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The Caribbean Roughhead Triplefin (*Enneanectes boehlkei*): DNA barcoding reveals a complex of four West Indian sympatric cryptic species (Teleostei: Blennioidei: Tripterygiidae)

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Abstract

Cryptic species with distinct DNA lineages and subtle morphological or marking differences are commonplace among some reef-fish families, especially the gobies and blennioids. Often the cryptic species correspond to sets of allopatric populations in species complexes long recognized by taxonomists as geographic variants (allospecies). However, recent large-scale mtDNA sequencing in the Barcode of Life project has revealed instances of sympatric cryptic species. This is particularly important to validate the species-level status of cryptic species in general, by confirming that barriers to interbreeding exist and there is no reason to single out some cryptic species from the spectrum of "normal" species. In the case of the Roughhead Triplefin Blenny (the *Enneanectes boehlkei* complex), four different barcode COI mtDNA lineages occur in the Lesser Antilles, at least three of which can be collected on the same shoreline on the island of Dominica. When examined closely, clear marking differences correspond to the DNA lineages and they are described here as species. The pairwise sequence divergences (minimum interspecific distance) among the four species range from 5.6% to 11.8%, on the same order or greater than divergences among traditional species in the family. The complex includes both widespread Caribbean species and apparent endemics to the Lesser Antilles. *Enneanectes matador* n. sp. has a red caudal fin, a differently marked second dorsal fin, and higher fin-ray counts and is found in the Lesser Antilles and Navassa, as well as in the W. Caribbean (and probably elsewhere). *Enneanectes wilki* n. sp. has a differently marked caudal peduncle and a dark banded caudal fin and is found only in the southern Lesser Antilles chain (Windward Islands). *Enneanectes deloachorum* n. sp., which also appears limited to the southeastern Caribbean, has two dark bars on the rear body, a dark-banded caudal fin, and higher fin-ray counts. *Enneanectes boehlkei* Rosenblatt 1960 has a single prominent dark bar on the caudal peduncle and a dark-banded caudal fin and ranges from the Bahamas to the Virgin Islands and partially down the Lesser Antilles chain, as well as across the northern Caribbean, including Florida, and along Central America from Yucatan down to Panama. An updated key to Western Atlantic triplefins is presented.

Key words: *Enneanectes*, triplefins, Tripterygiidae, coral reef fishes, cryptic species, endemic, new species, phylogenetics, barcode, DNA sequence, biogeography, biodiversity.

Introduction

The advent of highly efficient DNA sequencing and the concomitant development of a large database of a single "barcode" segment of the mitochondrial gene COI (BOLD, the Barcode of Life Database) has made it possible to conduct intensive surveys of the genetic structure of coral-reef fish populations (Ward *et al*. 2009). The results show that most reef-fish species show little divergence in the barcode sequence over the Caribbean region, as would be expected from species with pelagic larval dispersal, for example the snappers of *Lutjanus* (Victor *et al*. 2009). However, some taxa, particularly among the species-rich gobies and blennioids, show a propensity to break up into numerous lineages (Riginos & Nachman 2001, Taylor & Hellberg 2006, Eytan & Hellberg 2010, Tornabene *et al*. 2010, Victor 2010a, 2010b, Baldwin *et al*. 2011). These lineages are not just geographic variation in the frequencies of shared haplotypes, nor are they slight divisions in a background of high variation; typically there is an obvious division with low variation within lineages and divergences between lineages often to the same degree as among traditional species. Most significantly, when specimens of different lineages are closely examined, and especially when live colors are documented by underwater photography, the lineages often correspond to recognizable types. These lineages with clear phenotypic differences represent unrecognized species, typically varying in the same physical attributes as do well-established species in the same genus. In general, and perhaps not by coincidence, the phenomenon is manifested in groups taxonomically neglected because of small size, insignificance, or rarity. In some cases, such as in the triplefins of *Enneanectes* in the Caribbean, the recognition of species is made difficult by the geographic overlap of multiple cryptic species as well as the combination of widespread and regional-endemic cryptic species within a single collection.

The taxonomy of the western Atlantic triplefins, all in the genus *Enneanectes*, has remained unchanged since the original review by Richard Rosenblatt in 1960 (Greenfield & Johnson 1981, Smith & Williams 2002, Williams 2003, Fricke 2009, Patzner *et al*. 2009). One additional species, *Enneanectes smithi* Lubbock & Edwards 1981, has been described as endemic to St. Peter and St. Paul Archipelago along the mid-Atlantic Ridge off Brazil. Recently, Rosenblatt *et al*. (2013) described three new species of triplefins from the eastern Pacific Ocean and noted that additional undescribed species occur in the western Atlantic.

Identifications of live triplefins have been notoriously difficult using the literature descriptions of museum specimens and most underwater photographs in guides to date are misidentified, often labeling the Roughhead Triplefin, (*E. boehlkei*-complex) as the Redeye Triplefin *Enneanectes pectoralis* (Fowler 1941), a rarely photographed shallow-water species. Similarly, photos of Blackedge Triplefins, *Enneanectes atrorus* Rosenblatt 1960, are usually labeled as Lofty Triplefins, *Enneanectes altivelis* Rosenblatt 1960, a wary species infrequently photographed but often collected with rotenone. Unfortunately both red eyes and black fin-edges are typical of most species and they are singularly inappropriate adjectives for common names. Furthermore, the couplet in the original key separating the two naked-belly species, *E. boehlkei* and *E. atrorus*, contains two errors which further confuse identifications: *E. boehlkei* is supposed to never have black edges to the second dorsal-fin membranes (only "dark brown") and no strongly contrasted body bars; however, all species of the *E. boehlkei* complex can have dark to black fin-edges and strongly contrasting body bars to some degree.

The Roughhead Triplefin, *E. boehlkei*, described by Rosenblatt (1960) as one of the five western Atlantic species in the genus, is easily distinguished by the absence of scales on the belly and a spiny preorbital. The only other species with a naked belly is the Blackedge Triplefin *E. atrorus*, a more slender, long-snouted triplefin from deeper water and without a spiny preorbital. Review of my collections and barcode sequences of Roughhead Triplefins and comparison of them with underwater photographs from around the region revealed a variety of marking patterns which correlate with distinct lineages in the DNA sequence. Notably, the marking differences are prominent in display and signaling locations, on the caudal peduncle and caudal fin in particular, which are swished back-and-forth rapidly in over-excited triplefins. It would be expected that the first traits to diverge between closely related species are those involved in mating displays (Rocha & Bowen 2008). Indeed, cases of cryptic species recently described among reef fishes vary particularly in color patterns on the head (i.e. in *Centropyge* Bowen *et al*. 2006; *Gramma* Victor & Randall 2010), especially in mature males (e.g. Baldwin *et al*. 2011).

Three new species allied to *Enneanectes boehlkei* are described from the Caribbean and *E. boehlkei* is redescribed using specimens from the Virgin Islands, presumably representative of the type population from the Bahamas. Despite the broad similarity in markings, counts, and morphology, the barcode mtDNA sequences of the four species differ by several percent from each other, on the same order as the divergence among other species in the triplefin family.

Materials and Methods

Type specimens of the new species are deposited in the collections of the Division of Ichthyology at the Florida Museum of Natural History, University of Florida (UF). All fish were collected by handnet and promptly preserved in 90% ethanol. Sequenced specimens included in the neighbor-joining tree were collected in the Atlantic from Panama, Quintana Roo (Yucatan, Mexico; by Lourdes Vásquez-Yeomans *et al.*), Utila (Honduras), Puerto Rico, St. Thomas/St. John (USVI), Bahamas (by Louis Johnson [Exumas] and Carole Baldwin *et al.*), Tobago (by Carole Baldwin *et al.*), Barbados (by Henri Valles), and Dominica. The eastern Pacific *E. reticulatus* was collected from Baja California by Michael Brogan and the *Enneapterygius* specimens were collected in Bali.

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. A 652-bp segment was amplified from the 5′ region of the mitochondrial COI gene using a variety of primers (Ivanova *et al.* 2007). 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 (BOLD, www.barcodinglife.org; Ratnasingham & Hebert 2007). The sequence data is publicly accessible on BOLD and GenBank. Sequence divergence was 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 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 14 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. 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 frequently found within the series (usually the second). Total scale counts permit counts to be made when one or more scales are missing and their degree of notching is unknown.

Key to Species of *Enneanectes* in the central Western Atlantic Ocean

This new key mostly follows Rosenblatt (1960) and the revised key of Williams (2003). Some of the characters used in the first key which have proven unreliable are not included, such as the shape of the orbital cirrus and the absence of spiny preorbitals (in *E. altivelis*). Meristic and scale-pattern characters useful for preserved specimens, as well as color and marking characters that particularly apply to live fishes, are included. Photographs of living and preserved fishes, along with museum collections (see "Other material examined") and uncatalogued specimens, were reviewed for the key. Note that breeding males in some species can develop uniformly dark rear bodies and fins, obscuring the marking patterns on the anal and caudal fins.

1a. Abdomen and pectoral-fin base scaly; scales in row above rear pored scales much larger than in adjacent row above …...….…………..……...2

1b. Abdomen and pectoral-fin base naked; two scale rows above rear pored scales about equal size...............4

2a. First dorsal fin long and banner-like, first spine when depressed reaching past base of second spine of second fin (>17% SL) and with 4–6 dark (colored) bands; lateral-line pored scales usually 11 (10–12); pectoral-fin rays usually 14 (13–15); last body bar about same intensity as preceding bars and usually a vertical rectangle with an indented anterior upper corner (i.e. narrower at top than middle); usually six or more dark patches along anal fin; in life, mid-body bars edged with prominent dark-rimmed orange spots (Bahamas & Caribbean)..*E. altivelis*

2b. First dorsal fin short, first spine when depressed not reaching base of second spine of second fin (<14% SL) and with two dark bands (if banded); lateral-line pored scales usually 13 (12–14); pectoral-fin rays usually 15 (14–16); last body bar much darker than preceding bars, not indented; fewer than six dark patches along anal fin; in life, no prominent dark-rimmed orange spots along edges of mid-body bars.........................3

3a. Preoperculum behind eye with several scales; prominent dark bar below eye; series of dark spots along pored lateral-line; last body bar narrow-rectangular to square with corners well-rounded; rear body frequently orange to bright red in life (Florida, Bahamas, Caribbean)...……......…..……......*E. pectoralis*

3b. Preoperculum behind eye usually naked, rarely one or two scales; no prominent dark bar below eye; no dark spots along pored lateral-line; last body bar a wide rectangle with squared corners; rear body not orange to bright red in life (Bahamas to Puerto Rico, Providencia)..*E. jordani*

4a. Long sloping snout, horizontal distance forward of eye about equal to eye diameter; preorbital flange smooth (at most a few small spines along preorbital ridge on largest fish); first dorsal fin long, first spine when depressed usually reaching past base of second spine of second fin; last three body bars about equal intensity (in preservative) with anterior margin of last bar sloping down and back (bar wider dorsally); 13 pored lateral-line scales (Bahamas & Caribbean)..*E. atrorus*

4b. Blunt snout, horizontal distance forward of eye usually much less than eye diameter; preorbital flange spiny; first dorsal fin usually short, first spine when depressed usually not reaching base of second spine of second fin (exceptions in large males and *E. matador*); last one or two body bars distinctly darker than preceding bars (except some *E. wilki*); 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 patches at base of membranes of second dorsal fin; males with second dorsal fin broadly speckled black and head and body bright red in life (W. Caribbean, Greater and Lesser Antilles)..................................*E. matador* n. sp.

5b. Caudal fin with dark or dusky-red bands; three dark patches at base of membranes of second dorsal fin.....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 (particularly Bahamas and VI populations); no accessory interspace bar or dark patch in 4–5 interspace; no red bar at base of caudal fin following last body bar; four or five dark patches along anal fin (Florida, Bahamas, N. & W. Caribbean, & Antilles south 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. Last two body bars much darker than preceding bars; dusky red bar after last body bar variably present; two broad unbroken dark bands on caudal fin; three or four dark patches along anal fin (Dominica to S. Netherlands Antilles)..*E. deloachorum* n. sp.

7b. Last two body bars not much darker than preceding bars; dusky red bar after last body bar; often three or more and/or broken dark or dusky red bands on caudal fin; often six dark patches along anal fin (Dominica to St. Vincent)..*E. wilki* n. sp.

TABLE 1

	Dorsal fin spines			Dorsal fin soft rays			Anal fin soft rays		
	XI	XII	XIII	7	8	9	15	16	17
E. matador	1	17			8	10		9	9
E. wilki	2	9	1	1	9	2	1	9	2
E. deloachorum		3	2		1	4		3	2
E. boehlkei	2	21	1	4	17	3	1	23	

	Pored scales				Notched scale series							
	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	

Table 1. Table of meristic values for type specimens of three new species of *Enneanectes* and *E. boehlkei*. Scale counts include both sides, but only fully intact scale series are counted (some collections have few intact series). Pectoral fin-ray counts are almost always 15 and do not vary among species and are not included. Notched-scale series counts include unnotched scales within the series, thus higher than counted by Rosenblatt (1960). Only *E. boehlkei* specimens from the Virgin Islands are included in the table, presumably representative of the type population from the Bahamas (counts are about the same as those in the original description which comprised mostly Bahamian and Virgin Islands specimens): other populations from the Western Caribbean may not have identical counts.

Figure 1. *Enneanectes matador*, 15.7 mm SL male holotype, UF 185600, ethanol preserved, Roseau, Dominica.

Enneanectes matador, n. sp.

Figures 1–9; Table 1.

Enneanectes boehlkei [*non* Rosenblatt] Collette *et al*. 2003: 118, figure 122 (Navassa, a small island between Hispaniola and Jamaica).

Holotype. UF 185600, 15.7 mm SL, male, Dominica, Roseau (15.28°, -61.38°), B. Victor, July 12, 2011.

