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Enneanectes flavus, a new endemic species of triplefin blenny from the southeastern 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 flavus* n. sp., belonging to the unscaled-abdomen subgroup. The species is distinguished by having mature adults with black spinous dorsal fins and mature males with a bright yellow rear body and tail; other distinctive features include the third and fourth body bars closer together than the fourth and fifth, the last dark body bar usually extending onto the basal third of the caudal fin, three dark blotches along the anal fin, and two black blotches on each side of the anterior body. The species is apparently limited to the southeastern corner of the Caribbean Sea, i.e. northeast Venezuela and Tobago (and photographs from St. Vincent), where it replaces the widespread Redtail Triplefin, *Enneanectes matador*. This species is added to the small set of endemic marine species in this corner of the tropical western Atlantic Ocean, likely adapted to unusual local oceanographic conditions. The mtDNA-barcode COI sequence of the new species is 2.4% divergent from the two related allopatric lineages of *E. matador* in the Caribbean. A revised key to the 9 species of *Enneanectes* in the Greater Caribbean is presented.

Key words: taxonomy, ichthyology, systematics, coral reef fishes, Yellowtail Triplefin, DNA barcoding, Venezuela

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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 (Williams 2003). After a long period of stasis, the number of species has recently increased, with three new species described from the eastern Pacific Ocean by Rosenblatt, Miller & Hastings (2013) and 4 more from the Caribbean Sea by Victor (2013, 2017), with a present total of 15 species: 5 in the eastern Pacific and 10 in the western Atlantic (one from St. Paul's Rocks off Brazil only), including the new species described here.

The Greater Caribbean *Enneanectes* species described before 2013 were all wide ranging throughout the region. Some of the more recent descriptions, like many other newly described species of gobies and blennies in the region, have been from restricted localities, often part of cryptic-species complexes allopatrically dividing up the Greater Caribbean (Victor 2013). Different species complexes have shown somewhat different patterns of biogeography, but there are broad consistencies corresponding to known biogeographic boundaries, e.g. the Checkered Shy Blenny complex by Greenfield (1979), the Blackcheek Shy Blenny complex by Baldwin *et al*. (2011), and the cleaning gobies of *Elacatinus* by Colin (2010). The patterns include breaks between the Greater and Lesser Antilles and between the Mesoamerican Barrier Reef and the Panamic region, as well as regional foci of endemism in the Gulf of Mexico, Bahamas, western Caribbean, and southern Caribbean, including the southeast Caribbean around northeastern Venezuela, Trinidad & Tobago, and the southern (Windward) chain of the Lesser Antilles (Floeter *et al*. 2008, Robertson & Cramer 2014, Robertson & Van Tassell 2015).

The southeast corner of the Caribbean is a particularly interesting area with unusual local oceanographic conditions on the continental shelf and the southern Windward island chain, primarily upwelling in the area around northeastern Venezuela, the influence of the Orinoco/Amazon River outflow, and large inflows of equatorial waters from the North Brazil Current (Johns *et al*. 2002, Cherubin & Richardson 2007, Rueda-Roa *et al*. 2018). It contains a small set of endemic reef fish species, mainly blennies and gobies, limited to northeastern Venezuela and/or extending to Colombia or Tobago (e.g. Cervigón 1994, Almany & Baldwin 1996, Williams & Mounts 2003). In this study, an unusual-looking yellow triplefin species with a divergent mtDNA lineage is described from the area, where it replaces the widespread Redtail Triplefin, *Enneanectes matador* Victor, 2013.

Materials and Methods

Type specimens are deposited at the American Museum of Natural History, New York, NY, USA, and the National Museum of Natural History, Washington, D.C. (USNM).

Mitochondrial DNA sequences for the Tobago specimens were obtained from the Laboratories of Analytical Biology, NMNH (Weigt *et al*. 2012). Comparison sequences were obtained from the Centre for Biodiversity Genomics, Guelph, Canada, using the following procedure: 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 BOLD, 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 both by ocular micrometer and photomicrographs and are presented for the holotype followed in parentheses by the range for the paratypes; morphometrics are calculated only for individuals over 18 mm SL. Most measurements of Rosenblatt (1960) are followed, although oblique measurements were avoided (except upper-jaw, predorsal, prepelvic, preanal, and fin-element lengths), instead horizontal measurements were used for their greater consistency (as span). Lengths of specimens are mm standard length (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 span 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 naris, 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 span from edge to edge of the bony orbit; interorbital width is the least bony width; upper-jaw length is the oblique length; caudal-peduncle depth is the least depth and caudal-peduncle length is the horizontal span from the base of the last anal-fin ray to the caudal-fin base (one-third shorter than using the dorsal, as in Victor [2013, 2017]); lengths of fin spines and rays are measured to their junction with the body; caudal-fin length is the horizontal span 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. Triplefins typically have the last dorsal and anal-fin ray split to the base: they are counted as one 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 along the lateral midline 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, allowing counts to be made when some scales are missing and their degree of notching is unknown.

***Enneanectes flavus*, n. sp.**

Yellowtail Triplefin
Tres Aletas Cola Amarilla

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Figures 1–6.

BOLD mtDNA barcode lineage BIN BOLD:AAN4956

Holotype. AMNH 245238, 23.0 mm SL, male, Venezuela, Los Testigos Archipelago, Isla Noreste, north end, 11.41255°, -63.04725°, JVT 06-663, J.L. Van Tassell, D.R. Robertson & J. Posada, 7 September 2006

Figure 1. *Enneanectes flavus*, fresh holotype, AMNH 245238, 23.0 mm SL, mature male, Los Testigos, Venezuela (J.L. Van Tassell & D.R. Robertson).

Figure 2. *Enneanectes flavus*, fresh paratype, AMNH 249279, 27.9 mm SL, mature male, Paria Peninsula, Venezuela (J. L. Van Tassell & D.R. Robertson).

