

# Integrative taxonomy of the species complex *Haemulon steindachneri* (Jordan and Gilbert, 1882) (Eupercaria; Haemulidae) with a description of a new species from the western Atlantic

Cintia Oliveira Carvalho<sup>a,b,\*</sup>, Alexandre Pires Marцениuk<sup>a</sup>, Claudio Oliveira<sup>c</sup>,  
Wolmar Benjamin Wosiacki<sup>a</sup>

<sup>a</sup> Museu Paraense Emílio Goeldi, 66040-170, Belém, PA, Brazil

<sup>b</sup> Programa de Pós-Graduação em Biodiversidade e Evolução, Museu Paraense Emílio Goeldi, 66040-170, Belém, PA, Brazil

<sup>c</sup> Universidade Estadual Paulista - Campus Botucatu, 18618-689, Botucatu, SP, Brazil

## ARTICLE INFO

### Keywords:

Marine biogeography  
DNA barcode  
Morphology  
Western Atlantic  
Eastern Pacific  
Biodiversity

## ABSTRACT

*Haemulon steindachneri* (Jordan and Gilbert) (Haemulidae), popularly known as “cocoroca-de-boca-larga”, “latin-grunt” or “latin-burro”, represents a species complex found on the Atlantic western coast and on the Pacific eastern coast, condition confirmed recently by molecular phylogenies. In the present study, DNA barcoding analysis recognizes two distinct clusters; the first includes Brazil and Caribbean, and the second is composed of Pacific specimens, with genetic distance of 7.4%, differentiated by 35 base pairs. In addition to the molecular evidence, our results show morphological differences that distinguish the Atlantic lineage from that of the Pacific: anal fin, usually, with eight rays (vs. generally nine rays in Pacific); 13–15 scales below the lateral line, rarely 12 (vs. 12 scales below the lateral line, rarely 13 in Pacific), posterior margin of the maxilla robust with a slightly angled end (vs. smaller maxilla with moderately convex extremity), and presence of a spot on the preoperculum, broad and robust, with no definite shape (vs. narrow spot, with anterior extremity tuned and posterior straight, resembling a triangle in Pacific). Therefore, based on both molecular and morphological evidences, *H. steindachneri* is redescribed for the Pacific coast while a new species is described for the Atlantic coast.

## 1. Introduction

The different processes of species formation are still one of the most controversial topics in evolutionary biology (Gaither et al., 2015). When it comes to marine organisms, the challenges encountered in the understanding of the speciation process are even greater, as many marine species have wide distributions, large populations, and larval stages that provide genetic connectivity between different geographic areas (Lessios and Robertson, 2006; Bowen et al., 2013). Factors such as extinction, recolonization, fragmentation of populations, and area expansion resulting from different historical events may also influence the population genetic structure of marine organisms (Fauvelot and Planes, 2002). In this sense, the rise of the Isthmus of Panama was an important historical event, responsible for major changes in the marine environment of the New World, as well as its biota (O’Dea et al., 2016).

Beginning over 30 million years ago, the rise of the Isthmus of Panama was responsible for the separation of the Caribbean Sea from

the tropical east of the Pacific Ocean (O’Dea et al., 2016). At the end of the Pliocene to at least 3.2 million years ago, the cessation of this uplift occurred, which led to discontinuation of interoceanic channels that previously had a continuous body of water with gene flow between existing populations (Leigh et al., 2014; O’Dea et al., 2016). This paleogeographic event led to the divergence of many lineages, thus giving rise to some species pairs recognized as “geminata species” by Jordan (1908), which showed the presence of some supposed geminata species in haemulids of the New World, such as *Haemulon album* Cuvier/*H. sexfasciatum* Gill, or *H. parra* (Desmarest)/*H. scudderii* Gill, among others (Jordan, 1908). As seen, the genus *Haemulon* presents pairs of closely related sister species that have totally or partially overlapping distributions or with specimens found on both sides of the Isthmus of Panama (Rocha et al., 2008; Tavera and Wainwright, 2019). Considering this, the genus *Haemulon* (Haemulidae) is an excellent group to study the evolutionary history and dynamics of speciation in the tropics of the New World, since it has species distributed in both Atlantic and

\* Corresponding author at: Museu Paraense Emílio Goeldi, 66040-170, Belém, PA, Brazil.

