

ROBERT H. GIBBS, JR. AWARD CONTRIBUTION

Description of the First Species of *Polylepidion* (Teleostei: Labridae) from the Atlantic Ocean with Analysis of Evolutionary Relationships of the New Species

Carole C. Baldwin¹, Dahiana Arcila², D. Ross Robertson³, and Luke Tornabene⁴

Submersible diving in the 1980/90s in the Bahamas and Cuba and 2013–2018 at Curaçao, Dominica, and Roatan resulted in the collection of a new species of *Polylepidion*, a genus of wrasse previously known only from the Indian and Pacific Oceans. The new species, which inhabits the rariphotic reef-fish faunal zone at depths of 219–457 m, is another example of a deep-reef species belonging to a largely shallow-reef family, in this case the family Labridae. Here, we describe the new species and provide a phylogenetic placement for it by adding new sequence data from 12 genetic markers for the new species and one of its two congeners (*P. cruentum* from the eastern Pacific Ocean) to a previously published dataset comprising 336 species of wrasses that includes the other congener, *P. russelli*, from the Indian and West/Central Pacific Oceans. Our results resolve the phylogenetic history of the species of *Polylepidion* and provide the first molecular support for the monophyly of the genus.

THE marine-fish family Labridae comprises over 600 species in 82 genera displaying a broad array of anatomical and ecological adaptations across tropical and subtropical waters (e.g., Sanderson, 1990; Parenti and Randall, 2000; Tatom-Naecker and Westneat, 2018; Ghezelayagh et al., 2022). Although most wrasses inhabit shallow waters, a few species are limited to depths of ~100 to 400 m depth, including those in *Polylepidion* Gomon 1977. This genus is currently known from *P. cruentum* Gomon 1977 in the tropical eastern Pacific Ocean (Gomon, 1995; Britzke et al., 2021) and *P. russelli* (Gomon and Randall, 1975) in the Central Pacific (Gomon and Randall, 1975), West Pacific (Masuda et al., 1984; Hubert et al., 2011; GBIF, 2022; Rob Meyers, pers. comm.), and Indian (Béarez et al., 2013; Hobbs et al., 2014) Oceans. While exploring the fish fauna of deep reefs at Curaçao in 2013–2016 through human-occupied submersible diving as part of the Smithsonian Institution's Deep Reef Observation Project (DROP), several specimens of *Polylepidion* were collected at depths of 219–272 m using the *Curasub*. The genus is easily distinguished from closely related wrasse genera by numbers of dorsal- and anal-fin rays (Gomon, 1977, 1997). Subsequent correspondence with Grant Gilmore, formerly of the Harbor Branch Oceanographic Institute, revealed that he and colleagues had previously collected the same species decades earlier to depths of 367 m in the Bahamas and Cuba aboard the *Johnson Sea Link-I (JSL-I)* submersible and that he had made precise color-pencil sketches of juveniles

and adults of the species. Further DROP diving in Dominica (*Curasub*) in 2016 and Roatan Island (*Idabel*) in 2017–2018 resulted in the collection of additional specimens at depths of ~300 m. ROV imagery of the Atlantic *Polylepidion* was captured off the Florida Keys in 2011 and Puerto Rico in 2013 (see “Distribution and Habitat” below).

In his description of *Polylepidion*, Gomon (1977) noted that, morphologically, the genus closely resembles *Decodon*, *Pimelometopon*, *Semicossyphus*, and *Bodianus*, the last a historically catch-all wrasse genus to which *P. russelli* was originally assigned (Gomon and Randall, 1975) and to which *Semicossyphus* (including *Pimelometopon* based on Gomon [1997]) was recently provisionally relegated (Santini et al., 2016). Molecular phylogenies of the Labridae revealed a sister-group relationship between *Polylepidion* and *Decodon* (Aiello et al., 2017; Hughes et al., 2022; Larouche et al., 2022) and a paraphyletic *Bodianus* without the inclusion of *Clepticus*, *Decodon*, *Polylepidion*, and *Semicossyphus* (Aiello et al., 2017) or without the inclusion of *Clepticus* and *Semicossyphus* (Hughes et al., 2022; Larouche et al., 2022). By combining the recently published time-calibrated phylogenomic tree for the Labridae (Hughes et al., 2022) with genetic sequences for over 300 species of wrasses (Aiello et al., 2017), we investigated the evolutionary history and timing of speciation events of the genus *Polylepidion*, incorporating new genetic data for *P. cruentum* and the new species. Here we describe the new *Polylepidion* as the first species of the genus in

¹ Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560; ORCID: 0000-0002-2875-0474; Email: baldwinc@si.edu. Send correspondence to this address.

² Sam Noble Oklahoma Museum of Natural History and Department of Biology, University of Oklahoma, Norman, Oklahoma 73072; ORCID: 0000-0002-5126-1345; Email: dahiana.arcila@ou.edu; Present address: Scripps Institution of Oceanography, University of California San Diego, San Diego, California 92093-0244; Email: dkarcila@ucsd.edu.

³ Smithsonian Tropical Research Institute, Balboa, Republic of Panama; ORCID: 0000-0003-3972-149X; Email: robertsondr@si.edu.

⁴ University of Washington, School of Aquatic and Fishery Sciences, Burke Museum of Natural History and Culture, Seattle, Washington 98195; Email: luke.tornabene@gmail.com.

Submitted: 1 September 2022. Accepted: 8 December 2022. Associate Editor: M. T. Craig.

© 2023 by the American Society of Ichthyologists and Herpetologists DOI: 10.1643/i2022075 Published online: 13 April 2023

the Atlantic and report the results of the phylogenetic analysis.

MATERIALS AND METHODS

Specimen collection.—Specimens of the new species were collected from Caribbean and Bahamian deep reefs using human-occupied submersibles in Curaçao and Dominica (*Curasub*), Honduras (*Idabel*), and Bahamas (*Johnson Sea Link-I—JSL-I*). Both the *Curasub* and *Idabel* deployed a quinaldine fish-anesthetic solution to immobilize fishes prior to suction into a hose that transfers specimens into a collection bucket. Technology for collecting with the *JSL-I* was similar except that the fish toxicant rotenone was used. Most Caribbean specimens were photographed at the surface, and some *in situ* video was recorded at Curaçao and Roatan. Caribbean specimens were tissue sampled prior to fixation in formalin and then subsequently transferred to 75% ethanol. Bahamian specimens were collected prior to the onset of routine tissue sampling in the field and are not genetic vouchers; however, Richard G. Gilmore, Jr. made detailed color-pencil sketches of some specimens prior to preservation. Specimens were accessioned in fish collections at the Scripps Institution of Oceanography (SIO), Smithsonian Institution's National Museum of Natural History (USNM), University of Florida (UF), University of Washington (UW), and Museo Historia Natural at Universidad Nacional Autónoma de Honduras en el Valle de Sula (MUVS). Collecting at Curaçao, Dominica, and Roatan was done under ACUC permits 2014-13 and 2017-11 to Baldwin.