Paratypes. AMNH 249279, (3) male 27.9 & females 23.9 & 25.2 mm SL, Venezuela, Sucre, Paria Peninsula, Ensenada de San Francisco, 10.71211°, -62.00426°, D.R. Robertson & J. Posada, 3 December 2008; USNM 413224, female, 22.0 mm SL (TOB 9009), Trinidad & Tobago, Tobago, Mount Irvine Beach, 11.1964°, -60.7961°, 0–1 m, field number TOB 09-01, C.C. Baldwin, L.A. Weigt & D.G. Smith, 15 March 2009; USNM 413225, female, 22.5 mm SL (TOB 9010), same collection as prior; USNM 413227, male, 19.0 mm SL (TOB 9012), same collection as prior; USNM 413228, female, 17.4 mm SL (TOB 9013), same collection as prior; USNM 414291, female, 22.3 mm SL (TOB 9350), Trinidad & Tobago, Tobago, Arnos Vale Beach, 11.2267°, -60.7639°, 0–3 m, field number TOB 09-11, C.C. Baldwin, D.G. Smith, L.A. Weigt, R. Gonzalez & D. Rousseau, 19 March 2009; USNM 414292, male, 22.7 mm SL (TOB 9349), same collection as prior.

Non-type material. USNM 413226 (TOB 9011), front half of specimen, Trinidad & Tobago, Tobago, Mount Irvine Beach, 11.1964°, -60.7961°, 0–1 m, field number TOB 09-01, C.C. Baldwin, L.A. Weigt & D.G. Smith, 15 March 2009; AMNH 237336, male, Venezuela, Islas Los Frailes, Puerto Real, 11.2032°, -63.7405°, JVT 05-535, J.L. Van Tassell, D.R. Robertson, J. Posada & L. Rocha, 24 September 2005; AMNH 249262, Venezuela, Sucre, Paria Peninsula, Hueco del Indio, 10.73358°, -61.849819°, O.M. Lasso-Alcala & D.R. Robertson, 4 December 2008.

Diagnosis. A species of *Enneanectes* in the unscaled-abdomen subgroup (all with three scale rows above posterior pored lateral line), with a very short blunt snout, spiny preorbital flange, mode of 14 or 15 pored lateral-line scales; also with a broadly black-speckled second dorsal fin in adults, especially males (shared only with *E. matador*). Diagnostic for *E. flavus* is a yellowish rear body and tail, especially in mature males; melanophores extending from last body bar onto proximal third of caudal fin (unless obscured by bright yellow); interspace between third and fourth body bars half or less of interspace between fourth and fifth body bars; and three dark blotches along anal fin (except uniformly dusky in mature males); fresh and especially preserved specimens show two large black blotches on each side behind opercular flap, within a usually narrowly split first body bar.

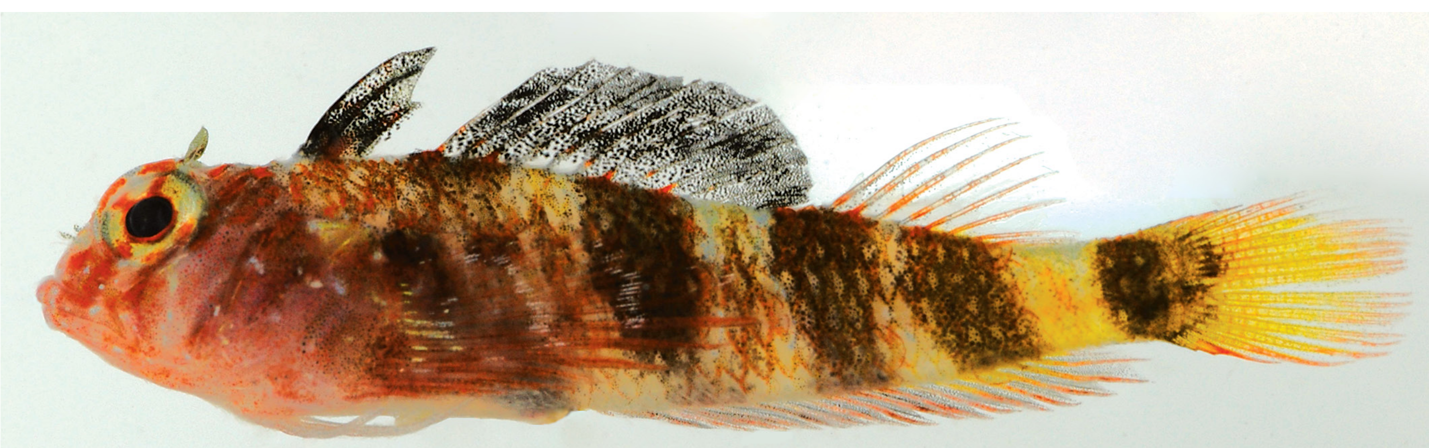

Figure 3. *Enneanectes flavus*, fresh, AMNH 237336, mature male, Los Frailes, Venezuela (J.L. Van Tassell & D.R. Robertson).

Figure 4. *Enneanectes flavus*, fresh paratype, USNM 414292, 22.7 mm SL, mature male, Tobago (C.C. Baldwin).