E-mail addresses: [cintiaoiveiracarvalho@yahoo.com](mailto:cintiaoiveiracarvalho@yahoo.com) (C. Oliveira Carvalho), [a\\_marцениuk@hotmail.com](mailto:a_marцениuk@hotmail.com) (A. Pires Marцениuk), [claudio.oliveira@unesp.br](mailto:claudio.oliveira@unesp.br) (C. Oliveira), [wolmar@museu-goeldi.br](mailto:wolmar@museu-goeldi.br) (W.B. Wosiacki).

<https://doi.org/10.1016/j.zool.2020.125782>

Received 2 July 2019; Received in revised form 20 March 2020; Accepted 23 March 2020

Available online 06 April 2020

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Pacific Oceans (Rocha et al., 2008).

The genus *Haemulon* Cuvier, 1829 has 19 valid species found in shallow tropical reef environments of the Atlantic and Eastern Pacific (Courtenay, 1961; Rocha et al., 2008). Species of this genus form schools with up to thousands of individuals, with commercial value and great trophic importance as prey/predators (Lindeman and Toxey, 2002; Ferreira et al., 2004). Fifteen species of *Haemulon* are known from the Western Atlantic and five from the Eastern Pacific, with *H. steindachneri* cited for both the Western Atlantic (Costa Rica to Santa Catarina, Brazil) and the Eastern Pacific (Gulf of California to Peru) (Lindeman and Toxey, 2002; Lindeman et al., 2016). The latter species is abundant in shallow areas and in rocky shores, with recognized importance in maintaining the integrity of these ecosystems (Furia, 1996; Rocha, 1997).

Recently, molecular phylogenies of Haemulidae and *Haemulon* have recognized two distinct forms of *H. steindachneri* from the Atlantic and Pacific (Rocha et al., 2008; Tavera et al., 2012, 2018). Rocha et al. (2008) showed that the populations of *H. steindachneri* from Brazil, the Caribbean, and Eastern Pacific have high intraspecific variation, with the Pacific and Atlantic forms showing differences in both mitochondrial and nuclear DNA, suggesting that the two recognized lineages could be treated as distinct species. Tavera et al. (2012; 2018; 2019) also concluded that *H. steindachneri* is represented by two distinct lineages, one in the Pacific and one in the Atlantic. Despite recent molecular studies showing species-level differences in *H. steindachneri*, no taxonomic study has reviewed the nomenclature adopted and/or the relationships between the Pacific and Atlantic lineages. In this sense, based on the combination of morphological and molecular characters, the present study redescribes *H. steindachneri* as a species restricted to the Eastern Pacific while a new species belonging to the *H. steindachneri* species complex is described for the Western Atlantic.

## 2. Material and Methods

### 2.1. Morphological data and analysis

Meristic and morphometric data were obtained following Courtenay (1961), with the following additions: HCP, height of the caudal peduncle: shortest distance between the dorsal and ventral margins of the caudal peduncle; WCP, width of the caudal peduncle: on the same axis as the HCP; CPL, caudal-peduncle length: between the posterior margin of the base of the last ray of the anal fin at the end of the hypural plate; DSPf, distance between the snout and the pelvic fin: from the tip of the snout to the base of the first ray of the pelvic fin; PvL, pelvic-fin length: from the base to the end of the longest ray; DL, dorsal-fin height: from the base of the fourth ray to its extremity; PtL, pectoral-fin length: from the base to the end of the longest ray; AH, anal-fin height: from the base of the second ray to its extremity; PPL, pre-pectoral length: from the tip of the snout to the base of the first ray of the pectoral fin; HH, head height: the highest vertical height of the head on the posterior margin of the operculum; ID, Interorbital distance: shorter distance between the inner margins of the orbits; POL, post-orbital length: distance from the posterior margin of the orbit to the end of the posterior membranous part of the operculum; DBL, dorsal-fin base length: from the anterior margin of the base of the first ray to the posterior margin of the base of the last ray; ABL, anal-fin base length: from the anterior margin of the base of the first ray to the posterior margin of the base of the last ray; WM, width of the mouth: distance between the inner margins of the angles of the mouth; PJW, pre-jaw width: greater distance between the outer side edges of the pre-jaw, considering the two plates; LCL, lower caudal-fin lobe length: from the base of the first ray to the end of the longer ray; UCL, upper caudal-fin lobe length: from the base of the first ray to the end of the longer ray.