Paratypes (17 specimens, 9.4–20.7 mm SL). UF 164454 (1, 14.6) U.S. Virgin Islands, St. Croix, Buck Island (17.796°, -64.591°), R. Spieler, T. Quinn, and P. Arena, Apr. 2, 2005; UF 164465 (2, 18–18.5) U.S. Virgin Islands, St. Croix, Buck Island (17.796°, -64.591°), D. Gilliam, L. Jordan, and B. Basten, Apr. 2, 2005; UF 164467 (2, 15.8–16) U.S. Virgin Islands, St. Croix, Buck Island (17.796°, -64.596°), D. Gilliam, L. Jordan, and J. Freeman, Apr. 3, 2005; UF 184841 (3, 16.4–17.7) U.S. Virgin Islands, St. Croix, Buck Island (17.796°, -64.595°), R. Spieler, P. Arena, and T. Quinn, Apr. 3, 2005; UF 185609 (3, 10.6–21) Panama, Colon, Mogote Afuera (9.637°, -79.524°), B. Victor, D. R. Robertson, J. Van Tassell, and L. Tornabene, May 29, 2007; UF 185608 (3, 14.1–19) Panama, Colon, Salmedina (9.563°, -79.696°), B. Victor, D. R. Robertson, J. Van Tassell, and L. Tornabene, May 31, 2007; UF 185607 (1, 9.4) U.S. Virgin Islands, St. Thomas, Outer Brass Island (18.396°, -64.976°), B. Victor and T. Smith, May 2, 2009; UF 185603 (1, 14.7) Dominica, Roseau (15.28°, -61.38°), B. Victor, July 17, 2011; UF 183137 (1, 20.7) U.S. Virgin Islands, St. Croix (17.734°, -64.610°), H. Jelks, W. Smith-Vaniz, W. Coles *et al*., Jan. 25, 2012.

Diagnosis. A species of *Enneanectes* with belly, pectoral-fin base, and cheek naked, spiny preorbital bone in adults, blunt snout, three rows of scales above rear pored scales, first two rows about equal-sized, relatively short first dorsal fin (all characters of *E. boehlkei* complex); red-barred or all-red caudal fin with no duskiness, dark bars, or black shading (or any concentrations of melanophores visible under microscopy); in life, white-black-red-white-red color bands extend from caudal peduncle rearward (in breeding males caudal fin can be all red); fifth body bar darker than preceding bars and usually narrower than preceding pale interspace; second dorsal-fin membranes with broad band of fine speckling covering most of fin membranes (more than outer half) and no distinct rounded dark spots near spine bases; fin rays D III+XII+8–9 and A II, 16–17; mode of 14 pored lateral-line scales and 22 scales in notched midline row.

Description. Body somewhat stout and elongate, body depth 20–24 (21)% SL, body width 17–23 (17)% SL; predorsal distance short, 24–29 (27)% SL; prepelvic distance shorter, 22–24 (22)% SL; preanal distance 47–54 (50)% SL; caudal peduncle length 11–16 (13)% SL, caudal peduncle depth 8–11 (10)% SL. Head short, large, and relatively deep, head length 29–34 (30)% SL; head depth (at midpoint of orbit) 17–20 (17)% SL or 54–68 (57)% HL; snout short and blunt, sloping sharply downward in front of eye, snout span 17–27 (21)% HL; eye large, orbit diameter 31–39 (38)% HL; single short flat tab-like orbital cirrus, longer than wide, tip narrowly to

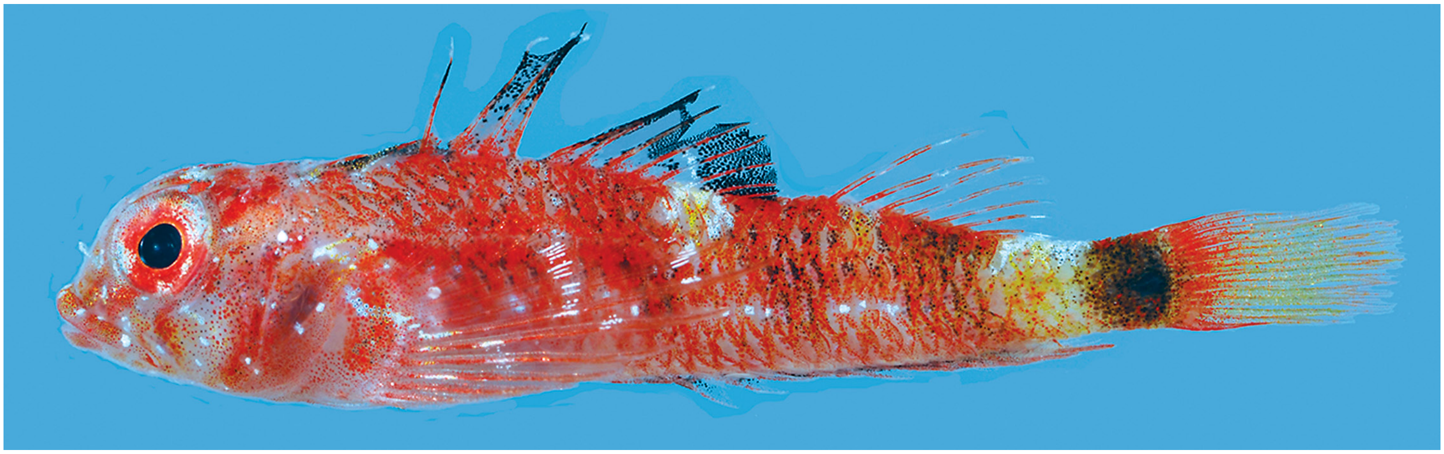

Figure 2. *Enneanectes matador*, paratype, 20.7 mm SL, UF 183137, St. Croix, U.S. Virgin Islands, male in breeding colors; photo by Howard L. Jelks.

broadly rounded (occasionally a wide point), speckled black, at most reaching just past vertical through rear orbital rim (usually shorter); interorbital narrow, mostly flat, width 9–12 (12)% HL; posterior orbital flange spiny, interorbital spiny, anterior orbital flange from minimally spiny to spiny; pores in rows around eye and in series along preopercle and mandible with single pore behind mandibular symphysis; mouth large, upper-jaw extending back past vertical through midpoint of eye, oblique length 31–44 (36)% HL (higher in larger and male fish); upper and lower jaws with variable-sized caniniform teeth, in multiple irregular rows with outermost largest; irregular vomerine tooth patch, no palatine teeth; anterior nostril a low tube with a speckled fingerlike cirrus about three times nostril diameter, posterior nostril an elliptical opening adjacent to orbital rim; 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.

Three dorsal fins, first two spinous, dorsal-fin rays III+XII+8–9; anal-fin rays II, 16–17; pectoral-fin rays 15; two pelvic-fin rays. Short first dorsal fin, in females all three spines when depressed reaching back to between base of first and second spine of second fin, in males first spine can be moderately extended, reaching back to base of 3rd or 4th spine, first dorsal-fin spine 10–18 (16)% SL, second spine 9–15 (13)% SL, third spine 6–10 (8)% SL; third spine of second dorsal fin 14–17 (14)% SL; third dorsal fin usually with unbranched soft rays (occasional branching in large fish), third ray 12–18 (16)% SL; anal-fin base long, 38–43 (40)% SL, with two short spindly spines rooted close together, second slightly longer than first and about half length of first ray, soft

Figure 3. *Enneanectes matador*, Antigua, note finely speckled membranes of the second dorsal fin; photo by Jason Phillip.

rays unbranched, antepenultimate ray longest 11–14 (12)% SL; pectoral fin long, 35–42 (39)% SL, uppermost 2–3 rays unbranched, lowermost two rays especially stout; inner pelvic-fin ray longest, 24–28 (25)% SL; caudal fin truncate, length 21–31 (24)% SL, 14–15 segmented caudal-fin rays, one or two uppermost and two or three lowermost unbranched, 4–7 upper and 3–5 visible lower procurrent rays.

Body covered with large ctenoid scales, except naked belly and pectoral-fin base; head generally unscaled, both operculum and cheek naked; fins bare except for about three large flat cycloid scales covering lower caudal-fin rays. Scales between lateral line and second dorsal-fin base in three rows, lower two about equal, dorsalmost small. Lateral line made up of anterior segment of 13–16 tubed scales above and partially overlying discontinuous posterior segment lying along lateral midline comprising 20–23 (one specimen with 16, mode of 22) mostly notched scales (frequently one unnotched scale after first notched scale) extending to caudal-fin base (two largest males from Panama have many unnotched scales in series).

Color in preservative. All color is lost in formalin except for dark melanophore pigment, while in ethanol some red erythrophores are frequently preserved (after two years in ethanol for Figs. 1,4 & 6). The background is pale to yellow (translucent in life) with a speckled dark overlay, mostly outlining individual scales, denser on the dorsal half, with the belly typically unmarked except for a few erythrophores edging the peritoneum and on the abdomen (pale in formalin), in contrast to other species where there can be deep melanophores at this location (Fig. 6). Overlying the speckling on the body are five dark bars, the first behind the pectoral-fin base and the fifth at the end of the caudal peduncle. The first four bars are somewhat slanted down and backwards and frequently fade away toward the ventral midline. The relative intensity of the five bars is an important taxonomic character and is conserved in well-preserved specimens. In *E. matador*, the first dark bar is least distinct, the next three are about equal in intensity and the fifth bar is darkest. The fifth bar is mostly rectangular, abruptly stopping at the base of the caudal-fin rays, and usually narrower than the pale interspace between the fourth and fifth bars. The caudal fin is transparent and unmarked, with at most a few isolated melanophores scattered close to the edge of the fifth bar.

The cranium is mostly covered in erythrophores (pale in formalin), but some fish have an additional dark-shaded overlay over the dorsal head, including the midline and edges of the cranium (Fig. 4), sometimes outlining

Figure 4. *Enneanectes matador*, center, compared with *E. wilki* (left) and a lightly marked *E. boehlkei* (right). Note cranium with predominantly erythrophores in *E. matador*. All fish preserved similarly in ethanol (Dominica, Dominica, and St. John).

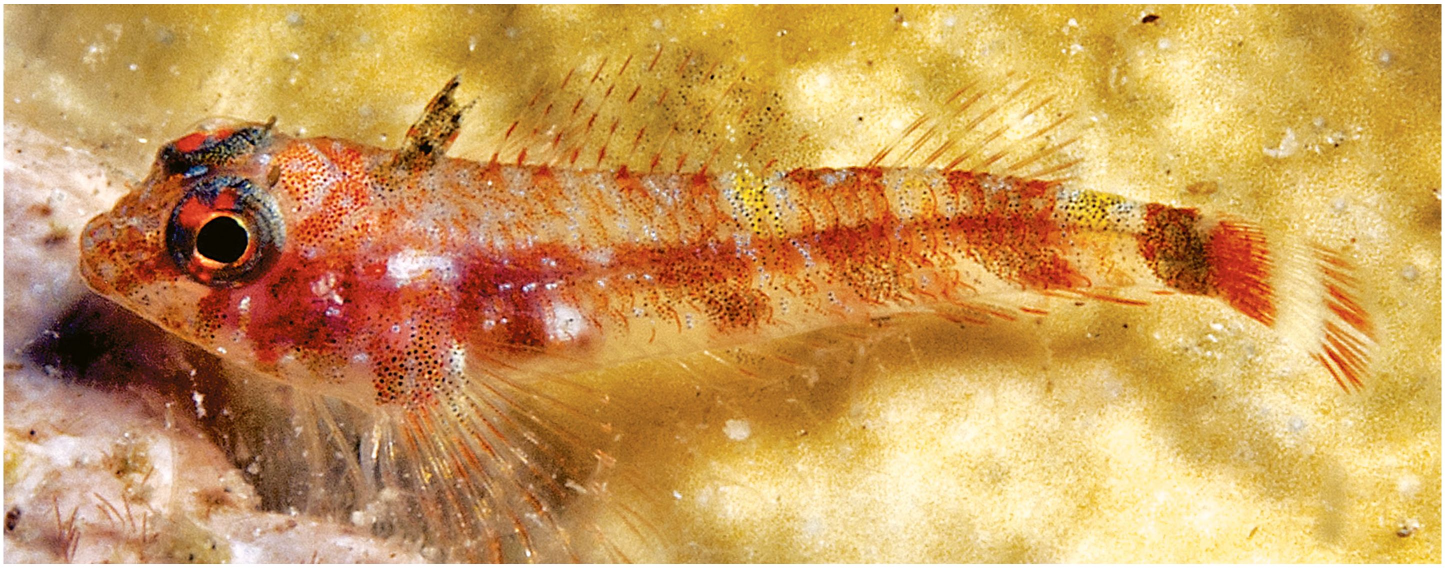

Figure 5. *Enneanectes matador*, Dominica; photo by Paul Humann.

rounded pale spaces that represent the bleached large erythrophores. The orbital cirrus remains darkly speckled or black. The iris is dark with bright red patches in a radiating-spoke pattern (uniform in faded specimens). There are patches of melanophores over the pectoral-fin base, the operculum, and preopercle with a darker bar along the outer preoperculum. A dark bar extends down below the eye and the snout and front half of the jaws are shaded with melanophores. The underside of the head is pale. Some specimens have very sparse melanophore shading overall, replaced with erythrophores (in life and ethanol).