Description. Three dorsal fins, first two spinous, dorsal-fin elements III+XII+8 (III+XII+7–8); anal-fin elements II,17 (II,16, one paratype with 17); pectoral-fin rays 15 (15, one paratype with 14); pelvic-fin elements I,2, with short spine embedded; combined dorsal-fin base long, 52 (57–65)% SL; first dorsal fin short in females to relatively long in males, when adpressed most extended spine (first or second) about reaching base of first spine (in females) to about base of third spine of second dorsal fin (in largest males); first dorsal-fin spine 7–10% SL in females, 12 (14–15)% SL in males; second spine 6–9% SL in females, 10 (10–11)% SL in male, third spine 5–7% SL in females, 7 (7–9)% SL in males; longest spine of second dorsal fin 13 (11–15)% SL; third dorsal fin with soft rays unbranched, last split to base, usually about second ray longest, 12 (13–18)% SL; anal-fin base long, 32 (29–40)% SL, with two short spindly spines rooted close together, second slightly longer than first, first anal-fin spine 3 (3–5)% SL; second anal-fin spine 3 (3–6)% SL; soft rays unbranched, last split to base, about antepenultimate ray longest 10 (10–13)% SL; pectoral fin long, longest ray about 8th from top, 33 (32–41)% SL, uppermost 2 or 3 rays unbranched, middle about 6 branched, lower rays unbranched; two pelvic-fin rays unbranched, inner longest, 24 (23–27)% SL; caudal fin truncate, length 18 (20–24)% SL, 14–15 segmented caudal-fin rays, one or two uppermost and two or three lowermost unbranched, 6 (5–7) upper and 5 (3–5) lower procurrent rays.

Body somewhat stout and elongate, body depth 20 (23–25)% SL, body width 17 (13–20)% SL; predorsal length short, 22 (27–30)% SL; prepelvic length shorter, 19 (21–24)% SL; preanal length 43 (50–61)% SL; caudal-peduncle length 8 (9–13)% SL, caudal-peduncle depth 7 (7–9)% SL. Head short, large, and relatively deep, head length 26 (28–32)% SL; head depth (at midpoint of orbit) 17 (18–21)% SL or 63 (61–72)% HL; snout short and very blunt, sloping sharply downward in front of eye, snout span 25 (17–25)% HL; eye large, orbit diameter 30 (30–39)% HL; single, unbranched, relatively short, paddle-shaped orbital cirrus, up to about pupil width; interorbital narrow, concave, minimum width 12 (10–14)% HL; bony orbital rim spiny (more so in large males), including anterior orbital flange; nasal surface barely spiny, cranial surface spiny; anterior naris a low tube with a speckled fingerlike cirrus about half pupil width from posterior rim, posterior naris a large elliptical opening adjacent to upper orbital rim; head pores two below naris, two rows of about 7 or 8 each flanking infraorbital canal, several additional along posterior upper orbital rim, one or a pair of small anterior interorbital pores, two rows of about 6 or 7 flanking preopercular canal and one larger before three mandibular pores on each side and a midline pore below lower jaw symphysis; mouth large, upper-jaw extending back past vertical through midpoint of eye in large males, oblique length 43 (35–45)% HL; upper and lower jaws with variable-sized caniniform teeth, in broad bands, with outermost largest in upper jaw; vomerine and palatine teeth a long thin crescent almost full length of upper palate, in tight multiple rows near midline, single file and larger, as large as jaw teeth, at distal ends; 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.

Body covered with large ctenoid scales, except naked abdomen and pectoral-fin base; head generally unscaled, except 3–7 ctenoid scales at upper end of opercle (preopercle naked); fins bare except for about three large flat cycloid scales covering base of caudal fin. 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 14 or 15 tubed scales above and partially overlying discontinuous posterior segment along lateral midline, comprising 20–23 mostly notched

Figure 5. *Enneanectes flavus*, underwater photograph, note touching third and fourth body bars under soft dorsal fin, and black extending onto the proximal caudal-fin rays, Tobago (P. H. Humann).

scales extending to caudal-fin base (but end of tubed series and most of lateral scales lost in paratypes). Urogenital papilla of males a short wide cone; urogenital opening of females with edges scalloped with fleshy processes.

Color when live or fresh. (Figs. 1–6) Body pale to translucent with scales prominently outlined in thin dark as well as golden and orange lines; 5 dark bars, first broad and indistinct, below anterior portion of second dorsal fin, often narrowly split into two dark halves with two prominent large dark blotches on skin below scales at lateral midline, above the proximal portion of the pectoral fin (underlying around tubed scales 2 and 3 and then 6 and 7); second and third bars more distinct, narrowing ventrally, centered below posterior half of second dorsal fin and gap to third dorsal fin, respectively; fourth bar below rear half of third dorsal fin, with a typically narrow pale interspace between third and fourth bars (about half or less of interspace between fourth and fifth body bars); fifth bar on caudal peduncle, sometimes darker than other bars (but typically same intensity), portion on caudal peduncle usually narrower than high and melanophores extending well onto the base of the caudal-fin rays, often up to a third of the length, with a varying degree of darkness, from a scattering of melanophores to solid black (e.g. Fig. 6); however, the melanophores can be obscured by bright yellow pigment on some mature males. Pale interspaces between last body bars with a bright white overlay in living fish, especially dorsally (Fig. 5); most specimens show a faint accessory interspace bar at center of last interspace. Rear body and caudal fin yellowish, ranging from barely yellow-tinged (especially in immature fish) to bright yellow in most mature males.

Head with markings ranging from dark in dusky fish to reddish in males with yellow rear bodies, primarily a bar below eye, bands from eye across upper jaw, and additional bars along margin of preopercle and on opercle; cranium with array of melanophores overlying erythrophores, more or less dusky in tandem with degree of darkness of body markings; iris with thin gold ring around pupil and then red to orange spokes; orbital cirrus can be black, especially in mature males, but can also appear white when melanophores are contracted in white-dominant individuals (e.g. Fig. 5).

Fins translucent, except first dorsal fin black in mature adults, banded in less mature fish; second dorsal fin broadly speckled black covering all of fin in mature adults, speckled black on most of membranes with unpigmented round spots, sparing basal membranes, in females (e.g. Fig. 6C) or immature fish; third dorsal fin translucent and red-banded to lightly speckled black; caudal fin black to dusky on proximal third (often obscured by bright yellow in mature males), followed by all bright yellow in mature males, or an unpigmented band and a dusky outer bar in some less mature fish; anal fin with three dark blotches corresponding to body bars on less mature fish, but uniformly dusky on mature males; pectoral fin translucent with sometimes prominent dark/light or red banding; pelvic fins unmarked.