Morphological characters, measurements, and counts were examined, preferably, on the left side of the specimens. The measurements were obtained using an ichthyometer with precision of 1 mm and

a digital caliper with an accuracy of 0.1 mm. The counts were made with the assistance of a stylet and fine-tipped tweezers under a stereoscopic microscope. The spines are presented as upper-case Roman numerals, branched rays as Arabic numerals, and the unbranched rays as lower-case Roman numerals. Values observed in the holotype are represented by asterisks “\*”. Osteological information such as number of vertebrae, pleural ribs, and accessory rays of the anal and dorsal fin were also collected from digital radiographs. The measures are presented as a percentage of the standard length, aiming for a comparative analysis between the lineages and geographic areas examined. The meristic and morphometric characters were compared by areas and presented in the form of tables.

We analyzed 115 specimens belonging to the *H. steindachneri* species complex, deposited in the following ichthyological collections: Academy of Natural Sciences of Drexel University (ANSP), Philadelphia; Zoological Collection of Santa Cecilia (AZUSC) at the University of Santa Cecília, Santos; California Academy of Sciences (CAS), San Francisco; Natural History Museum of Los Angeles County (LACM), Los Angeles; Museu Paraense Emílio Goeldi (MPEG), Belém; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo; Coleção do Laboratório de Biologia e Genética de Peixes (LBP) da Universidade Estadual de São Paulo (UNESP), Botucatu; National Museum of Natural History (USNM), Washington.

### 2.2. Molecular data and analysis

A total of 29 partial sequences of COI (517 bp) were obtained from *Haemulon atlanticus* sp. n., which will be deposited in GenBank. The vouchers were deposited in the ichthyological collection of MPEG. In addition, seven additional COI sequences from *H. atlanticus* sp. n. and 12 of *H. steindachneri* were obtained from GenBank and BOLD.

Molecular techniques were performed at the LBP-UNESP, Botucatu and at the MPEG. Total DNA was obtained using a DNeasy Blood and Tissue kit (Qiagen, Hilden, Germany) by the mouse-tail protocol. The 517 bp fragment at the 5' end of the mitochondrial COI gene was amplified by PCR using the primers FishF1 and FishR1 (Ward et al., 2005).

The reactions were performed in a reaction volume of 12.5 µL: 0.5 µL of DNTP (1.25 mM), 1.25 µL of buffer (10x), 0.5 µL of MgCl<sub>2</sub> (50 mM), 0.25 µL of each primer (200 ng/µL), 0.5–2.0 µL of total DNA (100 ng/µL), 0.2 µL of Taq DNA Polymerase (5U/µL) and purified water to complete the final volume of the reaction. The amplification protocol consisted of initial denaturation at 95 °C for two minutes, followed by 35 cycles of denaturation at 94 °C for 30 seconds, hybridization at 64 °C for one minute, extension at 72 °C for one minute, and final extension at 72 °C for ten minutes. PCR products were visualized on 1% agarose gel, and further purified using the ExoSap-IT kit (USB Europe GmbH, Staufen, Germany) at 37 °C for 60 min followed by 15 min at 80 °C. Sequencing reactions were conducted using a BigDye Terminators cycle kit (Applied Biosystems, California, USA) according to the manufacturer's instructions. Sequences were generated on ABI 3130-Genetic Analyzer (Applied Biosystems, California, USA) automated DNA sequencer at LBP and MPEG.