The first two membranes of the first dorsal fin are uniformly dark, contrasting sharply with the mostly pale body. The second dorsal fin of juvenile and smaller adults has only a distal band of melanophores, on larger fish the band is wider, typically more than half-way down the membranes. The third dorsal fin and pectoral fins are

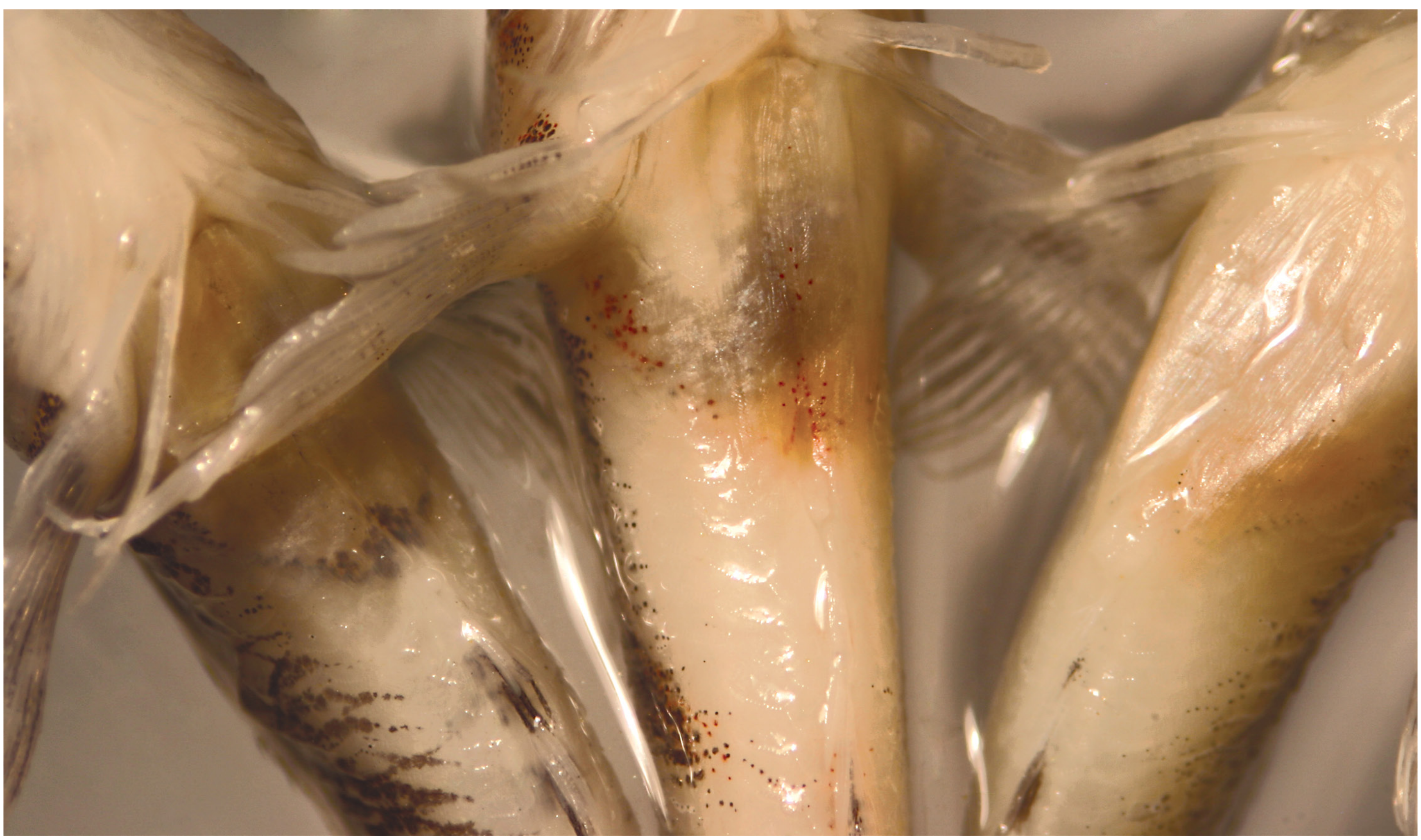

Figure 6. *Enneanectes matador*, center, compared with *E. wilki* (left) and a lightly marked *E. boehlkei* (right). Note abdomen edged with erythrophores in *E. matador*. All fish preserved similarly in ethanol (Dominica, Dominica, and St. John).

mostly transparent and crossed with a few dark bands. The caudal fin is transparent, with no dark or dusky bands, even in darker individuals. The anal fin has four or five spaced dark patches of sparse to moderate collections of melanophores along the fin membranes. In breeding males, the second dorsal fin is broadly speckled black and the anal-fin dark patches can merge, but notably the caudal fin remains transparent.

Color in life. The predominant color is red to reddish-orange with a variable degree of dark shading, ranging from fish that are almost entirely red to the rare individual with dark body bars and a dark head (but still with a purely red or red-barred caudal fin). The rear end of the fish has a characteristic series of color bands starting on the caudal peduncle in the array of white-black-red-white-red: the last body bar on the caudal peduncle is dark to black highlighted by a white band in front and a bright red band behind, then the red band on the base of the caudal fin is typically followed by a bright white band and a second red band. The entire caudal fin can be red on breeding males. The iris has gold ringing the pupil and bright-red spoke-like patches and there are bands of red covering the top of the head and snout. Some fish show additional prominent blue spots and bands on the head and rows of bluish-white rounded spots over the body (Fig. 7). The orbital cirrus ranges from white in lightly marked fish to black in larger fish and breeding males.

The first dorsal fin ranges from white in smaller lightly marked fish, especially those with mostly red to pink shading, to black in darker fish and breeding males with extended first spines. The second dorsal fin can be mostly unmarked in small fish, developing a broad band of melanophores along the outer half of the membranes in adult fishes and densely speckled black on most or all of the fin membranes in larger fish and breeding males. The pectoral fins are transparent to red with white and yellow thin banding.

Barcode sequence. A 652-nucleotide sequence of the section of the mitochondrial COI gene used for barcoding by the BOLD informatics database (Ratnasingham & Hebert 2007) was obtained for the holotype and some paratypes (Genbank accession numbers in Appendix 1). Following the database management recommendation of the BOLD the sequence of the holotype is presented here as well:

CCTCTACCTCGTATTCGGTGCTTGAGCTGGGATAGTAGGAACCGCCTTAAGCCTGCTTATCCGTGCA
GAACTTAGCCAGCCCGGCGCTCTTCTCGGAGACGACCAAATCTACAACGTTATCGTTACAGCCCAC
GCCTTTGTAATGATTTTCTTTATAGTAATGCCTATTCTTATTGGAGGTTTCGGTAACTGACTTATTCCC
CTAATGATCGGAGCGCCTGATATAGCATTCCCCCGAATGAACAACATGAGCTTTTGGCTTCTCCCTC
CCTCTTTCCTCCTCCTGCTGGCCTCTTCTGGGGTTGAAGCCGGAGCCGGGACTGGTTGAACAGTTT
ACCCTCCCCTGTCCGGCAACCTCGCCCATGCAGGGGCCTCCGTAGACCTAACAATCTTTTCTCTCC
ACTTAGCTGGTATCTCCTCTATTCTCGGTGCAATTAACTTTATCACCACTATCATTAATATGAAACCTC
CAGCTATCACGCAGTATCAAACACCACTGTTTGTATGAGCCGTGCTAATCACTGCTGTCCTTCTCTT

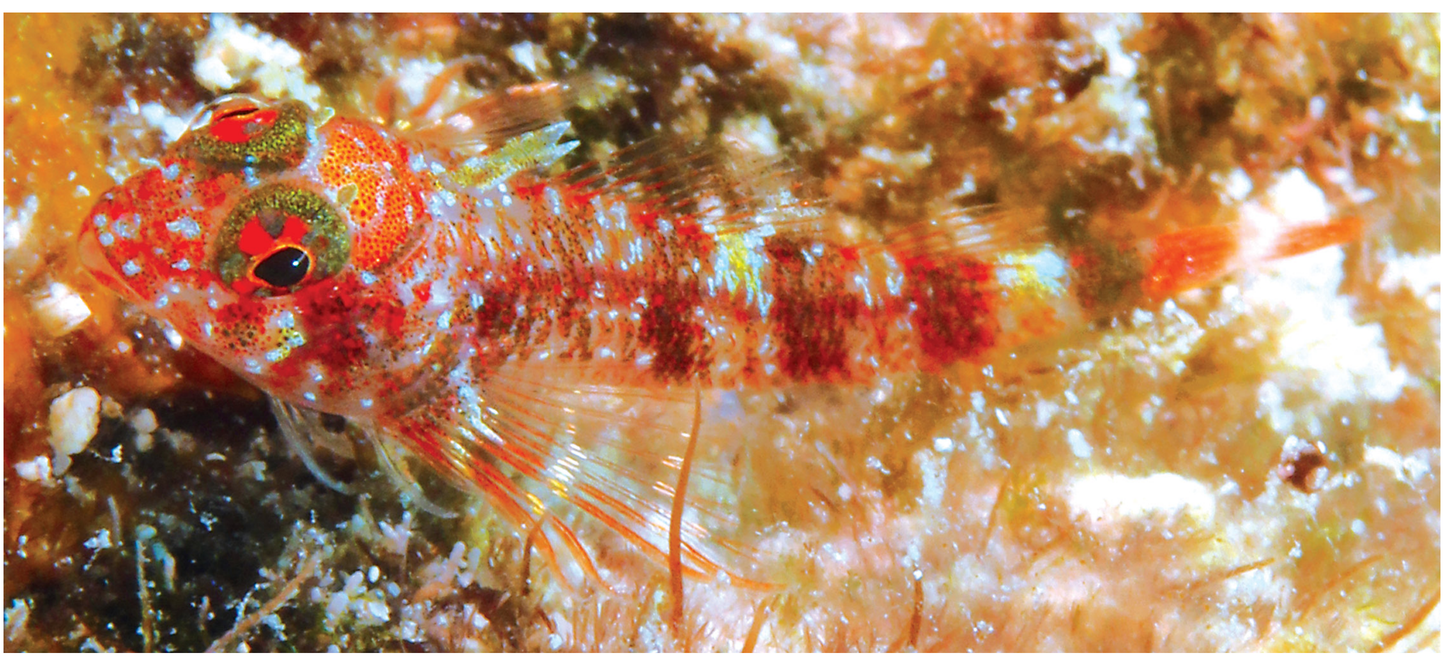

Figure 7. *Enneanectes matador*, Antigua; photo by Jason Phillip.

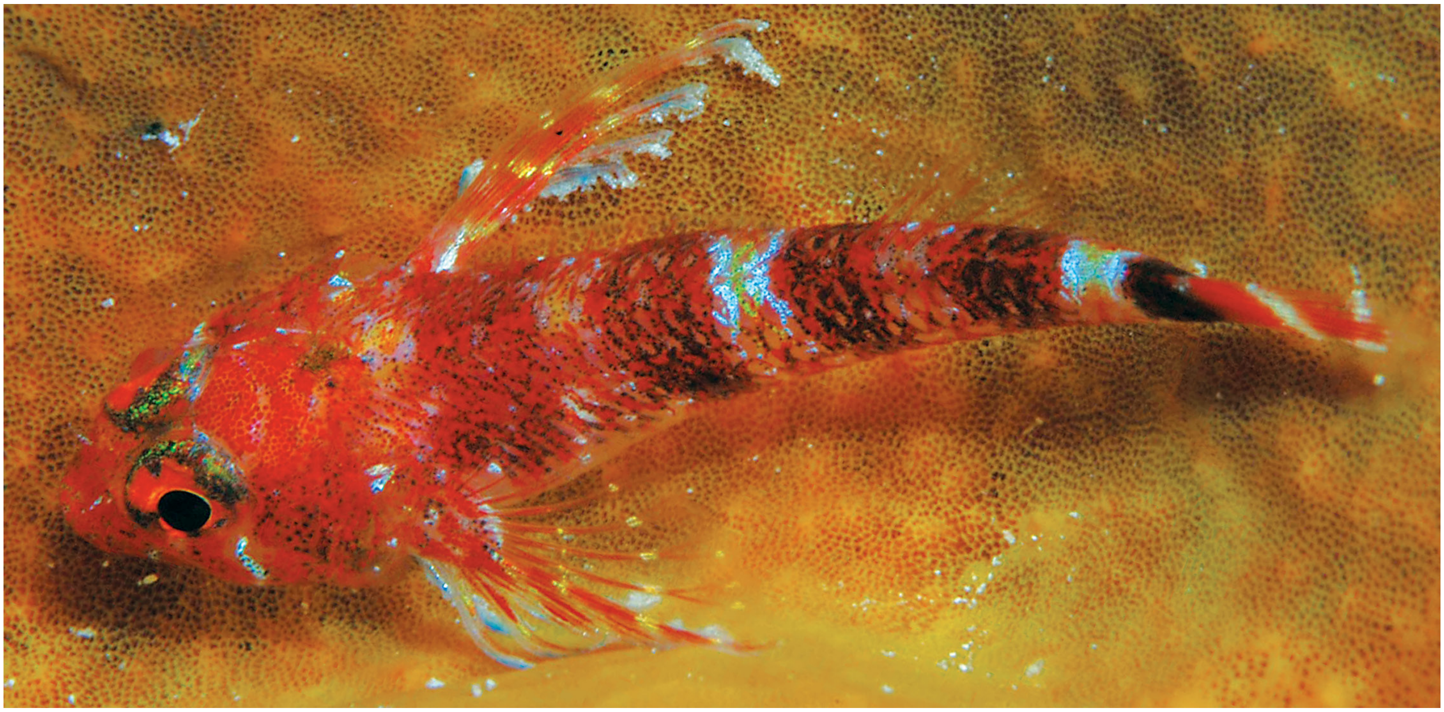

Figure 8. *Enneanectes matador*, Mona Island, Puerto Rico; photo by Keri Wilk.

ACTTTCCCTTCCGGTTCTTGCTGCAGGGATTACAATACTCCTGACAGACCGCAACCTAAACACCAC
ATTCTTTGACCCTGCTGGAGGAGGAGACCCCATTCTCTACCAACATCTC

Distribution. Type specimens have been collected from Dominica, the Virgin Islands, and Panama. Barcode mtDNA sequences in the BOLD database with somewhat close matches to the type specimens have been collected from Honduras, Belize, and Tobago (the latter two sites by Carole Baldwin *et al*.); but, because of the slight divergences of those lineages, they are not treated as types. The illustration of a 22.3 mm SL "*E. boehlkei*" from Navassa Island by Collette *et al*. 2003 matches *E. matador* in male breeding colors. Underwater photographs of red-tailed triplefins have been taken in Belize (Jack Randall), Bay Islands of Honduras (Les and Keri Wilk, Brad Ryon), Mona Island (Les and Keri Wilk), Puerto Rico (Paul Humann), Isla Aves (Juan Posada and Oscar Lasso-Alcala), St. Martin (Mark Yokoyama), Antigua and St. Kitts (Jason Phillip and Jim Garin), and Dominica (Ned Deloach and Paul Humann).

Etymology. Named for the bright red tail used in displays; the specific epithet is a noun in apposition. The common name Matador Triplefin is proposed.