Color in preservative. Head and body pale yellowish with dark markings as described for fresh specimens, all other colors lost; relative intensity of 5 dark body bars is an important taxonomic character and is conserved in well-preserved specimens– in *E. flavus*, bars are about same intensity, a few individuals with last bar darker than others (as in Fig. 6D). Notably, in preserved specimens melanophores extend well onto proximal caudal-fin rays and can be more distinct than in fresh individuals since overlying yellow chromatophores are lost.

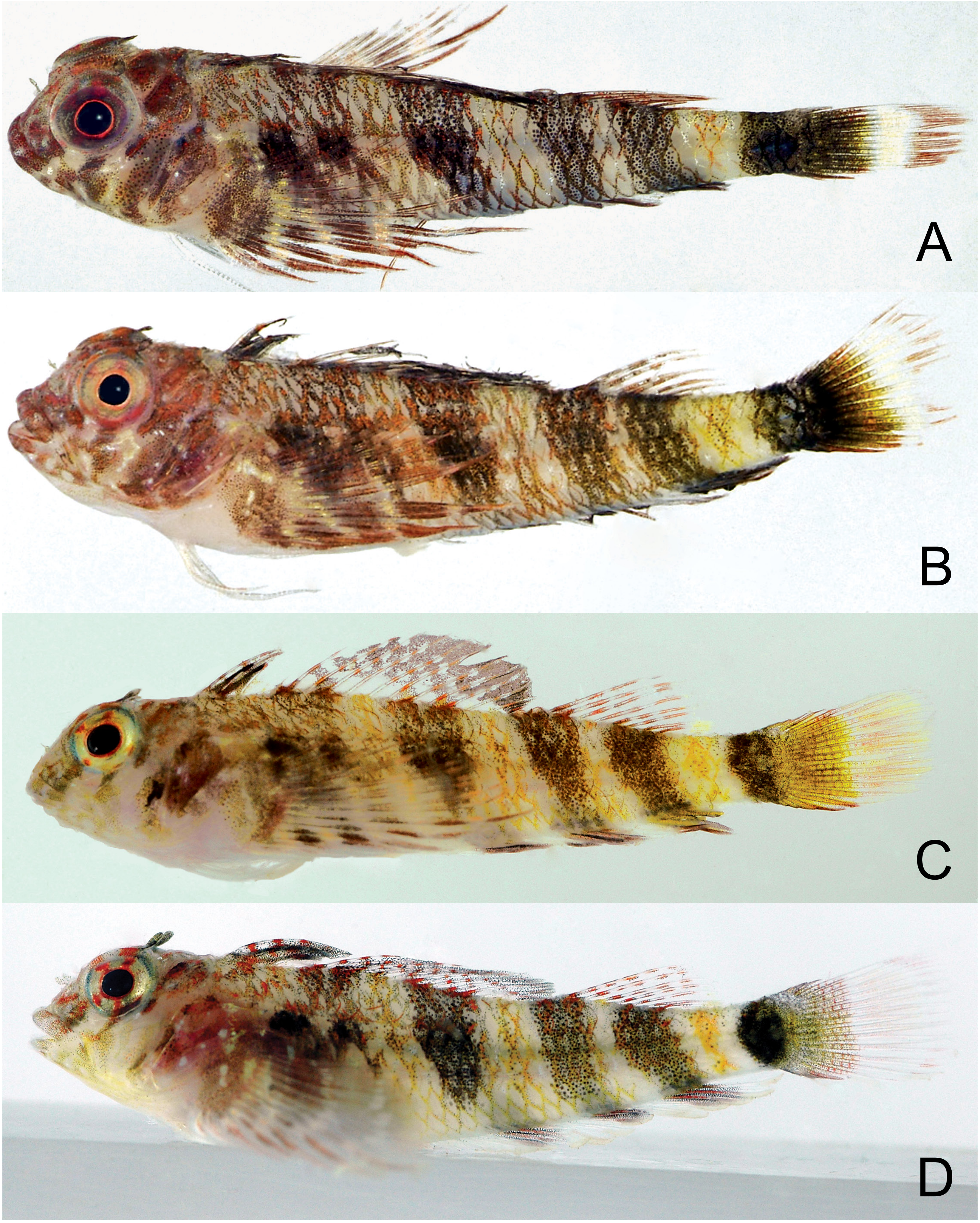

Figure 6. *Enneanectes flavus*, fresh paratypes: A: USNM 413227, 19.0 mm SL, male; B: USNM 413224, 22.0 mm SL, , female; C: AMNH 249279, female, 25.2 mm SL; D: AMNH 249262 (A & B, Tobago, C.C. Baldwin *et al*.; C & D, Paria Peninsula, Venezuela, J.L. Van Tassell & D.R. Robertson).

Etymology. The specific epithet *flavus* (Latin for yellow) is based on the bright yellow color of the mature male and treated as a masculine nominative singular adjective.

Distribution. Type specimens are from Tobago, Islas Los Frailes and Islas Los Testigos (off the northeastern coast of Venezuela), and the adjacent Paria Peninsula of Venezuela. Photographs of a similar yellow-tailed specimen from St. Vincent by Raymond Haberman appears to be *E. flavus* (Fig. 7); the new species may be overlapping with *E. matador* on St. Vincent.