Morphological character examination.—Counts and measurements follow Gomon and Randall (1978). Most specimens were X-rayed with a digital radiography system at USNM.

Molecular data and phylogenetic analyses.—Taxonomic sampling for genetic analyses comprised 336 species of wrasses from the most recent published dataset of the family Labridae (Aiello et al., 2017), including newly collected sequence data from *P. cruentum* and the new species (USNM 435298). For *P. cruentum*, we sequenced samples obtained from the Marine Vertebrate Collections at Scripps (SIO 10-18 and SIO 09-377). We follow Fricke et al. (2023, and references therein) in recognizing species of *Clepticus* and *Semicossyphus* as members of *Bodianus*.

DNA was extracted using the DNeasy tissue kit (Qiagen, Valencia, CA, USA) according to the manufacturer's protocol. Double-stranded DNA was synthesized via PCR using the same set of primers and PCR conditions described by Aiello et al. (2017) and Westneat and Alfaro (2005) for 12 genetic markers (12S, 16S, S7, CO1, CYTB, BMP4, DLX2, OTX1, RAG1, RAG2, TMO4C4, RHOD). The PCR products were electrophoresed in 1.5% low melting point agarose gels using a tris-acetate buffer for quality control and submitted for purification and sequencing in both directions at the Sequencing and Genomic Facilities of the University of Puerto Rico. Sequences were assembled, visualized, inspected, and concatenated in Geneious v10.0.9. All exon markers were aligned individually based on their underlying reading frame using the MAFFT aligner (Katoh and Standley, 2013). The 16S and 12S sequences were aligned with SATé using MAFFT and 25 iterations (Liu et al., 2009). The molecular dataset consisted of 6,209 sites for 336 species. All sequences

produced for this study have been deposited in NCBI (Supplemental Table S1; see Data Accessibility).

Phylogenetic relationships among maximum likelihood (ML) searches were conducted in RAXML v8.2.10 using the GTRGAMMA model (Stamatakis, 2014). All gene fragments were partitioned by codon position and concatenated in a single super matrix. A total of 30 tree replicates were conducted to obtain the best-scoring tree across the different searches for the concatenated dataset and each gene fragment. Branch support was estimated using the rapid bootstrapping algorithm with 1,000 replicates under the GTRGAMMA model; the collection of bootstrapped trees was used to draw bipartition frequencies onto the optimal tree. Species-trees analyses were conducted using ASTRAL-2 (Mirarab and Warnow, 2015). This method addresses gene tree incongruence due to incomplete lineage sorting using unrooted gene trees as input to maximize the number of quartet trees shared between the gene tree and the species trees.

Divergence time estimation analyses used a “congruification” approach (Eastman et al., 2013) that matches compatible nodes between a reference and target phylogenetic tree. The reference tree consisted of the genome-wide time-calibrated tree of the family Labridae (Hughes et al., 2022) based on seven fossil calibrations, †*Phyllopharyngodon longipinnis*, †*Trigonodon jugleri*, †*Tautoga* sp., †*Symphodus westneati*, †*Calotomus preisli*, †*Bolbometopon* sp., and †*Coris sigismundi*. The target tree consisted of the Labridae tree based on nine genetic markers and 336 species (Aiello et al., 2017), including the newly generated data for *P. cruentum* and the new species of *Polylepion*. To interpolate the dates for the same nodes as the reference in the target tree, an ML tree was estimated using a backbone constraint approach. Based on the tree assembled using nine genetic markers, 158 of the 336 species were placed on the backbone tree based on 1,105 exon markers (Hughes et al., 2022). The remaining 178 species were placed in the phylogenomic backbone tree using a constraint ML search in RAXML and by codon partitions. The resulting ML tree was calibrated in TreePL (Smith and O'Meara, 2012) using the secondary calibrations extracted from the reference backbone phylogeny and the function “congruify” implemented in the R package *geiger* (Harmon et al., 2008).

Polylepion gilmorei, new species

urn:lsid:zoobank.org:act:C3EE7A2D-AEA9-46C1-BBEA-A8541F6AC0CA

Red-barred Wrasse (English), Vieja de Barras Rojas (Spanish), Labre à barre rouge (French)

Figures 1–3, Supplemental Figures S1–S2, Tables 1–2, Supplemental Table T1

Polylepion species A, Curaçao, Robertson and Van Tassell (2016), <https://biogeodb.stri.si.edu/caribbean/en/gallery/genus/5244>.

Polylepion species A, Pichincho, Quattrini et al. (2017): fig. 11B.

Polylepion sp., Curaçao, Baldwin et al. (2018): fig. 2.

Holotype.—USNM 445945, 87.5 mm SL, not a genetic voucher, French Bay, San Salvador, Bahamas Islands, 23°57.47'N, 74°30.20'W, *Johnson Sea Link-I (JSL-I)* submers-



Fig. 1. *Polylepion gilmorei*, holotype, USNM 445945, 87.5 mm SL: (A) photograph of preserved holotype by S. Raredon; (B) color-pencil drawing of fresh holotype by R. G. Gilmore, Jr.

ible, dive #2028, 367 m, rotenone, C. R. Robins and D. Liberatore, 5 May 1987.

Paratypes.—Bahamas: UF 248937, 54.3 mm SL, not a genetic voucher, SE Sandy Pt., San Salvador, Bahamas Islands, *JSL-I* dive #1290, 280 m, rotenone, R. G. Gilmore, Jr. and M. Flake, 17 October 1982; USNM 445946, 48.0 mm SL, not a genetic voucher, same collection data as holotype; USNM 445947, 35.8 mm SL, not a genetic voucher, Riding Rock, San Salvador, Bahamas Islands, *JSL-I* dive #1294, 282 m, rotenone, C. Donohoe and R. Cook, 19 October 1982; USNM 445948, 41.1 mm SL, not a genetic voucher, Riding Rock, San Salvador, Bahamas Islands, 24°02.9'N, 74°30.35'W, *JSL-I* dive #2023, 309 m, rotenone, C. R. Robins and M. Adams, 2 May 1987; USNM 445949, 34.4 mm SL, not a genetic voucher, Riding Rock, San Salvador, Bahamas Islands, 24°03.5'N, 74°32.5'W, *JSL-I* dive #1513, 279 m, rotenone, C. R. Robins and D. Liberatore, 31 October 1983. Curaçao: SIO 22-91, 51.8 mm SL, genetic-voucher specimen number CUR15123, Curaçao, southern Caribbean Sea, west of Substation Curaçao downline, 12°4'58.8"N, 68°53'56.4"W, *Curasub* submersible, dive #CURASUB15-20, 250 m, C. Baldwin, B. Brandt, and D. Felder, 21 September 2015; USNM 413995, 114.2 mm SL,