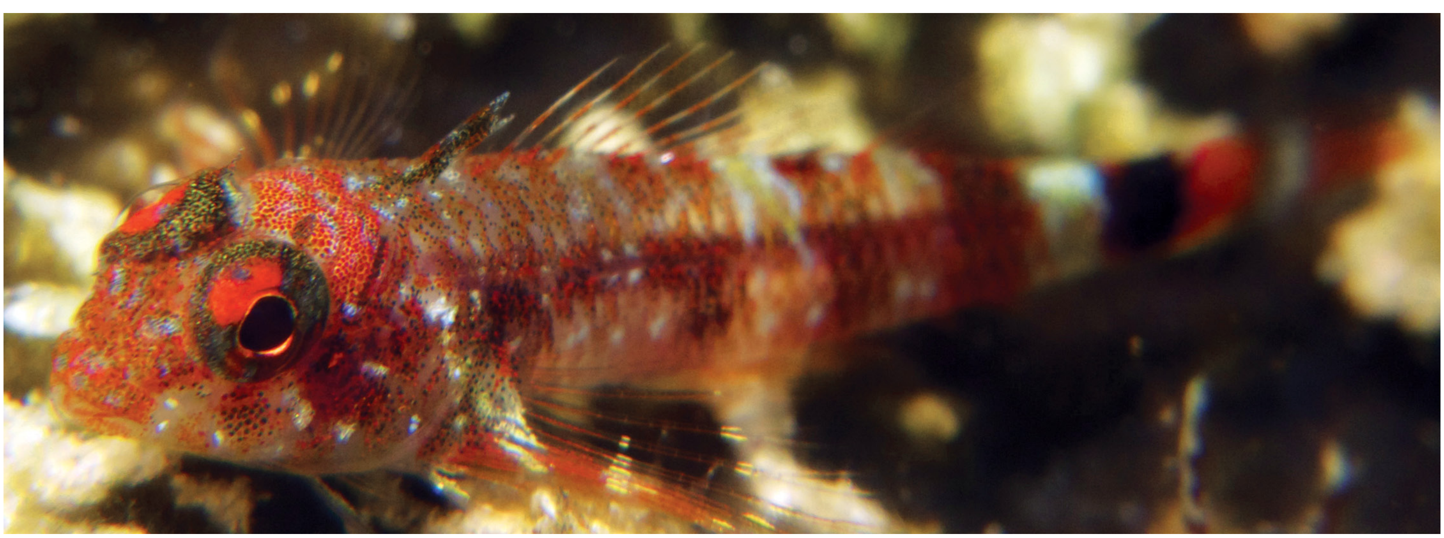

Figure 9. *Enneanectes matador*, St. Kitts, cranial pigment all erythrophores, dark orbital cirrus; photo by Jason Phillip.

Figure 10. *Enneanectes wilki*, 15.8 mm SL female holotype, UF 185610, ethanol preserved, Roseau, Dominica.

Enneanectes wilki, n. sp.

Figures 4, 6, 10–16; Table 1.

Holotype. UF 185610, 15.8 mm SL, female, Dominica, Roseau (15.28°, -61.38°), B. Victor, July 15, 2011.

Paratypes (11 specimens, 8.7–16.7 mm SL). UF 185604 (4, 13.7–16.7) Dominica, Roseau (15.28°, -61.38°), B. Victor, July 11, 2011; UF 185601 (3, 13.7–14.7) Dominica, Roseau (15.28°, -61.38°), B. Victor, July 12, 2011; UF 185635 (1, 8.7) Dominica, Roseau (15.28°, -61.38°), B. Victor, July 18, 2011 UF 185611 (3, 13.4–15.9) Dominica, Roseau (15.28°, -61.38°), B. Victor, July 22, 2011.

Diagnosis. A species of *Enneanectes* with belly, pectoral-fin base, and cheek naked, spiny preorbital bone in adults, blunt snout, three rows of scales above rear pored scales, first two rows about equal-sized, relatively short first dorsal fin (all characters of *E. boehlkei* complex); fifth body bar usually slightly darker than first four (not much darker than fourth) and usually narrower than 4–5 interspace; accessory interspace bar or darkened patch between the fourth and fifth body bars (yellow-ringed with dark-speckled center in life, especially ventrally); dusky red bar just behind fifth body bar; dark or dusky red bands on caudal fin, usually more than two, often broken; usually no pale band dividing dark snout forward of eye; second dorsal fin with three rounded dark spots on membranes near spine bases and thin band of fine speckling on outer rim of fin; anal fin with four to six dark patches; modal fin rays D III+XII+8 and A II, 16; mode of 14 pored lateral-line scales and 22 scales in notched midline row.

Description. Body somewhat stout and elongate, body depth 19–23 (21)% SL, body width 16–19 (19)% SL; predorsal distance short, 24–29 (26)% SL; prepelvic distance shorter, 22–26 (22)% SL; preanal distance 49–59 (54)% SL; caudal peduncle length 13–16 (13)% SL, caudal peduncle depth 8–10 (8)% SL. Head short, large, and relatively deep, head length 30–34 (30)% SL; head depth (at midpoint of orbit) 16–19 (16)% SL or 49–55 (53)% HL; snout short and blunt, sloping sharply downward in front of eye, snout span 16–22 (19)% HL; eye large, orbit diameter 35–38 (38)% HL; single short flat tab-like orbital cirrus, longer than wide, tip narrowly to broadly rounded (occasionally a wide point), speckled black, at most reaching just past vertical through rear orbital rim (usually shorter); interorbital narrow, mostly flat, width 7–13 (13)% HL; posterior orbital flange spiny, interorbital spiny, anterior orbital flange from minimally spiny to spiny; pores in rows around eye and in series along preopercle and mandible with single pore behind mandibular symphysis; mouth large, upper-jaw extending back past vertical through midpoint of eye, oblique length 36–39 (36)% HL; upper and lower jaws with variable-sized caniniform teeth, in multiple irregular rows with outermost largest; irregular vomerine tooth patch, no palatine teeth; anterior nostril a low tube with a speckled fingerlike cirrus about three times nostril diameter, posterior nostril an elliptical opening adjacent to orbital rim; 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.

Three dorsal fins, first two spinous, strong modal fin-ray count III+XII+8; anal-fin rays II, 16; pectoral-fin rays

Figure 11. *Enneanectes wilki*, Dominica, with white-predominant markings; photo by Jason Phillip.

15 (one with 16); two pelvic-fin rays. Short first dorsal fin with all three spines when depressed reaching back to between base of first and third spine of second fin; first dorsal-fin spine 13–15 (15)% SL, second spine 9–11 (11)% SL, third spine 7–9 (8)% SL; third spine of second dorsal fin 13–16 (15)% SL; third dorsal fin with unbranched soft rays, third ray 14–16 (14)% SL; anal-fin base long, 36–41 (38)% 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 9–13 (11)% SL; pectoral fin long, 33–41 (33)% SL, uppermost 2–3 rays unbranched, lowermost two rays especially stout; inner pelvic-fin ray longest, 25–30 (26)% SL; caudal fin truncate, length 22–26 (25)% SL, 14–15 segmented caudal-fin rays, one or two uppermost and two or three lowermost unbranched, 4–7 upper and 3–5 visible lower procurrent rays.

Body covered with large ctenoid scales, except naked belly and pectoral-fin base; head generally unscaled, both operculum and cheek naked; fins bare except for about three large flat cycloid scales covering lower caudal-fin rays. Scales between lateral line and second dorsal-fin base in three rows, lower two about equal, dorsalmost small. Lateral line made up of anterior segment of 13-16 tubed (raised) scales (mode of 14) above and partially overlying discontinous posterior segment lying along lateral midline comprising 20–23 (mode of 22) mostly notched scales (frequently one unnotched scale after first notched scale) extending to caudal-fin base.

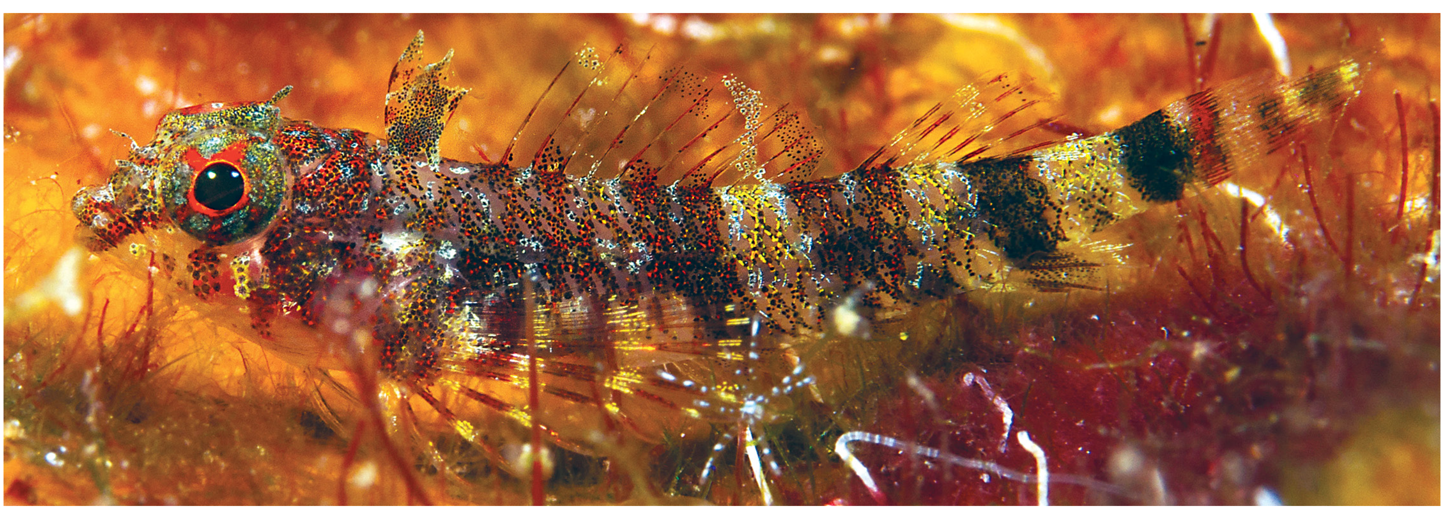

Figure 12. *Enneanectes wilki*, Dominica, note three reddish/dusky bands on the caudal fin; photo by Kris Wilk.

Figure 13. *Enneanectes wilki*, Dominica, with predominant dark markings, note dark patches at the base of the membranes of the second dorsal fin and no pale stripe dividing dark band from eye to front of upper jaw; photo by Kris Wilk.

Color in preservative. All color is lost after preservation except for dark melanophore pigment over a pale to yellow background (translucent in life). There is a speckled overlay, mostly outlining individual scales producing a distinct crosshatch pattern over the body. The belly is typically unmarked except for the edges of the dark peritoneum showing through along the flanks and in a V forward of the anus. Overlying the speckling on the body are five dark bars, the first behind the pectoral-fin base and the fifth at the end of the caudal peduncle. The bars are widest dorsally and slanted down and slightly backwards. The relative intensity of the five bars is an important taxonomic character and is conserved in well-preserved specimens. In *E. wilki*, the fifth bar is somewhat darker than the preceding bars, which are about equal. Notably, there is an intervening small dark bar or patch between the fourth and fifth bars (the accessory "interspace bar") often extending the full width of the body, but sometimes incomplete dorsally. The fifth bar is mostly rectangular and relatively narrow, extending a short way back to cover the base of the caudal-fin rays. The width of the fifth bar is typically less than the full space between the fourth and fifth bars.

The head is darkly marked, mostly on the dorsal half, with a pale underside including jaws, branchiostegals, and isthmus (except the front tip of the mandible is dark). The cranium is covered by a dense covering of melanophores and dark shading extends over the interorbital and snout. Usually the front of the snout is uniformly dark after preservation, without a pale stripe dividing the dark band running obliquely down from the front of the eye at 8-o'clock over the nasal area to cross the front of the upper jaw (occasional very lightly marked individuals may show a paler band and live fish often have a superficial white spot at that location on the upper jaw). The orbital cirrus is darkly speckled or black. The iris is dark with pale to reddish patches in a radiating-spoke pattern (uniform in faded specimens). The cheek and gill cover have dark patches, especially under the eye and on the operculum, with some individuals extensively speckled over that area, and the pectoral-fin base is fully shaded.

The first two membranes of the first dorsal fin are usually uniformly darkly shaded, while the second dorsal fin has the basic *E. boehlkei*-pattern made up of a narrow dark-speckled edge (less than the distal third of the first six spinous membranes at least, but often true for all but the last two membranes) and three dark spots (rounded patches of melanophores) at the base of the 2–3rd, 6th, and 8th membranes (often the latter two displaced forward to the 5th and 7th). The third dorsal fin and pectoral fins are mostly transparent and crossed with a few dark bands. The anal fin often has six spaced-apart dark patches on the fin membranes, but 4 or 5 are frequently encountered. The caudal fin has a series of dark bands often 3, sometimes with gaps interrupting the vertical continuity of the bars ("broken bands"). In breeding males, the posterior body and caudal fin become darkly shaded (progressively obscuring the anal-fin patches and the caudal-fin bands), but the distal dark edge of the second dorsal fin only expands up to at most half the length of the first six membranes, leaving the characteristic patches at the base of the membranes distinct.