Comparisons. The new species is apparently an allopatric sibling to *E. matador* from elsewhere in the Caribbean Sea (but may overlap in St. Vincent). DNA-confirmed *E. matador* are found on nearby Dominica, but which species occur on the intervening islands of Martinique, St. Lucia, and Barbados is unknown. The two species share the adult color pattern of a densely black-speckled second dorsal fin and the bright colors of yellow or red. They differ from each other in those colors and in the extent of black on the base of the caudal fin and over the cranium, and in the spacing of the last three body bars. Specifically, *E. matador* has only red on the caudal fin behind the dark last body bar, usually as a conspicuous narrow red bar (Figs. 8–10; no pigment remaining in preserved specimens) vs. the dark last body bar extending well onto the proximal third of the caudal fin, typically as relatively dense melanophores, in *E. flavus*. The patch of chromatophores over the cranium is almost all erythrophores in *E. matador*, but there is a clear uniform pattern of overlying melanophores in *E. flavus*.

An additional difference is in the spacing of the rear-body dark bars: while *E. matador* has the last three body bars usually somewhat evenly spaced, i.e. the 3–4 interspace is about the same as the 4–5 interspace, i.e. 97% as wide on average (range 0.74–1.47, n=27), compared to the 3–4 interspace being distinctly narrower than the last interspace in *E. flavus*, about half or less, on average 41% as wide (range 0–0.53%, n= 14; the zero represents the fish in Fig. 4 where the two bars are touching: note the interspace is measured at the lateral midline and is the pale area between bars). In addition, *E. flavus* has three dark blotches along the anal fin (Fig. 5C & D) vs. usually 4 (sometimes 5) in *E. matador*, although the anal fin of both species becomes uniformly dusky in colorful mature males.

The new species and *E. matador* share an unscaled abdomen, three rows of scales above the lateral line, and a blunt snout with *E. boehlkei*, *E. deloachorum*, and *E. wilki*. The latter three species form a widespread species complex dividing up the Caribbean in a somewhat similar way to *E. flavus* and *E. matador*: i.e. with *E. boehlkei*

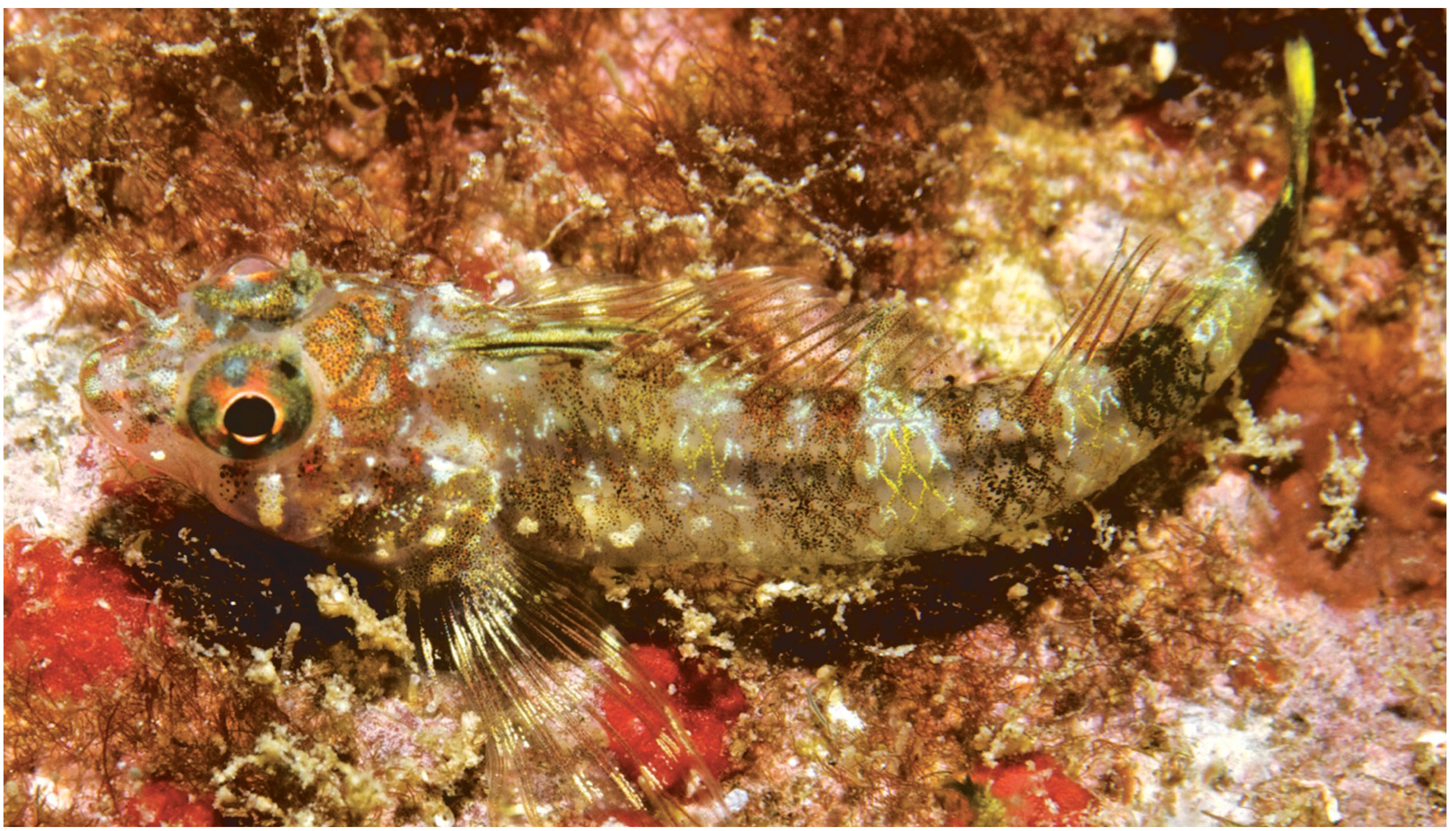

Figure 7. *Enneanectes flavus*?, note densely speckled second dorsal fin and yellowish caudal fin, St. Vincent (R. Haberman).

