani		1	20	2	23				23	1			2	45	1
E. quadra, n. sp.		3	7		9	1			9	1			1	17	

	Pored lateral-line scales							Notched-scale series							
	10	11	12	13	14	15	16	16	17	18	19	20	21	22	23
E. matador				1	11	9	2	1				1	3	4	1
E. wilki				3	12	6	1					1	6	9	1
E. deloachorum						3	1				1			2	1
E. boehlkei					3	18	5				2	5	9	3	
E. atrorus			5	5							1	1	2	4	
E. altivelis	3	11	1								1	4	4	1	
E. jordani			1	19					1	1	5	3			
E. quadra, n. sp.				11	1					1	2	3			

in deeper water (>10 m; *E. altivelis* and *E. atrorus*) are often the only species present in some museum rotenone collections and also are some of the most frequently photographed by divers, since the best scuba-diving sites are usually relatively deep. The key includes meristic and morphological characters as well as color patterns, and thus should allow identification of live, fresh, and preserved specimens, as well as most underwater photographs of triplefins.

1a. Abdomen and pectoral-fin base scaled; two scale rows above posterior pored lateral-line, upper row much smaller ……..…..……..…….....2

1b. Abdomen and pectoral-fin base naked; three scale rows above posterior pored lateral-line, two equal size plus one additional row much smaller near fin base 4

2a. Last body bar about equally dark to preceding bars and usually a narrow vertical rectangle with an indented anterior upper corner (i.e. narrower at top than middle); first dorsal fin long, when adpressed reaching past base of second spine of second fin and with 4–6 dark (colored) bands; pored lateral-line scales usually 11 (10–12); second dorsal-fin spines almost always 11; pectoral-fin rays almost always 14; six or seven dark bars along anal fin; in life, mid-body bars edged with prominent dark-rimmed orange spots (common on deeper reefs and walls; Florida, Bahamas, Caribbean) .....***E. altivelis***

2b. Last body bar much darker than preceding bars; first dorsal fin short, when adpressed not reaching base of second spine of second fin (often not reaching second fin origin) and with 2 dark bands, if banded; pored lateral-line scales almost always 13; second dorsal-fin spines mostly 12; pectoral-fin rays almost always 15; anal fin with or without dark bars; no prominent dark-rimmed orange spots along edges of mid-body bars in life 3

3a. Preoperculum behind eye with a patch of scales; series of dark rounded spots along pored lateral-line; last body bar narrower than high, corners usually rounded; dark band across snout and prominent curved dark bar below eye; caudal fin with a prominent narrow followed by a wide dark or dusky reddish band; anal fin usually unmarked on preserved specimens; rear body typically bright red in life (common, shallows; Florida, Bahamas, Caribbean) .....***E. jordani***

3b. Preoperculum behind eye naked; no series of dark spots along pored lateral-line; last body bar as wide or wider than high, corners usually squared off; snout reddish or pale and short dark bar below eye; caudal fin usually unbanded; anal fin with six to eight dark bars; rear body not bright red in life (uncommon, shallows; Bahamas, Virgin Islands, Belize, Honduras, Antigua, Yucatán & Providencia) .....***E. quadra*, n. sp.**

4a. Long sloping snout, horizontal distance forward of eye about equal to eye diameter; last three body bars usually about equally dark, with anterior margin of last body bar sloping down and back (bar wider dorsally); preorbital flange smooth (at most a few small spines along preorbital ridge on largest fish); 12–13 pored lateral-line scales (common on deeper reefs and walls; Bahamas & Caribbean) .....***E. atrorus***

4b. Blunt snout, horizontal distance forward of eye usually much less than eye diameter; last one or two body bars distinctly darker than preceding bars (except some *E. wilki*); preorbital flange spiny; usually 14–16 pored lateral-line scales 5

5a. Caudal fin red with no dark bands or any duskiness (unmarked in preserved fish); no dark rounded spots at base of membranes of second dorsal fin; males with second dorsal fin broadly speckled black; head and body bright red in life, pale in preservative (shallow reefs; W. Caribbean, Greater and Lesser Antilles) .....***E. matador***

5b. Caudal fin with dark or dusky-red bands; three dark rounded spots at base of membranes of second dorsal fin; head and body not bright red in life, cranium dark in preservative 6

6a. Fifth body bar much darker than first four and usually wider than 4–5 interspace; first four body bars usually indistinct, frequently barely distinguishable (esp. in Bahamas and Virgin Islands); no accessory interspace bar or dark patch in 4–5 interspace; no red bar following last body bar; usually four or five dark patches along anal fin (common, shallow reefs; Florida, Bahamas, N. & W. Caribbean, Antilles south only to St. Kitts) ....***E. boehlkei***