Color in life. Live fish show the same dark patterns described for preserved fish but have additional red, white, gold, and sometimes blue components. The iris has gold ringing the pupil and bright red spoke-like patches

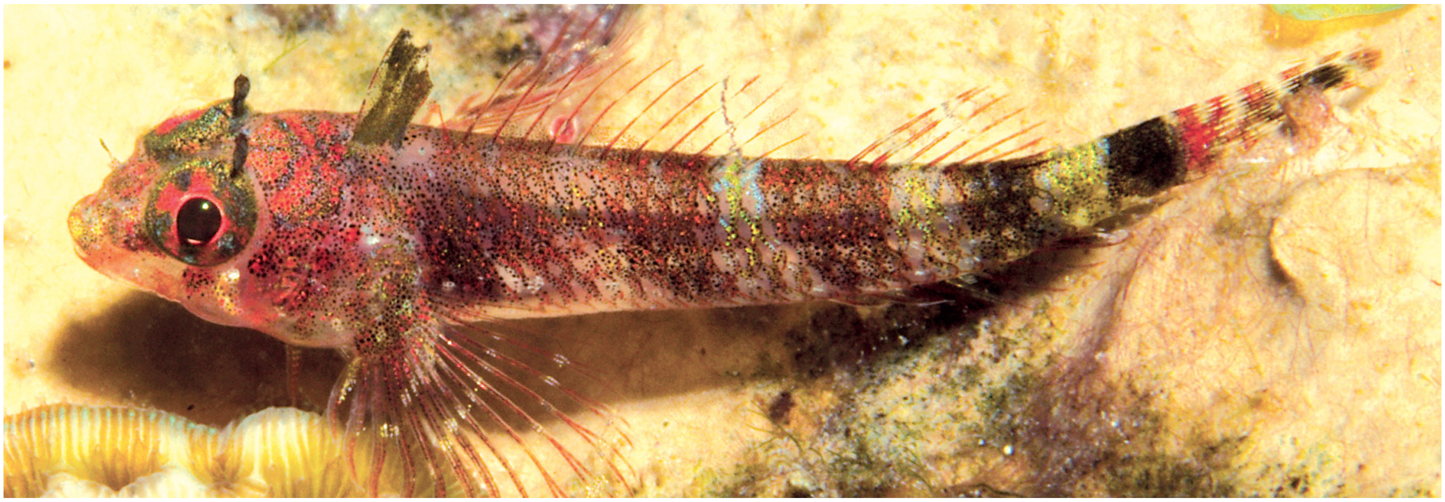

Figure 14. *Enneanectes wilki*, St. Vincent, note broken bands on caudal fin; photo by Ray Haberman.

and there are bands of red underlying the dark markings on top of the head and snout. Live specimens have an iridescent white spot overlying the dark shading on the upper lip, frequently with one or two more towards the eye, overlying the location of the pale stripe from the eye that is distinct in other species; these spots are typically lost in preservative leaving an undivided dark band across the snout and upper jaw (the other species typically retain a pale stripe dividing the dark band in preservative). There is a characteristic dusky red bar at the base of the caudal fin typically separated from the preceding dark fifth body bar by a whitish round patch on the upper fin base and sometimes on the lower fin base, to a lesser degree. The dark or dusky-red bands on the caudal fin, often three or more, can be broken or, if not broken, at least not evenly rectangular, and the intervening clear zones can show as white. Lightly marked fish have white predominating over the dark shading on the first dorsal fin and the fin can flash bright white. In addition, a prominent thin white bar on the rear second dorsal fin can show prominently. The pectoral fins are frequently white or yellow-banded. The pale areas between the body bars can be highlighted with white and are usually laced with yellow and gold, especially over the characteristic 4–5 interspace where the mid-portion has a dark speckled patch or bar, especially developed ventrally. A series of bluish-white rounded spots are arrayed over the body. There can be a blue iridescence to the light round spots over the head, particularly highlighting the darker bands over the cranium and the dark patches on the iris.

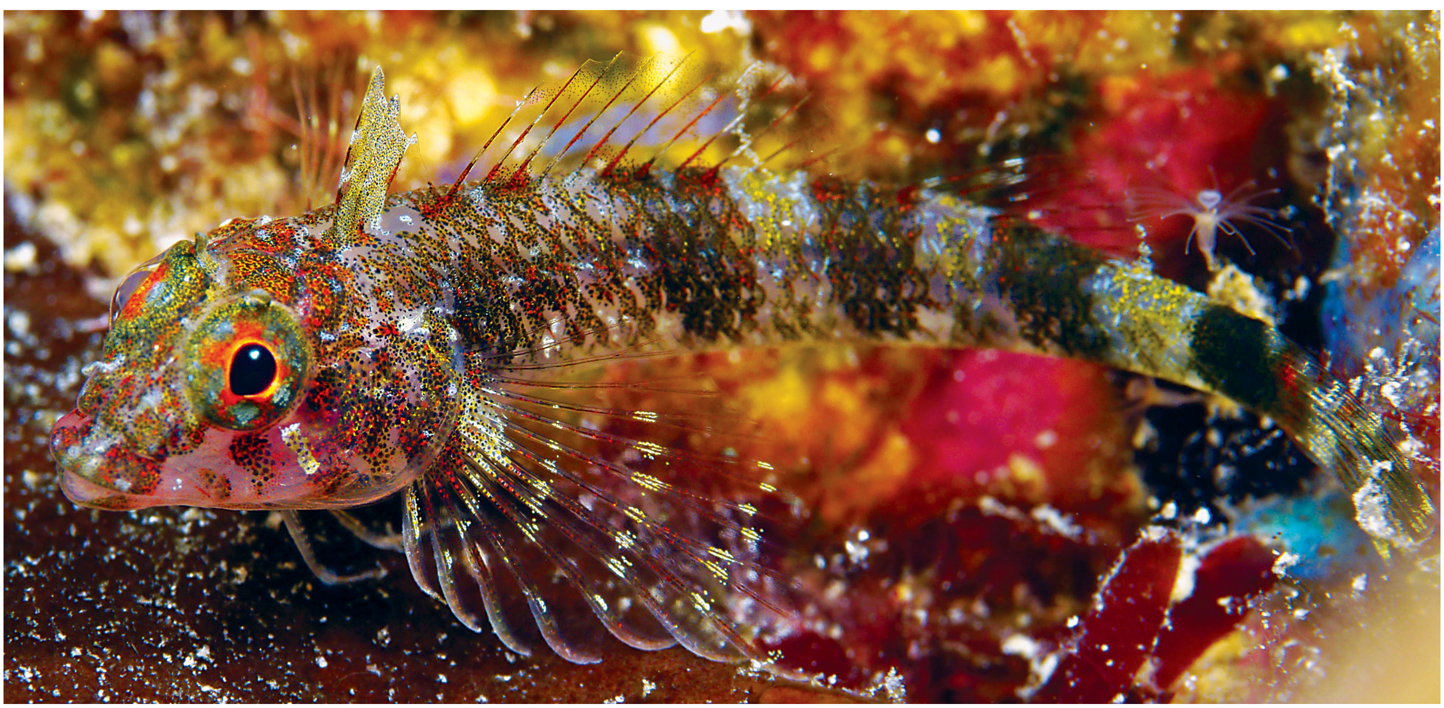

Figure 15. *Enneanectes wilki*, Dominica; photo by Kris Wilk.

Barcode sequence. A 652-nucleotide sequence of the section of the mitochondrial COI gene used for barcoding by the BOLD informatics database (Ratnasingham & Hebert 2007) was obtained for the holotype and paratypes (Genbank accession numbers in Appendix 1). Following the database management recommendation of the BOLD the sequence of the holotype is presented here as well:

CCTTTACCTCGTATTCGGTGCTTGAGCTGGAATAGTAGGAACCGCCCTAAGCCTGCTTATCCGAGCT
CAGCCAGCCCGGCGCCCTTCTCGGAGACGACCAAATTTACAACGTTATCGTTACAGCCCACGCCTT
TGTAATGATTTTCTTTATAGTAATGCCCATTCTTATTGGAGGTTTTGGTAATTGACTCATTCCGCTAAT
GATCGGGGCCCCTGATATGGCATTCCCCCGTATAAACAACATGAGCTTTTGACTTCTCCCCCCCTCT
TTCCTCCTATTACTAGCCTCCTCTGGCGTCGAAGCCGGAGCCGGGACTGGGTGGACAGTGTACCCC
CCACTGTCCGGCAATCTTGCCCATGCAGGGGCCTCCGTAGACCTAACAATCTTTTCTCTTCACTTAG
CTGGTGTATCTTCTATTCTTGGTGCAATTAACTTTATCACCACCATTATTAACATGAAGCCCCCGGCC
ATTACACAGTACCAAACACCATTATTTGTCTGAGCAGTGCTGATCACCGCCGTCCTGCTCCTTCTAT
CACTCCCAGTTCTTGCCGCAGGGATTACAATGCTCCTGACAGACCGCAACCTAAATACCACGTTCT
TTGACCCTGCTGGAGGGGGAGACCCTATTCTTTATCAACACCTC

Distribution. Type specimens have been collected from Dominica. A barcode DNA sequence in the BOLD database with a close match to the type specimens has been collected from Tobago (by Carole Baldwin *et al*.). Underwater photographs of triplefins generally corresponding to the species description have been taken in Dominica (Les and Kris Wilk, Ned Deloach, and Jonathan Lavan) and St. Vincent (Ray Haberman, Ned Deloach, and Keri Wilk).

Etymology. Named for Les Wilk in recognition of his contributions to the art of underwater photography of coral-reef animals, his development of the ReefNet underwater identification CDs, and his organization of the expedition to Dominica; the specific epithet is a noun in the genitive case. The common name of Windward Triplefin is proposed, since the species is mostly limited to that region of the Antilles.

Figure 16. *Enneanectes wilki*, St. Vincent, note multi-banded caudal fin; photo by Ray Haberman

Figure 17. *Enneanectes deloachorum*, 21.6 mm SL female holotype, UF 185602, ethanol preserved, Roseau, Dominica.

Enneanectes deloachorum, n. sp.

Figures 17–19; Table 1.

Holotype. UF 185602, 21.6 mm SL, Dominica, Roseau (15.28°, -61.38°), B. Victor, July 12, 2011.

Paratypes (4 specimens, 9–20.5 mm SL). UF 185612 (2, 9–10) Barbados, West Coast (13.3°, -59.6°), H. Valles, Aug. 1, 2004; UF 185605 (1, 20.5) Dominica, Roseau (15.28°, -61.38°), B. Victor, July 11, 2011; UF 185606 (1, 15) Dominica, Roseau (15.28°, -61.38°), B. Victor, July 11, 2011.

Diagnosis. A species of *Enneanectes* with belly, pectoral-fin base, and cheek naked, spiny preorbital bone in adults, blunt snout, three rows of scales above rear pored scales, first two rows about equal-sized, relatively short first dorsal fin (all characters of *E. boehlkei* complex); fourth and fifth body bars similarly dark and often much darker than preceding bars (which are about equal in intensity); accessory interspace bar or darkened patch between the fourth and fifth body bars; fifth bar sometimes narrower than the 4–5 interspace; two broad solid dark bands on the caudal fin; second dorsal fin with three rounded dark spots on the membranes near the spine bases and thin band of fine speckling on the outer rim of fin; anal fin with three or four dark patches; usually D III+XII–XIII+9 and A II, 16–17; mode of 15 pored lateral-line scales and 22 scales in notched midline row.

Description. Body somewhat stout and elongate, body depth 19–21 (21)% SL, body width 17–19 (19)% SL; predorsal distance short, 21–25 (24)% SL; prepelvic distance shorter, 19–20 (19)% SL; preanal distance 46–49 (49)% SL; caudal peduncle length 14–16 (16)% SL, caudal peduncle depth 8–9 (8)% SL. Head short, large, and relatively deep, head length 27–31 (27)% SL; head depth (at midpoint of orbit) 16–17 (16)% SL or 53–59 (59)% HL; snout short and blunt, sloping sharply downward in front of eye, snout span 19–22 (19)% HL; eye large, orbit diameter 33–39 (36)% HL; single short flat tab-like orbital cirrus, longer than wide, tip narrowly to broadly rounded (occasionally a wide point), speckled black, not reaching back to vertical through posterior orbital rim; interorbital narrow, mostly flat, width 9–10 (10)% HL; posterior orbital flange spiny, interorbital spiny, anterior orbital flange from minimally spiny to spiny; pores in rows around eye and in series along preopercle and mandible with a single pore behind mandibular symphysis; mouth large, upper-jaw extending back past the vertical through midpoint of eye, oblique length 39–43 (39)% HL; upper and lower jaws with variable-sized caniniform teeth, in multiple irregular rows with outermost largest; irregular vomerine tooth patch, no palatine teeth; anterior nostril a low tube with a speckled fingerlike cirrus about three times nostril diameter, posterior nostril an elliptical opening adjacent to orbital rim; 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.

Three dorsal fins, first two spinous, fin-ray count III+XII–XIII+8–9; anal-fin rays II, 16–17; pectoral-fin rays 15 (one with 16 on one side); two pelvic-fin rays. Short first dorsal fin with all three spines when depressed reaching back to base of first spine of second fin, first dorsal-fin spine 10–12 (10)% SL, second spine 9–11 (9)%

SL, third spine 13–15 (15)% SL; third spine of second dorsal fin 13–15 (15)% SL; third dorsal fin with unbranched soft rays, third ray 13–15 (14)% SL; anal-fin base long, 40–42 (40)% 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 13 (13)% SL; pectoral fin long, 33–35 (33)% SL, uppermost 2–3 rays unbranched, lowermost two rays especially stout; inner pelvic-fin ray longest, 23 (23)% SL; caudal fin truncate, length 20–24 (20)% SL, 14–15 segmented caudal-fin rays, one or two uppermost and two or three lowermost unbranched, 4–6 upper and 3–4 visible lower procurrent rays.

Body covered with large ctenoid scales, except naked belly and pectoral-fin base; head generally unscaled, both operculum and cheek naked; fins bare except for about three large flat cycloid scales covering lower caudal-fin rays. Scales between lateral line and second dorsal-fin base in three rows, lower two about equal, dorsalmost small. Lateral line made up of anterior segment of 15 or 16 tubed (raised) scales above and partially overlying discontinous posterior segment lying along lateral midline comprising 19–23 (mode of 22) mostly notched scales extending to caudal-fin base (frequently one unnotched scale after first notched scale).

Color in preservative. All color is lost after preservation except for dark melanophore pigment over a pale to yellow background (translucent in life). There is a speckled overlay, mostly outlining individual scales producing a distinct crosshatch pattern over the body. The belly is typically unmarked except for the edges of the dark peritoneum showing through along the flanks and in a V forward of the anus. Overlying the speckling on the body are five dark bars, the first behind the pectoral-fin base and the fifth at the end of the caudal peduncle. The bars are widest dorsally and slanted down and backwards. The relative intensity of the five bars is an important taxonomic character and is conserved in well-preserved specimens. In *E. deloachorum*, the fourth and fifth bars are about equal and distinctly darker than the preceding bars. There is often a dark patch or even a thin partial bar in the interspace between the fourth and fifth bar. The fifth bar is often narrower than the interspace, but on some larger fish the bar merges with the dark band at the base of the caudal fin to produce a broad dark band that can be wider than the pale space between the fourth and fifth bars.

The head is darkly marked, mostly on the dorsal half, with a pale underside including jaws, branchiostegals, and isthmus (except the front tip of the mandible is dark). The cranium is covered by a dense covering of melanophores and dark shading extends over the interorbital and snout. There is a pale stripe flanked by two dark stripes running obliquely down from the front of the eye at 8-o'clock over the nasal area to cross the front of the upper jaw. The orbital cirrus is darkly speckled. The iris is dark with pale to reddish patches in a radiating-spoke pattern (uniform in faded specimens). The cheek and gill cover have dark patches, especially under the eye and on the operculum, with some individuals extensively speckled over that area, and the pectoral-fin base is fully shaded.