Figure 8. *Enneanectes matador*, note densely speckled second dorsal fin and abruptly red caudal-fin base, Eleuthera, Bahamas (F.H. Krasovec).

widespread in the Caribbean but replaced by *E. deloachorum* and *E. wilki* in the southeast corner of the Caribbean region, although in a slightly wider area: both extend up to Dominica and *E. deloachorum* extends to the ABC Netherlands Antilles (Victor 2013).

Biogeography. The new species is limited to northeastern Venezuela and Tobago, and perhaps St. Vincent, a region influenced by the Orinoco/Amazon River outflow, as well as by local upwelling off the Venezuelan coast, (Cherubin & Richardson 2007, Rueda-Roa *et al*. 2018). The influence of upwelling and river outflow can produce colder and more turbid conditions and limit the extent of coral growth and the composition of the sediments. Oceanographic conditions are also quite different in the southernmost Windward Island chain, where there is extensive inflow into the Caribbean, carrying equatorial water from the North Brazil Current (Johns *et al*. 2002). Little is known about the processes leading to the development of endemic species to the area, but a small set of reef fish species are endemic to the region (also numerous invertebrates). These fishes are mostly blennioids and gobioids, groups that do tend to split up into species complexes within the Greater Caribbean, perhaps as a result of demersal egg guarding combined with relatively short pelagic larval durations (Victor 2015). It is theorized that reduced dispersal allows populations to diverge to adapt to local conditions, a much more difficult prospect for species with high dispersal distances.

This group of southeastern Caribbean (SEC) endemics typically center in northeastern Venezuela and spread out to adjacent regions to varying degrees (Robertson & Van Tassell 2015); in some cases, endemics are limited to the Gulf of Cariaco and the offshore islands around Margarita, in others their range extends westward along the

Figure 9. *Enneanectes matador*, note densely speckled second dorsal fin and abruptly red caudal-fin base, Saba, Lesser Antilles (J.D. Haines).

Figure 10. *Enneanectes matador*, note speckled second dorsal fin and abruptly red caudal-fin base, Antigua, Lesser Antilles (J.M. Phillip).

northern coastline of Venezuela or even to parts of Colombia or Panama, or eastward to the offshore islands of Los Testigos, the Paria Peninsula, and Trinidad and Tobago, or farther up the Windward chain of the Lesser Antilles, i.e. Grenada and St. Vincent. Interestingly, many of these SEC endemics do not occur on the offshore coral-rich islands of Bonaire, Curacao, and the Los Roques Archipelago, despite their close proximity to the mainland of Venezuela. Precise ranges of these species are often not well documented, and additional studies are needed to resolve the actual processes underlying these range variations.

Examples of SEC endemic blennies and gobies include the tight-range species found only in the northeast of Venezuela, such as *Emblemaria diphyodontis*, *Emblemariopsis randalli, Protemblemaria punctata*, and *Coryphopterus venezuelae* (*sensu* Cervigón 1994). In addition, there are species also found eastward to Tobago, such as *Acanthemblemaria johnsoni* (Almany & Baldwin 1996) and *Starksia rava* (Williams & Mounts 2003), and some onwards variously to the southernmost Lesser Antilles and/or westward across Venezuela (*Acanthemblemaria medusa* (*sensu stricto*), *Elacatinus randalli*, *Emblemariopsis bottomei, E. ramirezi*, and *Enneanectes flavus*, *E. deloachorum*, and *E. wilki*), or on to Colombia (*Acanthemblemaria* aff. *rivasi, Chaenopsis resh*), or even to Panama (*Tigrigobius zebrellus*). A few of these broad SEC endemics are also found on the nearby offshore coral-rich islands (*Acanthemblemaria medusa*, *Elacatinus randalli*, *Emblemariopsis bottomei*, and *Starksia guttata*). Supporting the case for reduced dispersal ability permitting local speciation in the SEC is the fact that some toadfishes are also endemic to the area, and toadfishes are one of the very few marine fish families that lack a pelagic larval phase. These toadfishes include *Batrachoides manglae*, common in the Cariaco Basin and extending westward to Colombia, and *Thalassophryne maculos*a also abundant in Venezuela, as well as westward to Colombia and Panama and eastward to Tobago (Cervigón 1994, Collette 2002, Robertson & Van Tassell 2015).

Genetic Analysis

Mitochondrial DNA sequences have been useful in delineating new species in the genus *Enneanectes*, which shows relatively deep divergences between lineages. 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. Victor (2017) presented a phenetic tree of mtDNA sequences for 7 species from the region. Despite the genetic divergence, related species are morphologically very similar and DNA identification assisted in confirming diagnostic differences in marking patterns.

In the case of *E. flavus*, the divergence between the two sibling species is relatively low (Fig. 11); *E. flavus* is only 2.1% divergent from *E. matador* (minimum interspecific distance by K2P; 2.36% p-distance). Notably, *E. matador* is comprised of two close but separate lineages, one wide ranging, from the Virgin Islands to Dominica