genetic-voucher specimen number CUR13087, Curaçao, southern Caribbean Sea, off Substation Curaçao downline, near 12°4'59.5"N, 68°53'56.8"W, *Curasub* dive #CURASUB13-MISC, no depth recorded, Substation Curaçao staff, 2012–2013; USNM 435298, 35.7 mm SL, genetic-voucher specimen number CUR15022, Curaçao, southern Caribbean Sea, off Substation Curaçao downline, 12°4'59.5"N, 68°53'56.8"W, *Curasub* dive #CURASUB15-06, 272 m, C. Baldwin, B. Van Bebber, D. R. Robertson, and C. Castillo, 11 February 2015; USNM 440432, 27.9 mm SL, genetic-voucher specimen number CUR16001, Curaçao, southern Caribbean Sea, east of Substation Curaçao downline, 12°4'59.5"N, 68°53'56.8"W, *Curasub* dive #CURASUB16-32, 219 m, C. Baldwin, B. Brandt, D. Pitassy, and T. Devine, 6 October 2016. Dominica: USNM 438664, 54.5 mm SL, genetic-voucher specimen number DOM16013, Saint George Parish, Roseau, Dominica (off Fisheries Dock), 15°17'40.6"N, 61°23'23.6"W, *Curasub* dive #CURASUB16-02, 262 m, A. Schrier, B. Brandt, and B. Van Bebber, 24 February 2016; USNM 440584, 34.1 mm SL, not a genetic voucher, western coast of Dominica, 15°37'11"N, 61°28'03"W, *Curasub* dive #CURASUB16-22, 244 m, B. Hoeksema, A. Schrier, B. Van Bebber, and D. Sipkema, 16 March 2016. Roatan: MUVS-447, 108 mm SL, genetic-

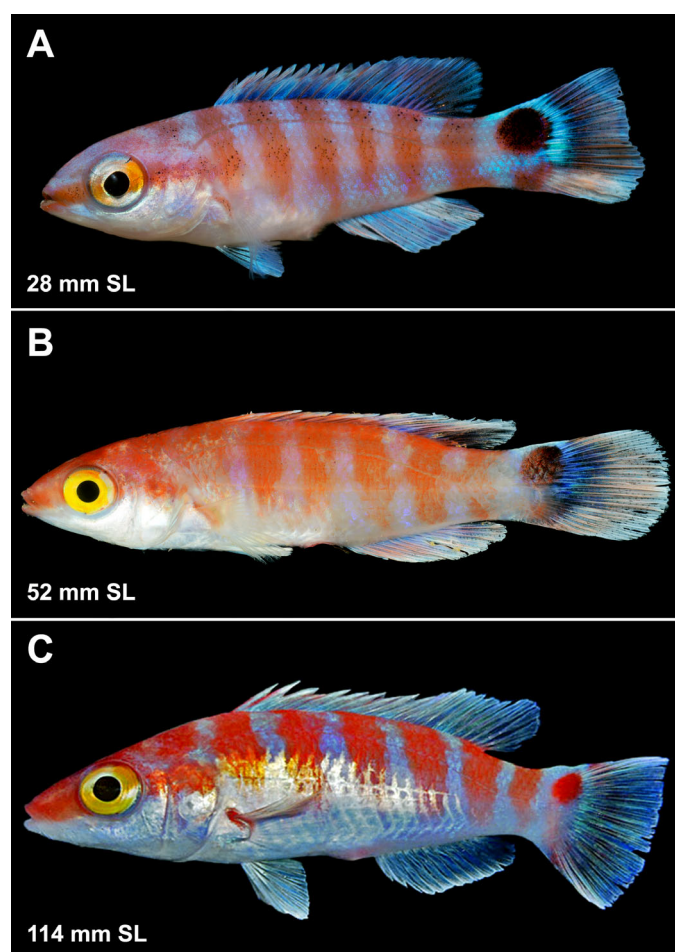


Fig. 2. Ontogeny of color pattern in selected paratypes of *Polylepion gilmorei*: (A) early juvenile, 27.9 mm SL, USNM 440432; (B) late juvenile, 51.8 mm SL, SIO 22-91; (C) adult, 114.2 mm SL, USNM 413995. Photographs by Barry Brown (A, C) and Darryl Felder (B).

voucher specimen number ROA17024, off Half Moon Bay, Roatan, *Idabel* submersible, dive #IDABEL 17-05, 305 m, L. Tornabene, R. Manning, and K. Stanley, 29 July 2017; UW 158149, 101 mm SL, genetic-voucher specimen number ROA18106, off Half Moon Bay, Roatan, *Idabel* dive #IDABEL 18-06, 305 m, R. Robertson, R. Manning, and K. Stanley, 8 June 2018.

Other Material (not examined): Cuba: juvenile (no length available), Cayo Rosario, Cuba, *JSL-I* dive #3054, 427 m, Rodolfo Claro, Dec. 1997 (illustrated by R. G. Gilmore, Jr.).

Diagnosis.—A revised diagnosis of *Polylepion* is presented after the species description. *Polylepion gilmorei*, the only species of *Polylepion* in the Atlantic Ocean, is distinguished from other wrasses by the following combination of characters: dorsal-fin rays usually XI, 11; anal-fin rays usually III, 11; pectoral-fin rays usually ii17; lateral-line complete, 38–44 tubed scales; scales above lateral line 2–4; scales not extending onto bases of dorsal and anal fins; scales on forehead extending anteriorly beyond or nearly to level of anterior nostrils; in life, multiple orange-red bars of pigment on dorsal portion of the trunk against an otherwise whitish background, and a red (adults) or black (juveniles) circular blotch on dorsal portion of caudal-fin base; inhabiting depths of 219–457 m.

Description.—Counts and measurements are summarized in Tables 1 and 2. Counts of holotype are given first, followed by any variation in the 13 paratypes in parentheses. Dorsal-fin rays XI, 11 (one paratype with XII, 10); anal-fin rays III, 11 (one paratype with III, 10); pectoral-fin rays ii17 (one paratype with ii16); pelvic-fin rays I, 5; dorsal unsegmented caudal-fin rays 8 (seven paratypes with 9); dorsal segmented, unbranched caudal-fin rays 2; segmented, branched caudal-fin rays 6+6 (one paratype with 6+5); ventral segmented, unbranched caudal-fin rays 2; ventral unsegmented caudal-fin rays 8 (four paratypes with 9); vertebrae 11+17; lateral-line scales 39, 41 (38–44, too many scales missing in four paratypes to obtain accurate counts); scales above lateral line 3 (2–4, too many scales missing in two paratypes to obtain accurate counts); scales below lateral line 11 (9–12, too many scales missing in six paratypes to obtain accurate counts); predorsal scales 21 (20–25, too many scales missing in eight paratypes to obtain accurate counts); gill rakers 7+10, last two tiny (6–8+9–10, last one to three tiny).