The first two membranes of the first dorsal fin are usually uniformly darkly speckled, while the second dorsal fin has the basic *E. boehlkei*-pattern made up of a narrow dark edge (less than the distal third of the first 10 spines) and three dark spots (rounded patches of melanophores) at the base of the 2–3rd, 6th, and 8th membranes. The third dorsal fin and pectoral fins are mostly transparent and crossed with a few dark bands. The anal fin usually has three or four spaced-apart dark patches on the fin membranes. The caudal fin has two prominent solid (unbroken)

Figure 18. *Enneanectes deloachorum*, Bonaire; photo by Michael W. Brogan.

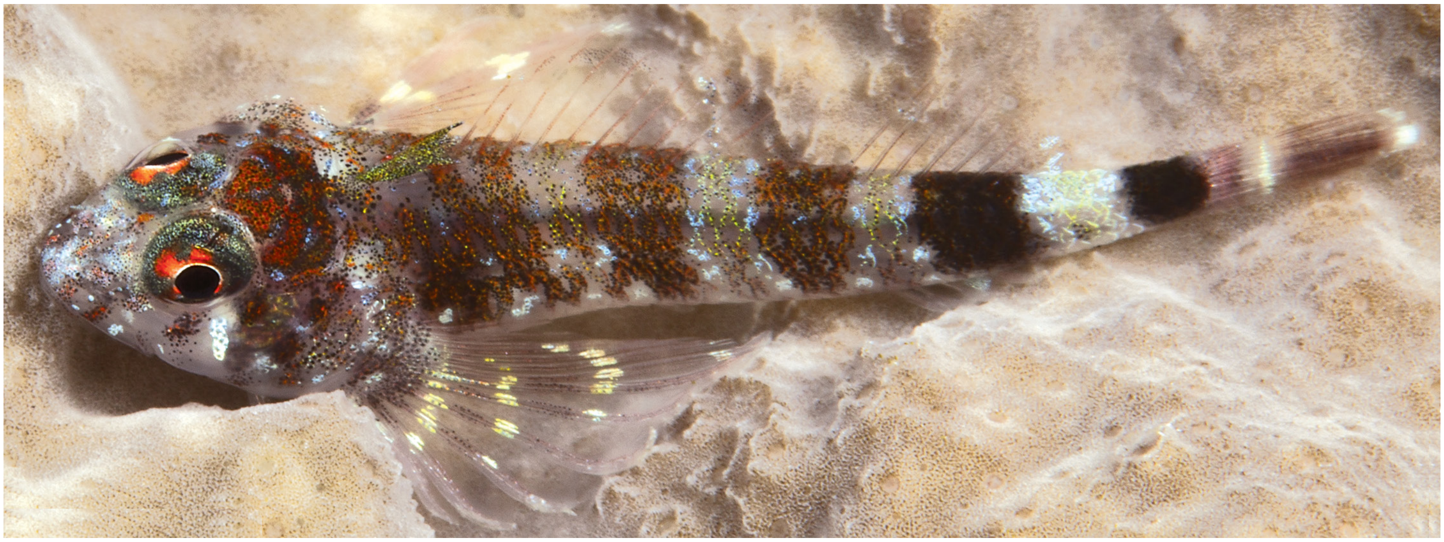

Figure 19. *Enneanectes deloachorum*, Bonaire; photo by André de Molenaar.

wide dark bands separated by a clear band before mid-fin. The marking pattern of breeding males from the type locations is unknown, but photographs from Bonaire show males with the posterior body and caudal fin darkly shaded (progressively obscuring the anal-fin patches and the caudal-fin bands).

Color in life. Live colors have not been documented for the species at the type locations, however similarly two-barred triplefins from Bonaire (Figs. 18 & 19) show mostly the same basic color patterns as described for *E. boehlkei* except for the fourth and fifth body bars being equally dark and prominent, the accessory dark patch or bar present in the 4–5 interspace, and a reddish bar present at the base of the caudal fin.

Barcode sequence. A 652-nucleotide sequence of the section of the mitochondrial COI gene used for barcoding by the BOLD informatics database (Ratnasingham & Hebert 2007) was obtained for the holotype and paratypes (Genbank accession numbers in Appendix 1). Following the database management recommendation of the BOLD the sequence of the holotype is presented here as well:

CCTCTACCTCGTATTCGGTGCTTGAGCTGGAATAGTAGGAACCGCTTTAAGCCTGCTTATCCGTGCA
GAACTTAGCCAGCCTGGCGCTCTCCTCGGAGATGACCAAATTTACAATGTTATCGTTACAGCCCAC
GCCTTTGTAATGATTTTCTTTATAGTAATACCCATTCTTATTGGAGGCTTCGGTAATTGACTCATCCCT
CTAATGATCGGGGCCCCTGATATAGCATTCCCCCGTATAAACAACATAAGCTTTTGACTTCTTCCCCC
CTCTTTCCTCCTCTTGCTAGCCTCCTCTGGGGTCGAAGCCGGGGCCGGGACTGGTTGAACAGTGTA
CCCCCCACTGTCCGGGAATCTTGCCCACGCAGGAGCCTCTGTAGACCTAACAATCTTTTCCCTTCAC
TTAGCCGGGATTTCTTCTATTCTTGGTGCCATTAATTTTATTACCACTATCATTAACATGAAACCCCCT
GCTATTACACAATATCAAACACCACTGTTCGTCTGAGCCGTACTAATTACTGCCGTCCTACTCCTTCT
CTCCCTCCCAGTCCTTGCTGCAGGGATTACCATGCTCCTGACAGATCGTAACCTAAACACCACATTC
TTTGACCCCGCCGGAGGAGGGGACCCTATTCTTTACCAACACCTC

Distribution. In addition to the type specimens from Dominica and Barbados, there are photographs of fish corresponding to the description for the species from Isla Aves (an isolated island west of Dominica; Juan Posada and Oscar Lasso-Alcala) and similar-appearing triplefins in photographs from Aragua and Sucre states in Venezuela, as well as Curaçao (Ross Robertson and Jim Van Tassell). Underwater photographs of the similarly two-barred form of triplefin from the S. Netherlands Antilles have been taken by Michael Brogan, Rick Coleman, Brian Mayes, André de Molenaar, Ellen Muller, Keri Wilk, and Peter Wirtz, but it is uncertain whether the Venezuelan, Curaçaoan, and Bonairean populations represent the same species.

Etymology. Named for Ned and Anna Deloach in recognition of their contributions to the art of underwater photography of coral-reef animals, their development of very useful guides to reef organisms, and their exceptional camaraderie on the expedition to Dominica; the specific epithet is a noun in the genitive case (plural). The common name Two-bar Triplefin is proposed.

Figure 20. *Enneanectes boehlkei*, 18 mm SL female, UF 185613, ethanol preserved, Coki Point, St. Thomas, U.S.V. I.

Enneanectes boehlkei, Rosenblatt 1960

Figures 4, 6, 20–25; Table 1.

Material examined (27 specimens, 10.7–21.4 mm SL). UF 185616 (2, 10.7–14.5) U.S. Virgin Islands, St. Thomas, Brewers Bay (18.341°, -64.977°), B. Victor, Sep. 3, 2006; UF 185614 (1, 15.2) U.S. Virgin Islands, St. Thomas, Brewers Bay (18.341°, -64.977°), B. Victor, May 3, 2009; UF 185615 (2, 19.4–20.4) U.S. Virgin Islands, St. Thomas, Brewers Bay (18.341°, -64.977°), B. Victor, May 5, 2009; UF 185613 (5, 14.5–19.6) U.S. Virgin Islands, St. Thomas, Coki Point (18.351°, -64.863°), B. Victor, Mar. 4, 2007; UF 185617 (1, 15.3) U.S. Virgin Islands, St. John, Klein Bay (18.319°, -64.769°), C. Caldow, Mar. 2, 2011; UF 149089 (10, 17.3–21.4) U.S. Virgin Islands, St. Croix, off Buck Island (17.789°, -64.612°), W. Smith-Vaniz and L. Rocha, Aug. 6, 2001; UF 164418 (6, 15.8–20.1) U.S. Virgin Islands, St. Croix, off Buck Island (17.799°, -64.617°), R. Spieler, K. Kilfoyle, and J. Freeman, Oct. 8, 2005.

Diagnosis. A species of *Enneanectes* with belly, pectoral-fin base, and cheek naked, spiny preorbital bone in adults, blunt snout, three rows of scales above rear pored scales, first two rows about equal-sized, relatively short first dorsal fin (all characters of *E. boehlkei* complex); fifth body bar prominently darker than first four and typically wider than 4–5 interspace; first four body bars usually indistinct, often barely distinguishable; 4–5 interspace without central dark patch or dark accessory bar; two broad and solid dark or dusky red bands on caudal fin (except breeding males with all dark); pale band flanked with dark or red stripes from eye across upper jaw; second dorsal fin with three rounded dark spots on membranes near the spine bases and thin band of fine speckling on outer rim of fin; anal fin with four or five dark patches; mode of D III+XII+8 and A II, 16; mode of 15 pored lateral-line scales and 21 scales in notched midline row.

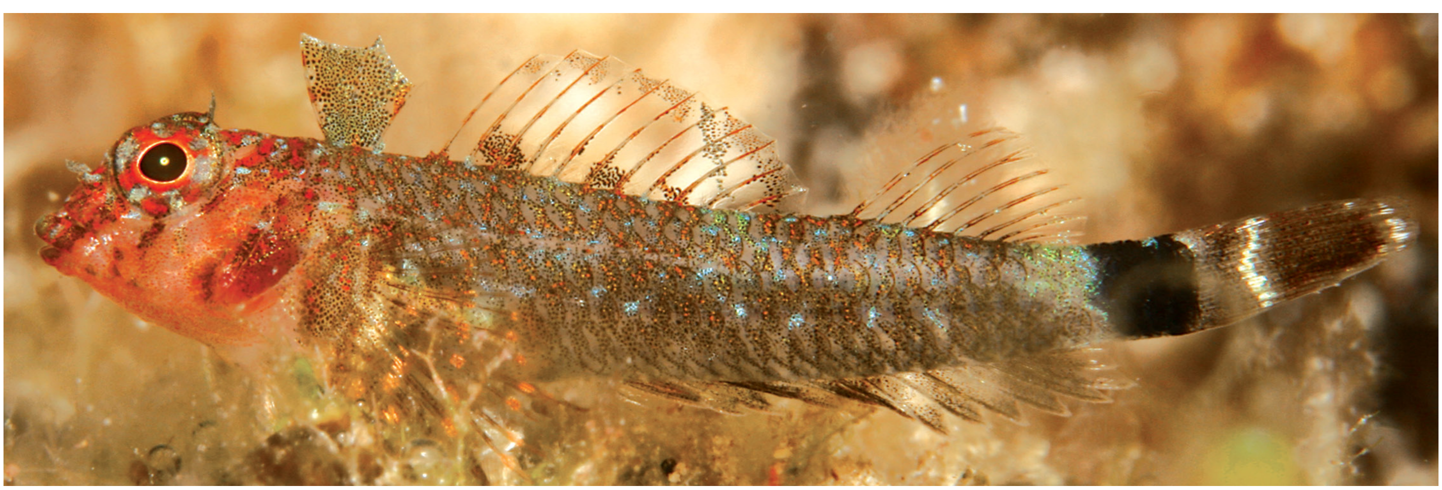

Figure 21. *Enneanectes boehlkei*, Exuma, Bahamas, darkly marked fish with indistinguishable anterior body bars; photo by Louis Johnson.

Figure 22. *Enneanectes boehlkei*, Exuma, Bahamas; photo by Louis Johnson.

Description. Body somewhat stout and elongate, body depth 18–22% SL, body width 15–20% SL; predorsal distance short, 22–28% SL; prepelvic distance shorter, 19–24% SL; preanal distance 47–56% SL; caudal peduncle length 11–14% SL, caudal peduncle depth 8–12% SL. Head short, large, and relatively deep, head length 28–32% SL; head depth (at midpoint of orbit) 16–19% SL, 53–61% HL; snout short and blunt, sloping sharply downward in front of eye, snout span 16–21% HL, eye large, orbit diameter 32–40% HL; single short flat tab-like orbital cirrus, longer than wide, tip narrowly to broadly rounded (occasionally a wide point), speckled black, usually not reaching back to vertical through posterior orbital rim (except in largest fish); interorbital narrow, mostly flat, width 9–12% HL; posterior orbital flange spiny, interorbital spiny, anterior orbital flange from minimally spiny to spiny; pores in rows around eye and in series along preopercle and mandible with a single pore behind mandibular symphysis; mouth large, upper-jaw extending back past the vertical through midpoint of eye, oblique length 35–45% HL; upper and lower jaws with variable-sized caniniform teeth, in multiple irregular rows with outermost largest; irregular vomerine tooth patch, no palatine teeth; anterior nostril a low tube with a speckled fingerlike cirrus about three times nostril diameter, posterior nostril an elliptical opening adjacent to orbital rim; 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 on first arch 1+7, short, stubby, and

Figure 23. *Enneanectes boehlkei*, St. Kitts, lightly marked fish with red-marked head, but note black cranial melanophores; photo by Jason Phillip.