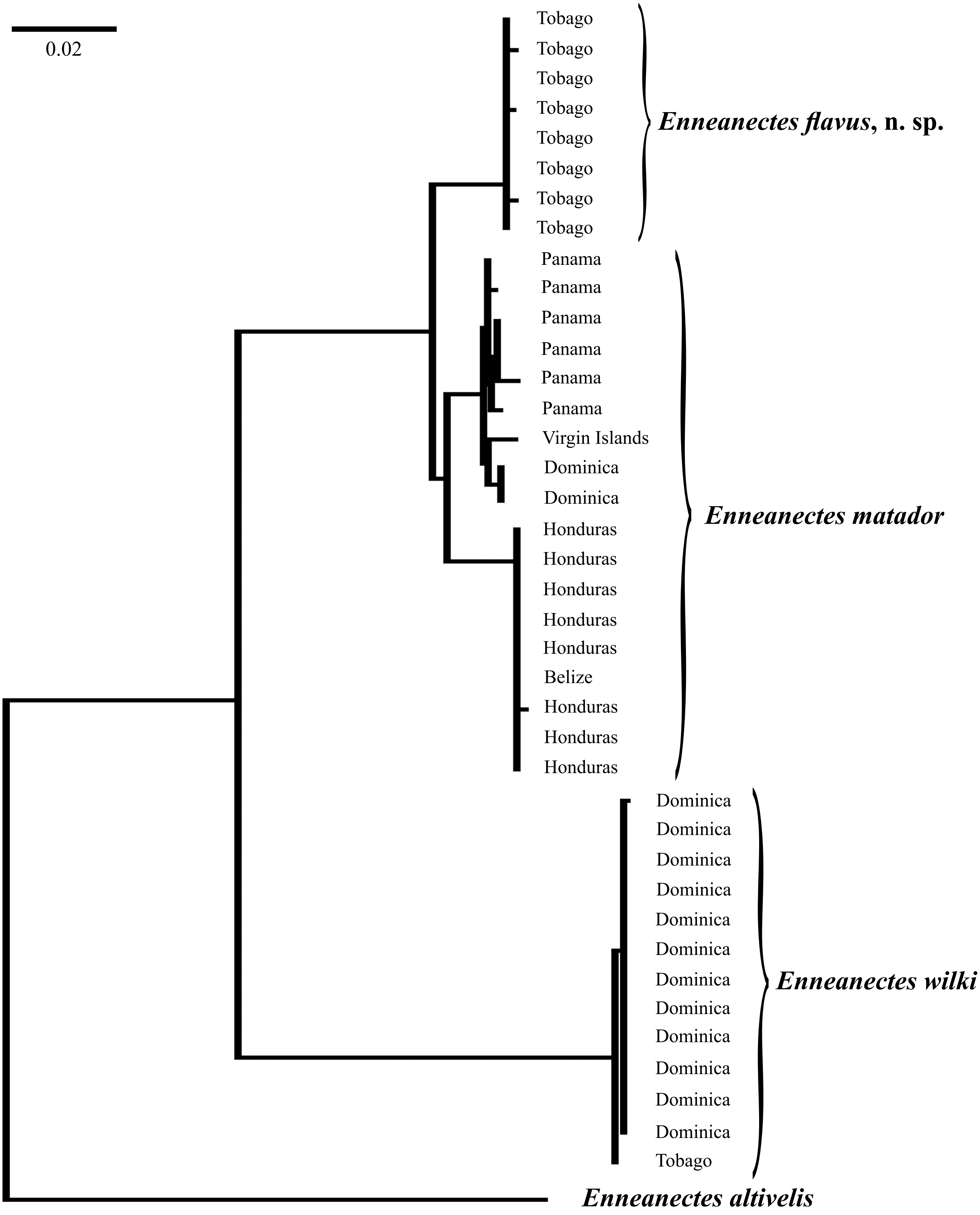

Figure 11. The neighbor-joining phenetic tree of species of the triplefin genus *Enneanectes* based on mtDNA COI sequences, following the Kimura two-parameter model (K2P) generated by BOLD (Barcode of Life Database). The scale bar at left represents a 2% sequence difference. Collection locations for specimens are indicated. GenBank accession numbers and collection data for the sequences in the tree are listed in Appendix 1. *Enneanectes altivelis* is used an outgroup.

and on the opposite side of the Caribbean in Panama, while the other so far is only from Belize and Honduras. Those two lineages diverge by 1.8% (minimum interspecific distance by K2P; 2.0% pairwise), but thus far appear to have the same phenotype, and therefore represent two genetically divergent lineages of the same species, or genovariants (*sensu* Victor 2015). Since the two genovariant lineages are (barely) monophyletic in this limited analysis, the description of *E. flavus* does not raise the prickly issue of new taxa creating paraphyly in the remaining branches of a multibranched lineage, which invalidates the status of the set of remaining branches (by making them not monophyletic). Monophyly is generally accepted as a condition of species definitions and genus designations, and reviews such as Mutanen *et al*. (2016) have highlighted the incidence of paraphyly among cryptic species complexes.

Revised Key to the *Enneanectes* species (9 spp.) of the Greater Caribbean

(note mature males have uniformly dusky anal fins; blotch patterns only in females and immature fish)

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, i.e. two equal sized plus one additional much smaller row 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 only 11 (10–12); second dorsal-fin spines almost always 11; pectoral-fin rays almost always 14; usually 6 or 7 dark blotches 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 blotches; 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 small 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 band followed by a wide dark or dusky reddish band; anal fin usually unmarked on preserved specimens; in life rear body typically bright red (common, shallows; Florida, Bahamas, Caribbean) .... ***E. jordani***

3b. Preoperculum behind eye naked; no series of small 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 6 to 8 dark blotches; in life rear body not bright red (uncommon, shallows; Bahamas, Virgin Islands, Belize, Honduras, Antigua, Yucatán & Providencia) .... ***E. quadra***

4a. Snout long and sloping, horizontal distance forward of eye about equal to eye diameter; last three body bars usually about equally dark, anterior margin of last body bar sloping down and back (i.e. 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. Snout blunt, horizontal distance forward of eye usually much less than eye diameter; last one or two body bars distinctly darker than preceding bars (except *E. flavus*, *E. matador*, and *E. wilki*); preorbital flange spiny; usually 14–16 pored lateral-line scales 5

5a. Second dorsal fin broadly speckled black in mature adults; caudal fin (and often rear body) yellowish or reddish, more brightly colored in mature males 6

5b. Second dorsal fin with only dark edge and three dark rounded spots at base of membranes; rear body of mature males not bright yellowish or reddish 7