Body deepest around midbody, tapering posteriorly. Head pointed, profile mostly straight except for convexity between orbits. Scales on trunk not extending onto dorsal- and anal-fin bases. Lateral line continuous, smoothly curved. Head mostly scaled except snout, lips, gular region, and branchiostegals. Scales extending anteriorly on forehead in advance of or nearly to anterior nostrils.

Posterior end of maxilla reaching vertical through anterior edge of orbit. Upper and lower jaws each with two pairs of large canines anteriorly. Anterior canines in upper jaw of similar size, followed by a row of much smaller canines (7 in holotype) and one moderately large canine at rear corner of jaw. Medial canines of large anterior pair in lower jaw smaller than more lateral ones.

Dorsal fin continuous, originating just anterior to vertical through base of pectoral fin. Membrane between dorsal- and anal-fin spines deeply incised, membrane forming small flags of tissue at tips of spines. Dorsal and anal fins slightly pointed posteriorly, longest rays not reaching margin of hypural plate in adults. Posterior margin of caudal fin somewhat rounded in juveniles, more truncate in adults. Posterior extent of pelvic fin not reaching anus.

Adults pale in alcohol with no dark markings on head, trunk, or fins (Fig. 1A). Juveniles similar except with circular blotch of melanophores on dorsal base of caudal fin. In addition to that blotch, smallest juvenile (27.9 mm SL) with six indistinct black bars on trunk, a dark stripe extending from snout to operculum, some dark pigment on pectoral-fin base, and dark spots present on lower caudal-fin base. A 35.7 mm juvenile with remnants of these dark markings.

In life (Figs. 1B, 2C), adults with six orange-red bars of pigment on dorsal portion of trunk, anteriormost bars terminating ventrally slightly below midbody, last bar extending from dorsal to ventral margins of caudal peduncle, bar much paler ventrally. Large red circular blotch on dorsal base of caudal fin, irregular and paler red bar below this blotch. Upper half of head red, eye mostly yellow. Indistinct stripe of red pigment extending along center of entire dorsal fin, stripe narrow on spinous dorsal fin, usually broader on soft dorsal fin. Uppermost and lowermost caudal-fin rays red, forming the margins of a broad, indistinct bar of red pigment on central area of caudal fin. Oblong blotch or streak of red pigment on pectoral-fin base. Gilmore's color-pencil sketch of the holotype (Fig. 1B) shows a broad red stripe centrally on

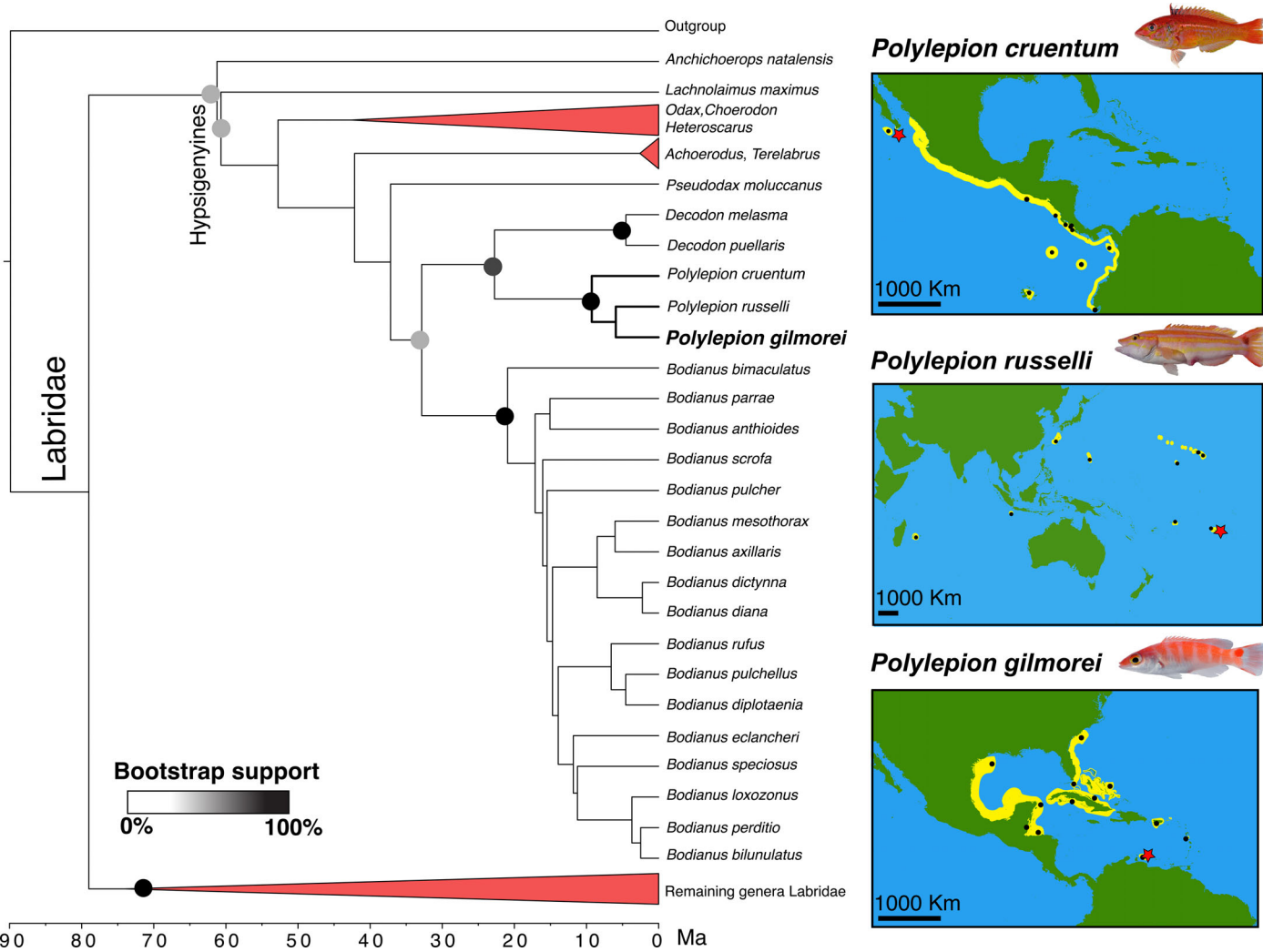


Fig. 3. Time-calibrated phylogeny and biogeographic distribution of species of *Polylepion*. Red stars indicate location of genetic voucher specimens; black spots indicate vouchered locations of other individuals of each species. A complete phylogeny with tip labels is available in Supplemental Fig. S2 (see Data Accessibility).