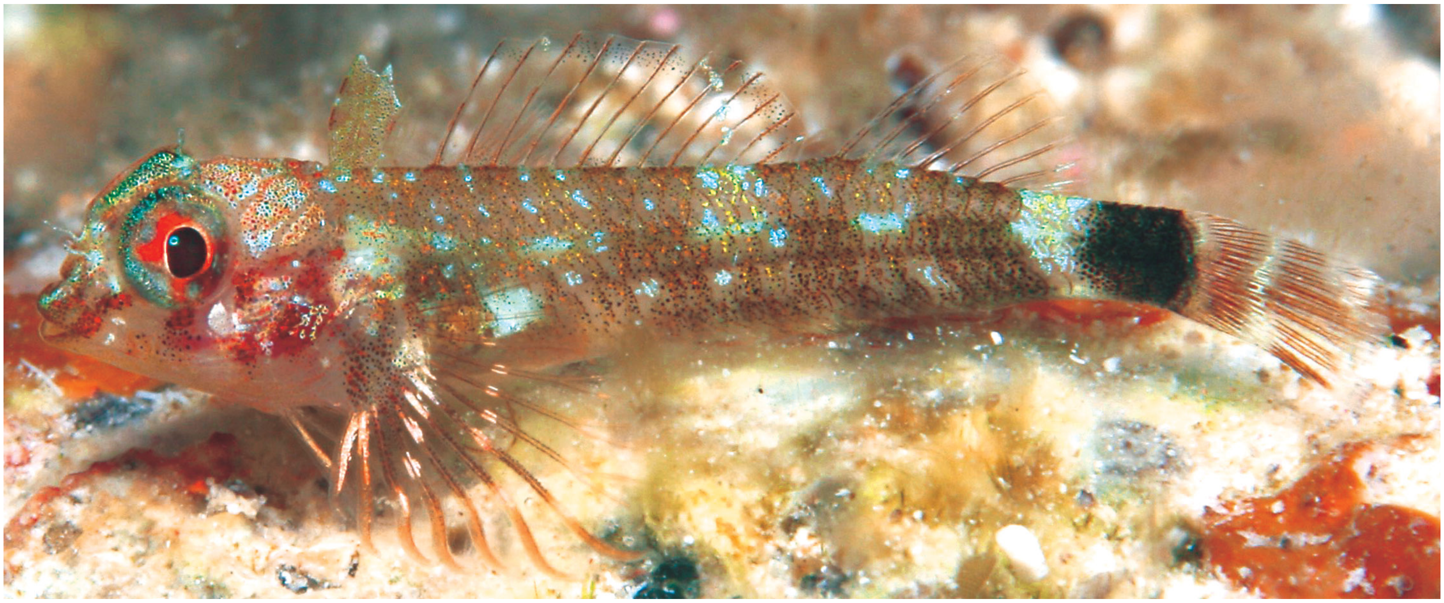

Figure 24. *Enneanectes boehlkei*, Exuma, Bahamas, note caudal fin has dusky orange bands (not a basal red bar); photo by Louis Johnson.

crowned with spines, dorsalmost lower-limb rakers split into inner and outer pairs (not counted separately).

Three dorsal fins, first two spinous, strong modal fin-ray count III+XII+8; anal-fin rays II, 16; pectoral-fin rays 15 (one with 16); two pelvic-fin rays. Short first dorsal fin with all three spines when depressed reaching back to between base of first and second spine of second fin (rarely to just past 2nd), first dorsal-fin spine 10–15% SL (lower in immature, largest males reach 15%), second spine 9–13% SL, third spine 6–10% SL; third spine of second dorsal fin 13–17% SL; third dorsal fin with unbranched soft rays, third ray 12–17% SL; anal-fin base long, 36–43% 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 10–14% SL; pectoral fin long, 35–42% SL, uppermost 2–3 rays unbranched, lowermost two rays especially stout; inner pelvic-fin ray longest, 23–31% SL; caudal fin truncate, length 23–28% SL, 14–15 segmented caudal-fin rays, one or two uppermost and two or three lowermost unbranched, 4–7 upper and 3–5 visible lower procurrent rays.

Body covered with large ctenoid scales, except naked belly and pectoral-fin base; head generally unscaled, both operculum and cheek naked; fins bare except for about three large flat cycloid scales covering lower caudal-fin rays. Scales between lateral line and second dorsal-fin base in three rows, lower two about equal, dorsalmost small. Lateral line made up of anterior segment of typically 15 tubed scales above and partially overlying discontinous posterior segment lying along lateral midline comprising 19–22 (mode of 21) mostly notched scales extending to caudal-fin base (frequently one unnotched scale after first notched scale).

Color in preservative. All color is lost after preservation except for dark melanophore pigment over a pale to yellow background (translucent in life). There is a speckled overlay, mostly outlining individual scales producing a distinct crosshatch pattern over the body. The belly is typically unmarked except for the edges of the dark peritoneum showing through along the flanks and in a V forward of the anus. Overlying the speckling on the body are five dark bars, the first behind the pectoral-fin base and the fifth at the end of the caudal peduncle. The bars are widest dorsally and slanted down and backwards. The relative intensity of the five bars is an important taxonomic character and is conserved in well-preserved specimens. In *E. boehlkei* the fifth bar is distinctly darker than the preceding bars, which are about equal and usually faint and frequently almost indistinguishable. The fifth bar is often wider than the preceding pale interspace and often extends farther forward on the upper half.

The head is darkly marked, mostly on the dorsal half, with a pale underside including jaws, branchiostegals, and isthmus (except the front tip of the mandible is dark). The cranium is covered by a dense covering of melanophores and dark shading extends over the interorbital and snout. There is a prominent pale stripe dividing the dark band running obliquely down from the front of the eye at 8-o'clock over the nasal area to cross the front of the upper jaw. The orbital cirrus is darkly speckled or black. The iris is dark with pale to reddish patches in

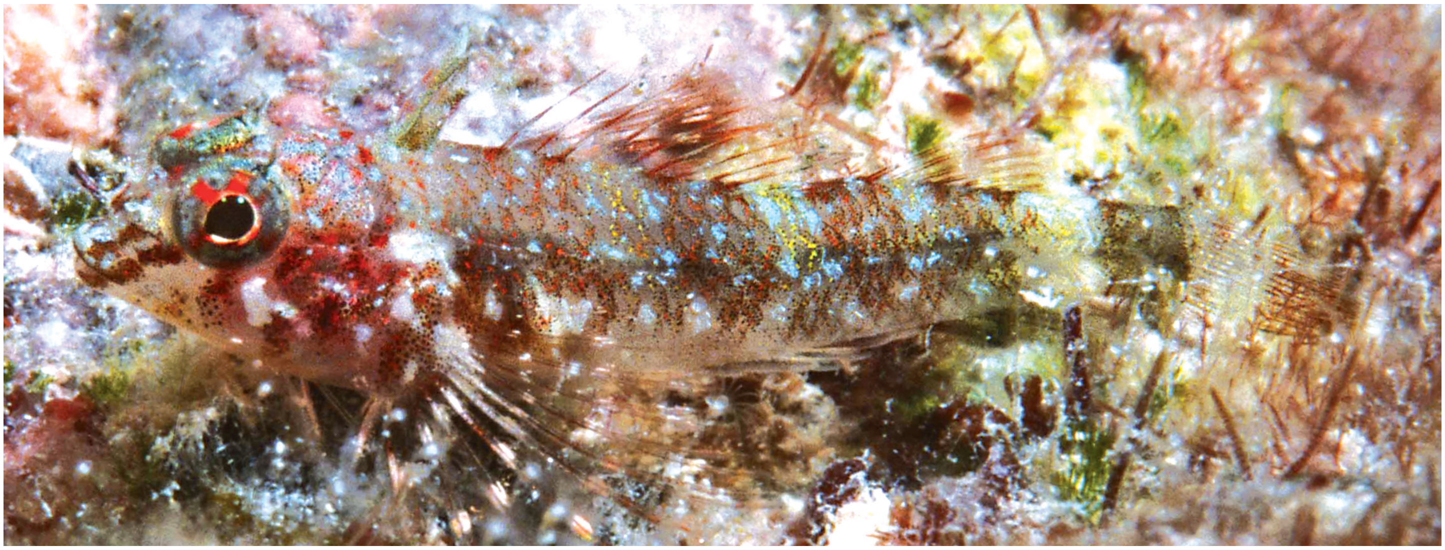

Figure 25. *Enneanectes boehlkei*, Dry Tortugas, Florida, note dark-light-dark stripes in front of eye; photo by Les Wilk.

a radiating-spoke pattern (uniform in faded specimens). The cheek and gill cover have dark patches, especially under the eye and on the operculum, with some individuals extensively speckled over that area, and the pectoral-fin base is fully shaded.

The first two membranes of the first dorsal fin are usually uniformly darkly shaded, while the second dorsal fin has the basic *E. boehlkei*-pattern made up of a narrow dark edge (less than the distal third of the first 10 spines) and three dark spots (rounded patches of melanophores) at the base of the 2–3rd, 6th, and 8th membranes (sometimes 2nd, 5th, and 7th). The third dorsal fin and pectoral fins are mostly transparent and crossed with a few dark bands. The anal fin usually has four, sometimes five, spaced-apart dark patches on the fin membranes. The caudal fin has two prominent solid (unbroken) dark bands, the outer one broad, separated by a clear band before mid-fin and ending in an irregular clear band at the rear edge. In breeding males, the posterior body and caudal fin become darkly shaded (progressively obscuring the anal-fin patches and the caudal-fin bands) and the distal dark edge of the second dorsal fin expands, but limited mostly to along the spine shafts and typically leaving at least the lower half of the first nine membranes unspeckled, except for the dark spots at the base of the 2–3rd, 6th, and 8th membranes.

Color in life. Live fish show the same dark patterns described for preserved fish but have additional red, white, gold, and sometimes blue components. The iris has gold ringing the pupil and bright red spoke-like patches. There are red bands underlying the dark markings on top of the head and snout. A series of bluish-white rounded spots are arrayed over the body. There is no red bar on the base of the caudal fin. Some otherwise lightly marked fish have bright orange to red markings predominating on the head, often with blue spots and bands and blue-dark patches on the iris (Fig 23). Lightly marked fish also have white predominating over the dark shading on the first dorsal fin and the fin can flash bright white. In addition, the thin white bar on the rear second dorsal-fin membranes can show prominently. The pectoral fins are white or yellow-banded. The pale areas between the body bars, when present, can be highlighted with white and are usually laced with gold. The darker bands on the caudal fin range from dusky red to black; note that the duskiness represents melanophores within the red-colored bands (vs. *E. matador*). The pale or transparent mid-band on the caudal fin can show a central bright white bar and the distal edge of the fin is usually white.

Distribution. Barcode DNA sequences in the BOLD database with close, but not identical, matches to the *E. boehlkei* specimens from the Virgin Islands from have been collected from Quintana Roo, Mexico (Lourdes Vásquez-Yeomans), Belize (Jack Randall and Carole Baldwin *et al.*), Honduras, and Panama. Underwater photographs generally corresponding to the *E. boehlkei* description have been taken in the Bahamas (Louis Johnson), Florida (Louis Johnson, Peter Leahy, and Les Wilk), Cuba (Bart Hazes), Cayman Islands (Cindy Abgarian, Everett Turner, and Ximena Olds), St. Kitts (Jason Phillip), Belize (Jack Randall), Honduras (Les and Keri Wilk, Brad Ryon), and San Andres in the Western Caribbean (Keri Wilk).

Comparisons. *E. boehlkei* is distinguished from the new members of the complex by a combination of markings: the fifth body bar much darker than the preceding four, which are about equal in intensity and frequently indistinct (vs. *E. deloachorum*; some *E. boehlkei* populations, like those from Panama, have a somewhat more distinct fourth bar); fifth body bar (defined rearward to edge of last dark pigmented scale) usually wider than preceding pale interspace (vs. *E. wilki* and *E. matador*); no interspace accessory bar or dark patch between the fourth and fifth body bars (vs. *E. wilki* and *E. deloachorum*); an inner and outer dark band on the caudal fin, broad and solid, i.e. vertically unbroken (vs. *E. matador* [red bands only, not dusky] and *E. wilki* [red bar at base, often more than two bands and bands often broken]); distinct dark-pale-dark eye stripes across upper jaw (vs. *E. wilki*, also not well-developed on *E. matador*); second dorsal fin with dark-speckled band limited to outer third (vs. *E. matador*); and usually 4 or 5 dark patches along the anal fin (vs. 3 or 4 in *E. deloachorum* and sometimes 6 in *E. wilki*).

The four species in the complex differ mostly in markings, but there are small meristic and morphological differences as well. The primary meristic differences are higher dorsal and anal fin-ray counts in *E. deloachorum* and *E. matador*, lower pored-scale counts in *E. matador* and *E. wilki*, and higher notched-scale counts in the three new species (Table 1). Morphological differences appear minimal, with broad overlap in the measurements, but the first dorsal-fin spines of *E. matador* are longer, up to 18% SL in males, folded back reaching the base of the 3rd or 4th second-dorsal spines, and apparently shorter in *E. deloachorum* (10% SL in the two large females). *E. deloachorum* appear to be more foreshortened, with the prepelvic length 20% SL or less, and slightly shorter pelvic-fin rays, 23% SL (vs. 25–30% SL in the other species).

DNA Sequences. The neighbor-joining phenetic tree of barcode mtDNA sequences for Caribbean *Enneanectes* presented in Fig. 26 includes all five previously known species from the western Atlantic and clearly shows that the original Roughhead Triplefin breaks up into four distinct lineages corresponding to the species described here. The degree of divergence between the species in the *E. boehlkei* complex is similar to the degree of divergence between other species in the genus. Indeed, the divergence from eastern Pacific congeners across the isthmus of Panama, a separation representing about 3 million years (Lessios 2008), is within the range of divergences among Caribbean species and not much greater than some divergences within the *E. boehlkei* complex (see the Pacific species *E. reticulatus* in the tree in Fig. 26).

Despite the close physical resemblance of species within the *E. boehlkei* complex, the four species form mostly well-circumscribed lineages of COI mtDNA sequences with relatively low intraspecific variation, i.e. maximum intraspecific distances range from 0.3 to 1.7% (*E. wilki* and *E. boehlkei* respectively; the latter including both W. Caribbean and Antillean populations) and high interspecific variation, i.e. minimum interspecific distances range from 5.6 to 11.8% for nearest-neighbor species (*E. boehlkei*/*E. deloachorum* and *E. matador*/*E. wilki* respectively). Using pairwise distances instead of K2P distances yield quite similar corresponding ranges of 0.3–1.7% and 5.4–10.8% respectively. *E. matador* populations from Honduras/Belize and Tobago diverge by about 2% and they, along with several other unexamined or unvouchered lineages in the BOLD database, are not included in the analysis since their taxonomic status is unresolved.

Discussion. The analysis of DNA sequences for Caribbean *Enneanectes* reveals a complex set of lineages that do not directly reflect the imperfect traditional taxonomy, similar to the situation found for other blennioids with abundant cryptic species, such as the *Acanthemblemaria* (Lin *et al*. 2009, Eytan & Hellberg 2010), *Emblemariopsis* (Victor 2010a), and *Starksia* (Baldwin *et al*. 2011); as well as some gobies, e.g. *Bathygobius* (Tornabene *et al*. 2010), *Elacatinus* (Taylor & Hellberg 2006), and *Tigrigobius* (ex-*Elacatinus*; Victor 2010b). Among many of these fishes, traditional species divide into sets of deeply divided lineages with subtle morphological or marking differences. A commonly encountered pattern is allopatric sets of lineages confined to distinct biogeographic areas, conforming to the "superspecies" model of species divided into regional species, subspecies, or populations (allospecies *sensu* Greenfield 1979). These sets of endemic species do not usually diverge equally in DNA sequence, but often exhibit the full range of divergences found within the genus.