6a. Caudal fin reddish (often a narrow red bar at base with an abrupt transition from black caudal peduncle to red) and no obvious melanophores on caudal fin proper (unmarked in preserved fish); cranium mainly red in life (pale in preservative), without melanophore concentrations; head and body often overall reddish; interspace between 3rd and 4th body bars roughly equal to interspace between other body bars (from 73-147% of last interspace), usually 4 or more dark blotches along anal fin (shallow reefs; W. Caribbean, Greater & Lesser Antilles down to Dominica) .... ***E. matador***

6b. Caudal fin yellowish with basal portion dark or dusky, merging with dark last body bar; cranium with melanophore array; rear body bright yellow in mature males; interspace between 3rd and 4th body bars about half or less of interspace between 4th and 5th body bars (from 0–53%); usually 3 dark blotches along anal fin (shallow reefs; N.E. Venezuela & Tobago [& St. Vincent?]) .... ***E. flavus*, n. sp.**

7a. Fifth body bar much darker than first four and usually wider than 4–5 interspace; first 4 body bars usually indistinct, frequently barely distinguishable (esp. in Bahamas & Virgin Islands); no accessory interspace bar or dark patch in 4–5 interspace; no red bar on base of caudal fin following last body bar; usually 4 or 5 dark blotches along anal fin (common, shallow reefs; Florida, Bahamas, N. & W. Caribbean, Antilles south only to St. Kitts) .... ***E. boehlkei***

7b. Fifth body bar not much darker than fourth bar and usually narrower than 4–5 interspace; an accessory interspace bar or dark patch within 4–5 interspace; often a dusky red bar following last body bar; frequently 3 or 6 dark blotches along anal fin 8

8a. 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 4 or fewer dark blotches along anal fin (common, shallow reefs; Dominica to ABC Netherlands Antilles) .... ***E. deloachorum***

8b. 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 6 dark blotches along anal fin (common, shallow reefs; Dominica to Tobago) .... ***E. wilki***

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Appendix 1. Specimen data and GenBank accession numbers for the mtDNA COI barcode sequences used in the phenogram in Figure 8, following the order in the tree.

Genus	species	Collection site	Voucher	GenBank #	Collector/Source
Enneanectes	*flavus*, n. sp.	Tobago	USNM 413225	JQ842850	C. Baldwin *et al*., USNM
Enneanectes	*flavus*, n. sp.	Tobago	USNM 413227	JQ842855	C. Baldwin *et al*., USNM
Enneanectes	*flavus*, n. sp.	Tobago	USNM 413344	JQ842844	C. Baldwin *et al*., USNM
Enneanectes	*flavus*, n. sp.	Tobago	USNM 413224	JQ842845	C. Baldwin *et al*., USNM
Enneanectes	*flavus*, n. sp.	Tobago	USNM 414291	JQ842849	C. Baldwin *et al*., USNM
Enneanectes	*flavus*, n. sp.	Tobago	USNM 413228	JQ842847	C. Baldwin *et al*., USNM
Enneanectes	*flavus*, n. sp.	Tobago	USNM 413226	JQ842848	C. Baldwin *et al*., USNM
Enneanectes	*flavus*, n. sp.	Tobago	USNM 414292	JQ842851	C. Baldwin *et al*., USNM
Enneanectes	*matador*	Panama, Portobelo	UF185609-10.6	KC860836	B. Victor
Enneanectes	*matador*	Panama, Portobelo	UF185608-14.1	KC860830	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	UF185608-18.8	KC860831	B. Victor
Enneanectes	*matador*	Panama, Portobelo	UF185608-19	KC860829	B. Victor
Enneanectes	*matador*	St. Thomas, USVI	UF185607	KC860835	B. Victor
Enneanectes	*matador*	Dominica	UF185603	KC860832	B. Victor
Enneanectes	*matador*	Dominica	UF185600	KC860834	B. Victor
Enneanectes	*matador*	Honduras	u872eb131	JN313599	B. Victor
Enneanectes	*matador*	Honduras	u872en98	KC860794	B. Victor
Enneanectes	*matador*	Honduras	u8630en156	KC860795	B. Victor
Enneanectes	*matador*	Honduras	u871en124	KC860797	B. Victor
Enneanectes	*matador*	Honduras	u873en161	KC860798	B. Victor
Enneanectes	*matador*	Belize	ECO-CH LP 4540	HQ573473	L. Vásquez-Yeomans
Enneanectes	*matador*	Honduras	u871enn89	KC860796	B. Victor
Enneanectes	*matador*	Honduras	u873en114	KC860792	B. Victor
Enneanectes	*matador*	Honduras	u873en101	KC860793	B. Victor
Enneanectes	*wilki*	Dominica	UF185601-13.7	KC860837	B. Victor
Enneanectes	*wilki*	Dominica	UF185611-15.9	KC860844	B. Victor
Enneanectes	*wilki*	Dominica	UF185601-14.7	KC860847	B. Victor
Enneanectes	*wilki*	Dominica	UF185611-13.4	KC860839	B. Victor
Enneanectes	*wilki*	Dominica	UF185604-13.7	KC860838	B. Victor
Enneanectes	*wilki*	Dominica	UF185604-16.7	KC860842	B. Victor
Enneanectes	*wilki*	Dominica	UF185635	KC860840	B. Victor
Enneanectes	*wilki*	Dominica	UF185604-15.7	KC860841	B. Victor
Enneanectes	*wilki*	Dominica	UF185601-13.8	KC860843	B. Victor
Enneanectes	*wilki*	Dominica	UF185610	KC860848	B. Victor
Enneanectes	*wilki*	Dominica	UF185611-14.3	KC860845	B. Victor
Enneanectes	*wilki*	Tobago	USNM 413343	JQ842854	C. Baldwin *et al*., USNM
Enneanectes	*altivelis*	Panama, Portobelo	n7531bea237	KC860802	B. Victor