6b. Fifth body bar not much darker than fourth bar and usually narrower than 4–5 interspace; an accessory interspace bar or dark patch in 4–5 interspace; often a dusky red bar following last body bar; frequently three or six dark patches along anal fin 7

7a. A wide solid dark band on outer half of caudal fin; last two body bars distinctly darker than preceding bars; dusky red bar on caudal fin after last body bar variably present; usually four or fewer dark patches along anal fin (common, shallow reefs; Dominica to ABC Netherlands Antilles) .....***E. deloachorum***

7b. Three or more and/or broken dark or dusky-red bands on caudal fin; last two body bars often not distinctly darker than preceding bars; dusky red bar on caudal fin after last body bar; usually six dark patches along anal fin (common, shallow reefs; Dominica to St. Vincent) .....***E. wilki***

Other material examined:

Enneanectes jordani (ex-*pectoralis*) (29, 9.5–28.0 mm SL): ANSP 118484 27.7 mm SL, USA, Puerto Rico, Puerto Yabucoa, J.V. Biaggi. UF 149102 (7, 15.4–24.0 mm SL), Virgin Islands (USA), St. Croix, off Buck Island, 17.789° N, 64.612° W, W. Smith-Vaniz & L. Rocha, 6 Aug. 2001. UF 239077 (8, 9.5–25.4 mm SL), Virgin Islands (USA), St. Croix, off N. shore of Buck Island Reef National Monument, 17.78925° N, 64.61789° W, 1–3 m, location 140, field number BUIS2001-050, W. Smith-Vaniz & L. Rocha, 19 Aug. 2001. UF 164426 (7, 10.1–22.4 mm SL), Virgin Islands (USA), St. Croix, N. of Buck Island Reef National Monument, 17.79913° N, 64.61673° W, 8 m, location 140, field number BUIS2005-134, R. Spieler, P. Quinn, D. Fahy & B. Buskirk (Nova Southeastern University Oceanographic Center), 8 Oct. 2005. UF 239080, 15.8 & 28.0 mm SL, Bahamas, Eleuthera, L. Johnson, 1 Jan. 2012. AMNH 235927, 25.1 mm SL, USA, Florida, Marathon Key, Hawks Channel, 24.409° N, 80.932° W, JVT-04-353, J. Van Tassell & D.R. Robertson, 29 Nov. 2004. AMNH 240738, 25.6 mm SL, Bahamas, Exuma Cays, N. of Lee Stocking Island, 23.792° N, 76.124° W, JVT-05-435, J. Van Tassell, D.R. Robertson & N. Delventhal, 4 June 2005. AMNH 243492, 27.6 mm SL, Venezuela, Carabobo, Laguna de Yapascua, 10.483° N, 67.900° W, JVT-07-741, J. Van Tassell, D.R. Robertson & J. Posada, 26 June 2007. AMNH 249725, 20.7 mm SL, Bahamas, Exuma Cays, Lee Stocking Island, 23.7814° N, 76.1116° W, JVT-05-432, J. Van Tassell, D.R. Robertson & N. Delventhal, 3 June 2005.
Enneanectes altivelis (29, 9.1–23.0 mm SL): UF 99211 (3, 19.3–20.9 mm SL), Bahamas, San Salvador, Rum Cay, M. Hancock & C. Koenig, 14 June 1968. UF 25332, 19.0 & 19.7 mm SL, Colombia, Isla Providencia, Santa Catalina Island, J. Tyler *et al.*, 22 Aug. 1968. UF 25394 (4, 9.1–22.0 mm SL), Colombia, Isla Providencia, Three Brothers, J. Tyler *et al.*, 24 Aug. 1968. UF 184969, 15.1 & 17.2 mm SL, USA, Florida, Pompano Beach, 26.27466° N, 80.07914° W, 11 m, field number FAU71-60, D. Herrema, J. Larsen & H. Sahlman, 21 Sept. 1971. USNM 387625, 18.0 & 20.2 mm SL, Saba, Saba Bank, 17.23450° N, 63.44919° W, 26–27 m, J.T. Williams *et al.*, 8 Jan. 2006. USNM 388394, 13.8 & 19.6 mm SL, Saba, Saba Bank, Poison Bank, 17.51253° N, 63.22719° W, 27–30 m, J.T. Williams *et al.*, 12 Jan. 2006. USNM 388446, 11.1 mm SL, Saba, Saba Bank, NE flats, 17.4675° N, 63.2497° W, 20 m, J.T. Williams *et al.*, 12 Jan. 2006. USNM 388560, 18.6 mm SL, Saba, Saba Bank, NE side, 17.56336° N, 63.29678° W, 21–24 m, J.T. Williams *et al.*, 9 Jan. 2006. UF 239081, 13.9 & 18.0 mm SL, Panama, Portobelo, Salmedina Reef, 9.565° N, 79.698° W, B.C. Victor, D.R Robertson, J. Van Tassell & L. Tornabene, 30 May 2007. UF 239082, 15.5 & 22.2 mm SL, Panama, Portobelo, Salmedina Reef, 9.565° N, 79.698° W, B.C.