Table 1. Counts and differences in head squamation of species of *Polylepion*. Data for *P. russelli* are from Gomon and Randall (1978) and Béarez et al. (2013), for *P. cruentum* from Gomon (1977) and Britzke et al. (2021).

	<i>P. russelli</i>	<i>P. cruentum</i>	<i>P. gilmorei</i>
Number of specimens	5	19	14
Dorsal-fin rays	XI, 11	XI, 11–12*	XI–XII, 10–11*
Anal-fin rays	III, 10–11*	III, 12–13*	III, 10–11*
Pectoral-fin rays	ii, 18–19	ii, 17	ii, 16–17*
Lateral-line scales	48–52	49–53	38–44
Predorsal scales	25–32	25–32	20–25
Scales above lateral line	5	2 ¹ / ₂ –4 ¹ / ₂	2–4
Scales below lateral line	17–18	16–18	9–12
Vertebrae	11+17	11+17	11+17
Caudal rays	9+2+12+2+9	9–11+2+12+2+9–11	8–9+2+12+2–3+8–9
Gill rakers	5–6+10–11=15–16	5–8+10–12=15–19	6–8+9–10=16–17
Squamation on forehead	Extending only to anterior extent of orbit or to anterior nostril*	Extending in advance of anterior nostril	Extending in advance of or nearly to anterior nostril

**Polylepion cruentum* from northern Peru was reported to have XI, 12 dorsal-fin rays and III, 13 anal-fin rays (Britzke et al., 2021), all others with counts of XI, 11 and III, 12; *P. gilmorei*, USNM 445948, with XII, 10 dorsal-fin rays, all others with XI, 11; holotype of *P. russelli* (Gomon and Randall) and one paratype of *P. gilmorei*, USNM 445948, with III, 10 anal-fin rays, other specimens with III, 11; *P. gilmorei*, USNM 445946, with ii, 16 pectoral-fin rays on both sides, all others with 17. Indian Ocean specimen of *P. russelli* with scales on forehead extending to anterior nostril (Béarez et al., 2013), Pacific specimens with scales extending only to anterior extent of orbit.

Table 2. Morphometric data for type specimens of species of *Polylepion*. Standard length is in mm, other measurements in percentages of standard length. Data for *P. russelli* are from Gomon and Randall (1978), for *P. cruentum* from Gomon (1977). Measurements for *P. gilmorei* were taken to the nearest tenth of a millimeter, and percentages of standard length are represented by appropriate number of significant digits.

	<i>P. russelli</i>		<i>P. cruentum</i>		<i>P. gilmorei</i>	
	Holotype	Paratypes (3)	Holotype	Paratypes (17)	Holotype	Paratypes (13)
Standard length (mm)	308.0	249.0–313.0	110.0	56.8–199.0	87.5	27.9–114
Body depth	26.6	24.9–29.3	27.3	23.5–29.4	28	24–31
Head length	35.6	35.6–37.7	40.4	38.9–43.8	36	31–39
Snout length	13.1	12.1–13.2	9.5	7.6–12.3	10	6.4–11
Orbit diameter	6.5	6.5–7.2	10.7	8.0–12.0	11	9.1–12
Bony interorbital width	6.3	6.3–8.1	5.6	4.5–6.0	9.1	7.9–12
Upper jaw length	11.2	11.2–11.9	11.1	9.7–14.2	9.9	7.8–11
Predorsal length	37.9	35.5–38.8	36.4	35.7–38.1	39	36–42
Length of dorsal-fin base	49.9	44.7–50.9	50.4	46.9–52.6	46	41–50
Length of depressed dorsal fin	59.9	59.9–64.6	64.1	59.9–68.2	59	52–61
Length of first dorsal-fin spine	5.7	5.1–7.1	7.9	7.0–8.6	7.2	6.1–10
Length of last dorsal-fin spine	9.8	9.8–10.6	10.2	9.1–12.2	13	12–15
Length of anal-fin base	20.5	20.2–21.3	22.8	21.8–25.3	21	19–25
Length of depressed anal fin	28.7	28.7–31.7	34.2	33.9–38.2	32	29–34
Length of third anal-fin spine	8.5	6.5–8.5	10.3	8.6–10.9	10	8.9–13
Least depth of caudal peduncle	13.9	13.9–15.5	13.0	11.8–13.6	15	13–16
Length of upper caudal-fin rays	23.0	23.0–25.2	21.4	19.5–23.1	23	8.8–28
Length of middle caudal-fin rays	20.1	19.8–20.9	21.0	20.7–24.2	22	20–31
Pectoral-fin length	17.1	17.0–18.4	18.2	17.3–20.6	18	16–21
Pelvic-fin length	18.1	14.4–18.1	20.4	14.7–25.0	17	13–19

soft portion of anal fin, but this pigment not apparent in photographs of freshly caught specimens, in which the extent of red pigmentation also varies on the dorsal fin (Fig. 2).

Juveniles (Fig. 2A, B) with the six orange-red trunk bars extending further ventrally than in adults, bars containing some melanophores mixed in with the red chromatophores in smallest juveniles. Spot on upper base of caudal fin relatively larger than in adults, black or a black/red mix and broadly rimmed with iridescent white. Head pigment similar to that of adults except red on upper portion of head pale, setting off a distinctive narrow red stripe running from tips of jaws through center of eye to upper rear corner of operculum. Other fin pigment similar to that of adults.

Distribution and habitat.—Known from specimens collected in the Bahamas, Cuba, Curaçao, Dominica, and Roatan; from imagery taken by the ROV *Kraken* aboard the NOAA R/V *Nancy Foster* on 28 September 2011 at 300 m on the Pourtales Terrace, south of the Florida Keys (Andrew David, NOAA, pers. comm.); and from imagery taken at 240–457 m by the ROV *Deep Discover* tethered to the camera sled *Seirios* deployed from the NOAA Ship *Okeanos Explorer* on seamounts east and west of Puerto Rico (Quattrini et al., 2017; fig. 11B). The Pourtales Terrace image is reproduced here in Supplemental Fig. 1A (see Data Accessibility). *Polylepion gilmorei* inhabits depths of 219–457 m and associates with hard substrates, including rocky ledges and patches of dead corals or rocks lying on silty sand bottoms (Supplemental Fig. 1B [see Data Accessibility]; *in situ* video from Roatan is available from the Zenodo digital repository: <https://doi.org/10.5281/zenodo.7304806>).