In contrast to the superspecies pattern, other lineages can be broadly distributed in the region or even pan-Caribbean. In addition, and more intriguing, there are sympatric lineages, both endemic and widespread, that represent cryptic species that maintain their genetic distinction despite the opportunity to interbreed. By any definition, they are no different from "normal" species, just eluding easy recognition, especially as preserved

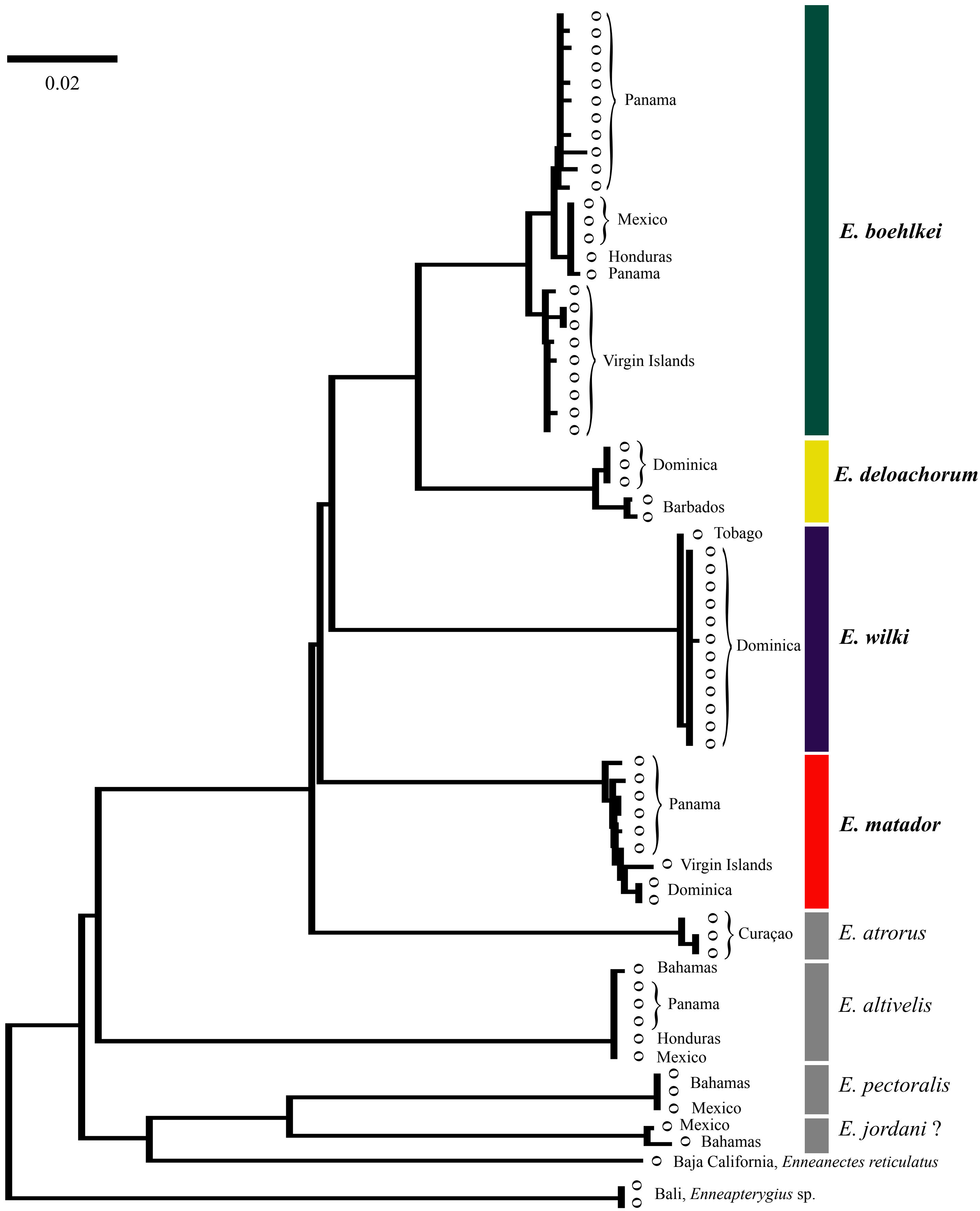

Figure 26. The neighbor-joining phenetic tree based on the COI mtDNA sequences of *Enneanectes*, following the Kimura two-parameter model (K2P) generated by BOLD (Barcode of Life Database). The colored bars at right delineate the *E. boehlkei* species-complex, while grey bars represent the other Atlantic species in the genus. The scale bar is a 2% sequence difference. *Enneapterygius* sp. from Bali is used as an outgroup. GenBank accession numbers and collection data for the sequences in the tree are listed in Appendix 1.

museum specimens. These overlooked species run the gamut from clearly morphologically and meristically distinct to those only slightly differing in markings and unresolvable without the power of sequencing to separate the specimens and reveal the diagnostic characters. Frequently there are also additional close, but often quite distinct, lineages that are not visibly different and cannot practically be considered species- a continuing conundrum for taxonomists. It should be noted that the importance of underwater photography cannot be over-estimated in evaluating differences between cryptic species which diverge primarily in colors and markings, amply illustrated here by the triplefins of the Caribbean Sea.

Other material examined:

Enneanectes atrorus: UF 17094 (1, 23.6) Bahamas, S. Andros Island, C. Gilbert and P. Heemstra, Aug. 22, 1966; UF 12345 (7, 17.3–25.4 mm SL) Grand Cayman, Paradise Rocks, C. Gilbert and J. Tyler, Aug. 23, 1964; UF 13405 (3, 17.9–25.5) Bahamas, Little San Salvador, C. Gilbert and P. Heemstra, Sep. 9, 1966.

Enneanectes altivelis: UF 99211 (3, 19–20.3) Bahamas, San Salvador, Rum Cay, M. Hancock and C. Koenig, June 14, 1968; UF 25332 (2, 19.2–19.7) Colombia, Isla Providencia, Santa Catalina Island, J. Tyler *et al*., Aug. 22, 1968; UF 25394 (4, 13.5–21.2) Colombia, Isla Providencia, Three Brothers, J. Tyler *et al*., Aug. 24, 1968.

Enneanectes jordani: UF 25332 (1, 19.4) Colombia, Isla Providencia, Santa Catalina Island, J. Tyler *et al*., Aug. 22, 1968; UF 25394 (5, 17–19.9) Colombia, Isla Providencia, Three Brothers, J. Tyler *et al*., Aug. 24, 1968; UF 24974 (2, 16.9–17.4) Colombia, Isla Providencia, Crab Cay, C. Gilbert, W. Clerke, and I. Stevens, Aug. 20, 1970.

Enneanectes pectoralis: UF 149102 (7, 15–23.8) U.S. Virgin Islands, St. Croix, off Buck Island (17.789°, -64.612°), W. Smith-Vaniz and L. Rocha, Aug. 6, 2001.

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Appendix 1. Specimen data and GenBank accession numbers for the mtDNA COI barcode sequences used in the phenogram in Figure 26, following the order in the tree. Holotypes in bold type.

Genus	species	Collection site	Voucher	GenBank #	Collector/Source
Enneanectes	*boehlkei*	Panama, Portobelo	n7527ae95	KC860821	B. Victor
Enneanectes	*boehlkei*	Panama, San Blas	sb92enn92	KC860804	B. Victor
Enneanectes	*boehlkei*	Panama, Portobelo	n7529be146	KC860810	B. Victor
Enneanectes	*boehlkei*	Panama, Portobelo	n7529benn104	KC860815	B. Victor
Enneanectes	*boehlkei*	Panama, Portobelo	n7527ae180	KC860807	B. Victor
Enneanectes	*boehlkei*	Panama, Portobelo	n7527ae85	KC860808	B. Victor
Enneanectes	*boehlkei*	Panama, Portobelo	n7527ae93	KC860806	B. Victor
Enneanectes	*boehlkei*	Panama, Portobelo	n7527ae188	KC860814	B. Victor
Enneanectes	*boehlkei*	Panama, Portobelo	n7527aeb165	KC860812	B. Victor
Enneanectes	*boehlkei*	Panama, Portobelo	n7527aeb151	KC860818	B. Victor
Enneanectes	*boehlkei*	Panama, Portobelo	n7529ben166	KC860803	B. Victor
Enneanectes	*boehlkei*	Quintana Roo, Mexico	MFLIV1628	HM389342	L. Vásquez Yeomans
Enneanectes	*boehlkei*	Quintana Roo, Mexico	MFLIV1518	HM389249	L. Vásquez Yeomans
Enneanectes	*boehlkei*	Quintana Roo, Mexico	MFLIV1637	HM389351	L. Vásquez Yeomans
Enneanectes	*boehlkei*	Utila, Honduras	u872eb151	KC860824	B. Victor
Enneanectes	*boehlkei*	Panama, Portobelo	n7529be142	KC860816	B. Victor
Enneanectes	*boehlkei*	St. Thomas, USVI	UF185616-10.7	KC860809	B. Victor
Enneanectes	*boehlkei*	St. Thomas, USVI	UF185615-19.4	KC860805	B. Victor
Enneanectes	*boehlkei*	St. Thomas, USVI	UF185613-17.1	KC860817	B. Victor
Enneanectes	*boehlkei*	St. Thomas, USVI	UF185614	KC860819	B. Victor
Enneanectes	*boehlkei*	St. Thomas, USVI	UF185613-18	KC860811	B. Victor
Enneanectes	*boehlkei*	St. Thomas, USVI	UF185613-19.6	KC860822	B. Victor
Enneanectes	*boehlkei*	St. John, USVI	UF185617	KC860820	C. Caldow/ B. Victor
Enneanectes	*boehlkei*	St. Thomas, USVI	UF185613-17.5	KC860813	B. Victor
Enneanectes	*boehlkei*	St. Thomas, USVI	UF185613-14.5	KC860823	B. Victor
Enneanectes	*deloachorum*	Dominica	UF185605	KC860852	B. Victor
Enneanectes	**deloachorum**	**Dominica**	**UF185602**	**KC860851**	**B. Victor**
Enneanectes	*deloachorum*	Dominica	UF185606	KC860849	B. Victor
Enneanectes	*deloachorum*	Barbados	UF185612-9	JN313598	H. Valles/ B. Victor
Enneanectes	*deloachorum*	Barbados	UF185612-10	KC860850	H. Valles/ B. Victor
Enneanectes	*wilki*	Tobago	TOB9206	JQ842854	C. Baldwin *et al*., USNM
Enneanectes	*wilki*	Dominica	UF185604-16.7	KC860842	B. Victor
Enneanectes	*wilki*	Dominica	UF185611-14.3	KC860845	B. Victor
Enneanectes	**wilki**	**Dominica**	**UF185610**	**KC860848**	**B. Victor**
Enneanectes	*wilki*	Dominica	UF185601-13.8	KC860843	B. Victor
Enneanectes	*wilki*	Dominica	UF185611-15.9	KC860844	B. Victor
Enneanectes	*wilki*	Dominica	UF185601-13.7	KC860837	B. Victor
Enneanectes	*wilki*	Dominica	UF185601-14.7	KC860847	B. Victor
Enneanectes	*wilki*	Dominica	UF185604-16.2	KC860846	B. Victor
Enneanectes	*wilki*	Dominica	UF185604-15.7	KC860841	B. Victor
Enneanectes	*wilki*	Dominica	UF185604-13.7	KC860838	B. Victor

Enneanectes	*wilki*	Dominica	UF185611-13.4	KC860839	B. Victor
Enneanectes	*wilki*	Dominica	UF185XXX-8.7	KC860840	B. Victor
Enneanectes	*matador*	Panama, Portobelo	UF185608-18.8	KC860831	B. Victor
Enneanectes	*matador*	Panama, Portobelo	UF185608-19	KC860829	B. Victor
Enneanectes	*matador*	Panama, Portobelo	UF185609-19.8	KC860828	B. Victor
Enneanectes	*matador*	Panama, Portobelo	UF185609-21	KC860833	B. Victor
Enneanectes	*matador*	Panama, Portobelo	UF185608-14.1	KC860830	B. Victor
Enneanectes	*matador*	Panama, Portobelo	UF185609-10.6	KC860836	B. Victor
Enneanectes	*matador*	St. Thomas, USVI	UF185607	KC860835	B. Victor
Enneanectes	**matador**	**Dominica**	**UF185600**	**KC860834**	**B. Victor**
Enneanectes	*matador*	Dominica	UF185603	KC860832	B. Victor
Enneanectes	*atrorus*	Curaçao	CURA8103	JQ842097	C. Baldwin *et al*., USNM
Enneanectes	*atrorus*	Curaçao	CURA8102	JQ842096	C. Baldwin *et al*., USNM
Enneanectes	*atrorus*	Curaçao	CURA8101	JQ842098	C. Baldwin *et al*., USNM
Enneanectes	*altivelis*	Bahamas	BAHA8180	JQ839760	C. Baldwin *et al*., USNM
Enneanectes	*altivelis*	Panama, Portobelo	n762aea250	KC860799	B. Victor
Enneanectes	*altivelis*	Panama, Portobelo	n762aea160	KC860801	B. Victor
Enneanectes	*altivelis*	Utila, Honduras	u873ea138	KC860800	B. Victor
Enneanectes	*altivelis*	Panama, Portobelo	n7531bea237	KC860802	B. Victor
Enneanectes	*altivelis*	Quintana Roo, Mexico	MFLIV1627	HM389341	L. Vásquez Yeomans
Enneanectes	*pectoralis*	Quintana Roo, Mexico	MFLIV1599	HM389321	L. Vásquez Yeomans
Enneanectes	*pectoralis*	Eleuthera, Bahamas	el11ep273	KC860826	L. Johnson/ B. Victor
Enneanectes	*pectoralis*	Eleuthera, Bahamas	el11ep156	KC860825	L. Johnson/ B. Victor
Enneanectes	*jordani*?	Quintana Roo, Mexico	MFL812	GU224787	L. Vásquez Yeomans
Enneanectes	*jordani*?	Bahamas	BAHA8172	JQ839758	C. Baldwin *et al*., USNM
Enneanectes	*reticulatus*	Baja California, Mexico	mwb11er320	KC860827	M. Brogan/ B. Victor
Enneapterygius	sp.	Bali, Indonesia	bali11700c118	KC860855	B. Victor
Enneapterygius	sp.	Bali, Indonesia	bali11700h140	KC860856	B. Victor