Victor, D.R Robertson, J. Van Tassell & L. Tornabene, 31 May 2007. UF 239083 (6, 12.8–23.0 mm SL), Panama, Portobelo region, Isla Dos Hermanas, 9.596° N, 79.668° W, B.C. Victor, D.R Robertson, J. Van Tassell & L. Tornabene, 2 June 2007. UF 239095, 13.7 mm SL, Honduras, Utila, B.C. Victor, 3 July 2008. UF 239084, 11.4 mm SL, Cayman Islands, Grand Cayman, Georgetown, 19.27° N, 81.39° W, B.C. Victor, 28 April 2014.
Enneanectes atrorus (13, 11.9–25.8 mm SL): UF 12345 (7, 17.6–25.8 mm SL), Cayman Islands, Grand Cayman, Georgetown, Paradise Rocks, Station 6, field number CRG64-35, 16–18 m, C.R. Gilbert & J.C. Tyler, 23 Oct. 1964. UF 13405 (3, 22.5–25.6 mm SL), Bahamas, Little San Salvador, off south-central, field number CRG66-55, 32–35 m, C.R. Gilbert & P.C. Heemstra, 9 Sep. 1966. UF 17094, 24.0 mm SL, Bahamas, South Andros, 17 miles E., field number CRG66-27, 24.05° N, 77.17° W, 18–22 m, C.R. Gilbert & P.C. Heemstra, 22 Aug. 1966. UF 239085, 11.9 & 21.6 mm SL, Cayman Islands, Grand Cayman, Georgetown, 19.27° N, 81.39° W, B.C. Victor, 28 April 2014.

Acknowledgments

The cooperation of William Smith-Vaniz and Rob Robins of the Division of Ichthyology at the Florida Museum of Natural History was instrumental in resolving the species and their assistance is greatly appreciated. The excellent underwater photographs by Louis Johnson from Eleuthera, Mickey Charteris from Roatan, and Ari Dimitris from Florida, as well as the fresh photographs by D. Ross Robertson, Jim Van Tassell, and Carole Baldwin, were invaluable. The cooperation of and photographs by the following museum staff is greatly appreciated: Jeffrey T. Williams, Sandra Raredon, and Diane Pitassy of the Smithsonian's National Museum of Natural History; Philip Hastings, H.J. Walker, and Benjamin Frable at the Scripps Institution of Oceanography Fish Collection; Mark Sabaj Pérez, at the fish collection of the Academy of Natural Sciences of Drexel University, Philadelphia and Caleb McMahan at The Field Museum of Natural History. Specimens, tissues, or sequences for comparisons of the DNA barcodes were contributed by Carole Baldwin of the Smithsonian's National Museum of Natural History; Andrew Bentley of the Kansas University Biodiversity Institute Collection, Michael Brogan, Chris Caldow, Louis Johnson, Henri Valles, and Lourdes Vásquez-Yeomans of ECOSUR (Chetumal, Quintana Roo, Mexico). Preparation and printing were sponsored by Walsh Paper Distribution, Inc. of Westminster, CA. The DNA barcoding was performed at the Centre for Biodiversity Genomics and supported by the International Barcode of Life Project (iBOL.org) with funding from the Government of Canada via the Canadian Centre for DNA Barcoding as well as from the Ontario Genomics Institute (2008-OGI-ICI-03), Genome Canada, the Ontario Ministry of Economic Development and Innovation, and the Natural Sciences and Engineering Research Council of Canada. The manuscript was reviewed by David Greenfield and William Smith-Vaniz.

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Appendix 1. Specimen data and GenBank accession numbers for the mtDNA COI barcode sequences used in the phenogram in Figure 17, following the order in the tree.