Etymology.—Named in honor of Richard Grant Gilmore, Jr., in recognition of the contributions he has made to our

knowledge of the western Atlantic and Caribbean deep-reef fish fauna, including the first discovery of the new *Polylepion*.

Comparisons.—Counts and measurements of the species of *Polylepion* are summarized in Tables 1 and 2. Currently the only known species of the genus in the Atlantic Ocean, *P. gilmorei* differs from *P. cruentum* in having fewer anal-fin rays (III, 10–11, almost always 11, vs. III, 12–13, usually 12 in *P. cruentum*). It differs from *P. russelli* in having fewer pectoral-fin rays (ii, 16–17, usually 17, vs. ii, 18–19 in *P. russelli*) and fewer scales above the lateral line (2–4 vs. 5 in *P. russelli*). *Polylepion gilmorei* differs from both congeners in having fewer lateral-line scales (38–44 vs. 48–52 in *P. russelli* and 49–53 in *P. cruentum*) and scales below the lateral line (9–12 vs. 17–18 in *P. russelli* and 16–18 in *P. cruentum*). The new species further differs from its congeners in color pattern, especially in having multiple red bars of pigment on the dorsal portion of the trunk against an otherwise whitish background (vs. color pattern of trunk variable in *P. cruentum* and *P. russelli*, usually with at least some yellow stripes on the trunk against a pinkish background in small specimens, never with distinct red bars). The largest specimen of *P. gilmorei* is 114 mm SL, whereas that of *P. cruentum* is 199 mm SL and *P. russelli* 313 mm SL, which could indicate that *P. gilmorei* is a smaller species than its congeners.

Relationships.—(Fig. 3) Early morphological studies noted the resemblance among *Bodianus*, *Decodon*, and *Polylepion* and suggested a close relationship between species of *Polylepion* and *Decodon* (Gomon, 1997). The results of our phylogenomic analysis are congruent with those of Aiello et al. (2017), Hughes et al. (2022), and Larouche et al. (2022) in strongly supporting a sister-group relationship between the deep-reef genera *Polylepion* and *Decodon* (bootstrap support = 97%) and with those studies and Santini et al. (2016) in

revealing that *Bodianus* includes species formerly classified in the genera *Clepticus* and *Semicossyphus* (Supplemental Fig. S2; see Data Accessibility). Unlike the phylogeny of Aiello et al. (2017), in which *Decodon* and *Polylepion* were embedded in the *Bodianus* clade, our results agree with those of Hughes et al. (2022) and Larouche et al. (2022) in resolving *Decodon* and *Polylepion* as distinct from *Bodianus*. Further taxonomic study of *Bodianus* is needed to resolve the species composition of that genus.

Our results provide the first molecular evidence for the monophyly of the genus *Polylepion* (bootstrap support = 100%) and support the recognition of *P. gilmorei* as a distinct species. The phylogeny further suggests that the eastern Pacific *P. cruentum* is sister to the clade comprising the western Atlantic *P. gilmorei* and Indo-Central-West Pacific *P. russelli*.

Biogeography.—One possible biogeographic scenario for the current distribution of *Polylepion* based on the time-calibrated phylogeny (Fig. 3) involves an initial split of the eastern Pacific population approximately 10 mya, with westward migration that ultimately isolated *P. russelli*. That occurred at about the same time as the separation of the other Neotropical genus of deep-reef wrasses, *Decodon*, into eastern Pacific and western Atlantic populations, suggesting a linkage of these events in both genera to shoaling of the central American isthmus prior to its final closure ~2 mya (Lessios, 2008; O'Dea et al., 2016). Since *P. russelli* is known as far west as Réunion Island in the southwest Indian Ocean, further westward migration around the tip of South Africa approximately 6 mya could have led to the establishment of an isolated Atlantic population. Colonization from the Indian Ocean directly into the western Atlantic has been hypothesized for some shallow-reef fishes, including *Centropyge* (Bowen et al., 2006, and references therein), which, like *Polylepion*, is not known from the tropical eastern Atlantic. Gordon (2003) noted that dispersal directly from the Indian Ocean into the western Atlantic could occur via the surface-flowing South Equatorial Current, which runs below the equator from the eastern Atlantic to Brazil. However, given that the global tropical deep-reef fish fauna is poorly known, additional species of *Polylepion* may be discovered, and other biogeographic scenarios are possible.

Revised diagnosis of *Polylepion*.—Gomon (1977) proposed the generic name *Polylepion* (“many small scales”) in reference to large number of lateral-line scales (48–53) relative to those in the closely related genera *Bodianus* (30–48), *Decodon* (26–30), and *Semicossyphus* (42–45), although he noted that *Pimelometopon* has 53–57 (Gomon, 1977: table 1). *Polylepion gilmorei* has fewer lateral-line scales (38–44) than its congeners, a count that overlaps those of *Bodianus* and “*Semicossyphus*.” Discovery of the new Atlantic species necessitates minor changes in the diagnosis of *Polylepion*, and the new diagnosis follows with Gomon’s (1977) diagnostic characters given in parentheses if different: dorsal-fin rays XI, 10–12, usually 11 (XI, 11); anal-fin rays III, 10–13, usually 11 or 12 (III, 11–12); pectoral-fin rays ii, 16–19, usually 17 or 18 (ii, 17–19); lateral-line scales 38–53 (48–52); scales above lateral line 2–5 ($2\frac{1}{2}$ –5); scales below lateral line 9–18 (16–19, usually 17 or 18); predorsal scales approximately 20–32 (25–32); scales on forehead reaching forward to a vertical between anterior edge of orbit and one

anterior to anterior nostrils; color in alcohol pale with dusky spot on dorsal base of caudal fin in juveniles. Since neither *P. gilmorei* nor *P. russelli* has black interspinal membranes in the anterior portion of the dorsal fin, that character in Gomon’s (1977) diagnosis is removed from the revised diagnosis.