Genus	species	Collection site	Voucher	GenBank #	Collector/Source
Enneanectes	*quadra*, n. sp.	Berry Islands, Bahamas	BAHA8172	JQ839758	C. Baldwin *et al.*, USNM
Enneanectes	*quadra*, n. sp.	Berry Islands, Bahamas	BAHA8174	JQ839757	C. Baldwin *et al.*, USNM
Enneanectes	*quadra*, n. sp.	Xcalak, Mexico	ECO-CH LP 3788	GU224787	L. Vásquez-Yeomans
Enneanectes	*jordani*	Eleuthera, Bahamas	el11ep156	KC860825	L. Johnson/ B. Victor
Enneanectes	*jordani*	Carrie Bow Cay, Belize	BZLW7230	JQ841147	C. Baldwin *et al.*, USNM
Enneanectes	*jordani*	Carrie Bow Cay, Belize	BZLW7286	JQ841159	C. Baldwin *et al.*, USNM
Enneanectes	*jordani*	Xcalak, Mexico	ECO-CH-LP 3762	HM389346	L. Vásquez-Yeomans
Enneanectes	*jordani*	Berry Islands, Bahamas	BAHA8173	JQ839759	C. Baldwin *et al.*, USNM
Enneanectes	*jordani*	Carrie Bow Cay, Belize	BZLWD7751	JQ841152	C. Baldwin *et al.*, USNM
Enneanectes	*jordani*	Eleuthera, Bahamas	el11ep273	KC860826	L. Johnson/ B. Victor
Enneanectes	*jordani*	Xcalak, Mexico	ECO-CH-LP 4535	HQ573414	L. Vásquez-Yeomans
Enneanectes	*jordani*	Xcalak, Mexico	ECO-CH-LP 3743	HM389322	L. Vásquez-Yeomans
Enneanectes	*jordani*	Carrie Bow Cay, Belize	BZLWD7229	JQ841150	C. Baldwin *et al.*, USNM
Enneanectes	*jordani*	Carrie Bow Cay, Belize	BZLWD7752	JQ841157	C. Baldwin *et al.*, USNM
Enneanectes	*jordani*	Carrie Bow Cay, Belize	BZLWD7285	JQ841155	C. Baldwin *et al.*, USNM
Enneanectes	*jordani*	Carrie Bow Cay, Belize	BZLWD7242	JQ841154	C. Baldwin *et al.*, USNM
Enneanectes	*jordani*	Xcalak, Mexico	ECO-CH-LP 3762	HM389347	L. Vásquez-Yeomans
Enneanectes	*jordani*	Carrie Bow Cay, Belize	USNM 329832	KF929842	KUIT/ A. Bentley
Enneanectes	*jordani*	Xcalak, Mexico	ECO-CH-LP 3742	HM389321	L. Vásquez-Yeomans
Enneanectes	*reticulatus*	Baja California, Mexico	mwb11er320	KC860827	M. Brogan/ B. Victor
Enneanectes	*altivelis*	Berry Islands, Bahamas	BAHA8180	JQ839760	C. Baldwin *et al.*, USNM
Enneanectes	*altivelis*	Utila, Honduras	u873ea138	KC860800	B. Victor
Enneanectes	*altivelis*	Panama, Portobelo	n762aea250	KC860799	B. Victor
Enneanectes	*altivelis*	Panama, Portobelo	n7531bea237	KC860802	B. Victor
Enneanectes	*altivelis*	Quintana Roo, Mexico	MFLIV1627	HM389341	L. Vásquez-Yeomans
Enneanectes	*matador*	Panama, Portobelo	UF 185609-19.8	KC860828	B. Victor
Enneanectes	*matador*	Dominica	UF 185600	KC860834	B. Victor
Enneanectes	*matador*	Dominica	UF 185603	KC860832	B. Victor
Enneanectes	*matador*	St. Thomas, USVI	UF 185607	KC860835	B. Victor
Enneanectes	*matador*	Panama, Portobelo	UF 185609-10.6	KC860836	B. Victor
Enneanectes	*wilki*	Dominica	UF 185604-15.7	KC860841	B. Victor
Enneanectes	*wilki*	Dominica	UF 185601-13.8	KC860843	B. Victor
Enneanectes	*wilki*	Dominica	UF 185610	KC860848	B. Victor
Enneanectes	*wilki*	Dominica	UF 185611-14.3	KC860845	B. Victor
Enneanectes	*wilki*	Tobago	TOB9206	JQ842854	C. Baldwin *et al.*, USNM
Enneanectes	*deloachorum*	Dominica	UF 185605	KC860852	B. Victor
Enneanectes	*deloachorum*	Dominica	UF 185606	KC860849	B. Victor
Enneanectes	*deloachorum*	Dominica	UF 185602	KC860851	B. Victor
Enneanectes	*deloachorum*	Barbados	UF 185612-10	KC860850	H. Valles/ B. Victor
Enneanectes	*deloachorum*	Barbados	UF 185605	KC860852	H. Valles/ B. Victor
Enneanectes	*boehlkei*	St. Thomas, USVI	UF 185613-14.5	KC860823	B. Victor
Enneanectes	*boehlkei*	St. John, USVI	UF 185617	KC860820	C. Caldow/ B. Victor
Enneanectes	*boehlkei*	Panama, Portobelo	n7527ae95	KC860821	B. Victor
Enneanectes	*boehlkei*	Utila, Honduras	u872eb151	KC860824	B. Victor
Enneanectes	*boehlkei*	Xcalak, Mexico	ECO-CH-LP 3761	HM389342	L. Vásquez-Yeomans
Emblemariopsis	*carib*	Barbados	hv0248es130	HQ654578	H. Valles/ B. Victor