DISCUSSION

Baldwin et al. (2018) presented a classification of reef-fish faunal zones at Curaçao that comprises the altiphotic (0 to ~40 m), mesophotic (~40 to ~130 m), and rariphotic (~130 to at least 300 m). The new species joins a growing list of new Caribbean deep-reef fish species discovered at mesophotic and rariphotic depths and collected with the aid of robotic arms and fish anesthetics using human-occupied submersibles (Robertson et al., 2022). Including the new species of *Polylepion*, exploration of the Caribbean deep-reef fish fauna by the Smithsonian’s Deep Reef Observation Project (DROP) has resulted in the description of one new genus and more than 25 new species, with additional new species yet to be described (e.g., Tornabene and Baldwin, 2019, and references therein; McFarland et al., 2020; Tornabene et al., 2023). While some of the new species inhabit mesophotic depths, *P. gilmorei* and several new species in the genera *Birdsongichthys*, *Haptoclinus*, *Liopropoma*, *Lipogramma*, *Robinsichthys*, and *Varicus* live in the rariphotic, below the mesophotic but above the deep aphotic zone (Baldwin et al., 2018; Tornabene et al., 2023). While the rariphotic reef-fish assemblage is taxonomically distinct from shallower faunas, the two faunas share strong evolutionary affinities, as most rariphotic species belong to reef-fish families inhabiting altiphotic and mesophotic reefs (Baldwin et al., 2018). At Curaçao, the seabass family Serranidae, with eight rariphotic species, Gobiidae (6), Grammatidae (4), and Labridae (3, including the new species of *Polylepion*) are the most common families of typical reef fishes with species that primarily inhabit the rariphotic zone (Baldwin et al., 2018; Tornabene et al., 2023).

Tornabene et al. (2016, 2023) used time-calibrated phylogenies of some members of the Gobiidae to hypothesize multiple transitions from shallow- to deep-reef habitats, all of which occurred approximately 10–30 mya. Our time-calibrated phylogeny of the Labridae (Fig. 3) suggests that by 30 mya, a split had occurred between the deep-reef clade comprising *Decodon* + *Polylepion* and the shallower-reef clade comprising *Bodianus* + *Clepticus* + *Semicossyphus*, with *Decodon* and *Polylepion* diverging slightly more than 20 mya. Future exploration of tropical deep reefs is likely to reveal additional new fish species and possibly new genera, which may alter our phylogenetic and biogeographic hypotheses. For now, the discovery of the new *Polylepion* provides another example of the value of continued exploratory expeditions to enhance our globally poor knowledge of tropical deep reefs.

DATA ACCESSIBILITY

Supplemental material is available at <https://www.ichthyologyandherpetology.org/i2022075>. Unless an alternative copyright or statement noting that a figure is reprinted from a previous source is noted in a figure caption, the published images and illustrations in this article are licensed by the American Society of Ichthyologists and Herpetologists for use if the use includes a citation to the original source (American Society of Ichthyologists and Herpetologists, the

DOI of the *Ichthyology & Herpetology* article, and any individual image credits listed in the figure caption) in accordance with the Creative Commons Attribution CC BY License. ZooBank publication urn:lsid:zoobank.org:pub:1FA0F7E4-3DF9-41EF-99B9-4BADF08E1AD5.

ACKNOWLEDGMENTS

We thank G. Gilmore for valuable specimens, data, artwork, and discussion related to the new species. B. Brandt, B. Brown, T. Christiaan, L. Schenk, A. “Dutch” Schrier, K. Stanley, T. Trudel, and B. van Bebber assisted in various ways with submersible operations; C. Castillo and T. Devine provided project management and DNA technician services; R. Manning provided assistance in the field; M. Westneat provided the original gene alignments published by Aiello et al. (2017); L. Hughes provided the time-calibrated phylogenetic tree of the Labridae; D. Pitassy and K. Maslenikov provided collection-management assistance; S. Raredon provided photographs and radiographs of type material; A. David (NOAA) provided the image in Supplemental Fig. 1 and information on depth and habitat of the fish in that image, and J. Reed was chief scientist on the NOAA expedition that secured the image; C. Lardizabal at MUVS helped facilitate collecting in Roatan and assisted with cataloging specimens. Funding for the Smithsonian Institution’s Deep Reef Observation Project was provided by the Smithsonian’s Consortium for Understanding and Sustaining a Biodiverse Planet to CCB, the Smithsonian’s Competitive Grants for the Promotion of Science program to CCB and DRR, the Herbert R. and Evelyn Axelrod Endowment Fund for systematic ichthyology to CCB, the Prince Albert II of Monaco Foundation’s grant and gift to CCB, STRI funds to DRR, and University of Washington School of Aquatic and Fishery Sciences funds to LT. Aspects of the work by CCB and DA were completed under National Science Foundation grants DEB-1541552, DEB-2015404, and DEB-2144325. This is Ocean Heritage Foundation/Curaçao Sea Aquarium/Substation Curaçao (OHF/SCA/SC) contribution number 52.

LITERATURE CITED

- Aiello, B. R., M. W. Westneat, and M. E. Hale. 2017. Mechanosensation is evolutionarily tuned to locomotor mechanics. *Proceedings of the National Academy of Sciences of the United States of America* 114:4459–4464.
- Baldwin, C. C., L. Tornabene, and D. R. Robertson. 2018. Below the mesophotic. *Science Reports* 8:4920.
- Béarez, P., A. Dettai, and M. F. Gomon. 2013. *Polylepion russelli* (Labridae), a trans-Indo-Pacific species. *Cybio* 37: 305–306.
- Bowen, B. W., A. Muss, L. A. Rocha, and W. S. Grant. 2006. Shallow mtDNA coalescence in Atlantic pygmy angelfishes (genus *Centropyge*) indicates a recent invasion from the Indian Ocean. *Journal of Heredity* 97:1–12.
- Britzke, R., Z. R. Siccha-Ramierz, and M. L. Guevara-Torres. 2021. Crossing the borders: first record of Bleeding Wrasse, *Polylepion cruentum* Gomon, 1977 (Labriformes, Labridae), in the northern Peru. *Papeles Avulsos de Zoología* 61:e20216185.
- Eastman, J. M., L. J. Harmon, and D. C. Tank. 2013. Congruification: support for time scaling large phylogenetic trees. *Methods in Ecology and Evolution* 4:688–691.
- Fricke, R., W. N. Eschmeyer, and R. Van der Laan (Eds.). 2023. Eschmeyer’s catalog of fishes: genera, species, references. <http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>. Electronic version accessed 18 March 2023.
- GBIF. 2022. GBIF Occurrence Download. <https://doi.org/10.15468/dl.5g5scn>
- Ghezelayagh, A., R. C. Harrington, E. D. Burrell, M. A. Campbell, J. C. Buckner, P. Chakrabarty, J. R. Glass, W. T. McCraney, P. J. Unmack, C. E. Thacker, M. E. Alfaro, S. T. Friedman, W. B. Ludt, P. F. Cowman . . . T. J. Near. 2022. Prolonged morphological expansion of spiny-rayed fishes following the end-Cretaceous. *Nature Ecology and Evolution* 6:1211–1220.
- Gomon, M. F. 1977. A new genus and eastern Pacific species of bodianine labrid fish. *Proceedings of the Biological Society of Washington* 89:621–630.
- Gomon, M. F. 1995. Labridae. Viejas, doncellas, señoritas, p. 1201–1225. *In: Guía FAO para Identificación de Especies para lo Fines de la Pesca. Pacífico Centro-Oriental*. Vol. III. W. Fischer, F. Krupp, W. Schneider, C. Sommer, K. E. Carpenter, and V. Niem (eds.). FAO, Rome.
- Gomon, M. F. 1997. Relationships of fishes of the labrid tribe Hypsigynini. *Bulletin of Marine Science* 60:789–871.
- Gomon, M. F., and J. E. Randall. 1975. A new deep-water fish of the labrid genus *Bodianus* from Hawaii and the Ryukyu Islands. *Bulletin of Marine Science* 25:443–444.
- Gomon, M. F., and J. E. Randall. 1978. Review of the Hawaiian fishes of the labrid tribe Bodianini. *Bulletin of Marine Science* 28:32–48.
- Gordon, A. L. 2003. The brawniest retroflexion. *Science* 421: 904–905.
- Harmon, L. J., J. T. Weir, C. D. Brock, R. E. Glor, and W. Challenger. 2008. GEIGER: investigating evolutionary radiations. *Bioinformatics* 24:129–131.
- Hobbs, J-P. A., S. J. Newman, G. E. A. Mitsopoulos, M. J. Travers, C. L. Skepper, J. J. Gilligan, G. R. Allen, H. J. Choat, and A. M. Ayling. 2014. Checklist and new records of Christmas Island fishes: the influence of isolation, biogeography and habitat availability on species abundance and community composition. *Raffles Bulletin of Zoology Supplement* 30:184–202.
- Hubert, N., E. Paradis, H. Bruggemann, and S. Planes. 2011. Community assembly and diversification in Indo-Pacific coral reef fishes. *Ecology and Evolution* 1:229–277.
- Hughes, L. C., C. M. Nash, W. T. White, and M. W. Westneat. 2022. Concordance and discordance in the phylogenomics of wrasses and parrotfishes (family Labridae). *Systematic Biology* 2022:syac072.
- Katoh, K., and D. M. Standley. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30:772–780.
- Larouche, O., S. M. Gartner, M. W. Westneat, and K. M. Evans. 2022. Mosaic evolution of the skull in labrid fishes involves differences in both tempo and mode of morphological change. *Systematic Biology* 2022:syac061.
- Lessios, H. A. 2008. The great American schism: divergence of marine organisms after the rise of the Central American Isthmus. *Annual Review of Ecology, Evolution, and Systematics* 39:63–91.
- Liu, K., S. Raghavan, S. Nelesen, C. R. Linder, and T. Warnow. 2009. Rapid and accurate large-scale coestima-

- tion of sequence alignments and phylogenetic trees. *Science* 324:1561–1564.
- Masuda, H., K. Amaoka, C. Araga, T. Uyeno, and T. Yoshino (Eds.). 1984. *The Fishes of the Japanese Archipelago*. Volume I. Tokai University Press, Tokyo.
- McFarland, E. P., C. C. Baldwin, D. R. Robertson, L. A. Rocha, and L. Tornabene. 2020. A new species of *Chromis* damselfish from the tropical western Atlantic (Teleostei, Pomacentridae). *ZooKeys* 1008:107–138.
- Mirarab, S., and T. Warnow. 2015. ASTRAL-II: coalescent-based species tree estimation with many hundreds of taxa and thousands of genes. *Bioinformatics* 31:i44–i52.
- O'Dea, A., H. A. Lessios, A. G. Coates, R. I. Eytan, S. A. Restrepo-Moreno, A. L. Cione, L. S. Collins, A. de Queiroz, D. W. Farris, R. D. Norris, R. F. Stallard, M. O. Woodburne, O. Aguilera, M-P. Aubry . . . J. B. C. Jackson. 2016. Formation of the Isthmus of Panama. *Science Advances* 2016:e1600883.
- Parenti, P., and J. E. Randall. 2000. An annotated checklist of the species of the labroid fish families Labridae and Scaridae. *Ichthyological Bulletin* 68:1–97.
- Quattrini, A. M., A. W. J. Demopoulos, R. Singer, A. Roa-Varon, and J. D. Chator. 2017. Demersal fish assemblages on seamounts and other rugged features in the northeastern Caribbean. *Deep-Sea Research I* 123:90–104.
- Robertson, D. R., L. Tornabene, C. C. Lardizabal, and C. C. Baldwin. 2022. Submersibles greatly enhance research on the diversity of deep-reef fishes in the Greater Caribbean. *Frontiers in Marine Science* 8:800250.
- Robertson, D. R., and J. Van Tassell. 2016. *Shorefishes of the Greater Caribbean: online information system*. Version 2.0. Smithsonian Tropical Research Institute, Balboa, Panamá.
- Sanderson, S. L. 1990. Versatility and specialization in labrid fishes: ecomorphological implications. *Oecologia* 84:272–279.
- Santini, F., L. Sorenson, and M. E. Alfaro. 2016. Phylogeny and biogeography of hogfishes and allies (*Bodianus*, Labridae). *Molecular Phylogenetics and Evolution* 99:1–6.
- Smith, S. A., and B. C. O'Meara. 2012. treePL: divergence time estimation using penalized likelihood for large phylogenies. *Bioinformatics* 28:2689–2690.
- Stamatakis, A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30:1312–1313.
- Tatom-Naecker, T.-A. M., and M. W. Westneat. 2018. Burrowing fishes: kinematics, morphology and phylogeny of sand-diving wrasses (Labridae). *Journal of Fish Biology* 93:860–873.
- Tornabene, L., and C. C. Baldwin. 2019. *Psilotris vantasselli*, a new species of goby from the tropical western Atlantic (Teleostei: Gobiidae: Gobiosomatini: Nes subgroup). *Zootaxa* 4624:191–204.
- Tornabene, L., R. Manning, D. R. Robertson, J. L. van Tassell, and C. C. Baldwin. 2023. A new lineage of deep-reef gobies from the Caribbean, including two new species and one new genus (Teleostei: Gobiidae: Gobiosomatini). *Zoological Journal of the Linnean Society* 197:322–343.
- Tornabene, L., J. L. Van Tassell, D. R. Robertson, and C. C. Baldwin. 2016. Repeated invasions into the twilight zone: evolutionary origins of a novel assemblage of fishes from deep Caribbean reefs. *Molecular Ecology* 25:3662–3682.
- Westneat, M. W., and M. E. Alfaro. 2005. Phylogenetic relationships and evolutionary history of the reef fish family Labridae. *Molecular Phylogenetics and Evolution* 36:370–390.