The bidirectional sequence "contigs" were assembled, and the sequences were aligned using Geneious v.5.6 (Kearse et al., 2012) to obtain consensus sequences and to check for indels or possible stop codons. The MEGA v 7.0 program (Kumar et al., 2016) was used to construct neighbor joining (NJ) dendrograms (see Supplement I Appendix A) and to estimate the Kimura 2-parameter (K2P) (Kimura, 1980) genetic divergence within and between clades. In addition, a cladistic haplotype analysis (Brower, 1999) was made based on a network created in Haploviewer (Salzburger et al., 2011) following the parameters recommended by the software's authors.

The construction of an ultrametric tree with a strict clock was performed using a log-normal time distribution model through the BEAUTi and BEAST programs (Drummond et al., 2012). The evolutionary

nucleotide model used to estimate the ultrametric tree was the HKY model with Gamma correction. We used a Yule prior speciation method, which is the most suitable for species-level phylogenies (Drummond and Rambaut, 2007). In total, 30,000,000 trees per 10,000 generations were sampled. The data was checked through the TRACER v.1.7 program (Rambaut et al., 2018) in order to evaluate if extra races would be necessary to achieve convergence. All topologies sampled below the asymptote (10,000 generations) were discarded as part of a burn-in procedure. The remaining trees were used to build a consensus tree by majority in the Tree Annotator program.

Additionally, species delimitation analyses (see Supplement I Appendix A) were performed to see if their results corroborate the separation between the species of the *Haemulon steindachneri* species complex. Automatic Barcode Gap Discovery analysis (ABGD) (Puillandre et al., 2012), was processed using the “graphic” web version available at <http://www.wabi.snv.jussieu.fr/public/abgd/abgdweb.html>, under the default parameters of  $P_{min} = 0.001$  to  $P_{max} = 0.1$ , steps = 10, X (relative gap width) = 1.5, Nb bins (for distance distribution) = 20, and the Kimura (K80) molecular model.

For the generalized mixed Yule Coalescent (GMYC) method, an ultrametric tree was estimated in Beast v1.8.2 (Drummond et al., 2012), employing an uncorrelated lognormal relaxed clock and speciation Yule process, and the General Time Reversible (GTR) model (Lanave et al., 1984; Tavaré, 1986). The Bayesian topology reconstruction started with a UPGMA tree and the Markov Chain Monte Carlo (MCMC) method was performed for 500 million generations; a tree was sampled for every 20,000 generations. We used the software Tracer v1.7 (Rambaut et al., 2018) to check the convergence of the values. All sampled topologies beneath the asymptote (20,000,000 generations) were discarded as part of a burn-in procedure, and the remaining trees were used to construct a 90% majority-rule consensus tree using Tree Annotator v1.8.2 (Drummond et al., 2012). The GMYC analysis was performed with the package Species Limits by Threshold Statistics (“splits”) (Fujisawa and Barraclough, 2013) using R v 3.0.0 (R Development Core Team, 2014). For the Bayesian Poisson tree process (bPTP) analyses, the same ultrametric input tree was used as in the GMYC analysis. The analyses were run on the web server (<http://species.h-its.org/ptp>) with 100,000 MCMC generations, a burn-in of 0.1 and other parameters left as default.

### 2.3. Comparative material

*Haemulon aurolineatum* Cuvier. MPEG 34253 (4, 115–127), Alagoas; MPEG 34268 (2, 117–126), Alagoas; *H. melanurum* (Linnaeus). AZUSC 4504 (4, 145–164 mm SL), Ceará; MZUSP 53092 (1, 113 mm SL), Maranhão; *H. parra*. MPEG 34588 (6, 148–188 mm SL), Ceará; MPEG 34571 (1, 189 mm SL), Ceará; MPEG 34531 (4, 169–215 mm SL), Ceará; MZUSP 46479 (2, 131–136), Fernando de Noronha; MZUSP 65671 (1, 169 mm SL), Pernambuco; *H. plumierii* (Lacepède). MPEG 34549 (5, 136–147 mm SL), Ceará; MPEG 34629 (7, 141–156), Ceará; USNM 398053 (2, 119–166 mm SL), Mexico; USNM 37089 (4, 147–166 mm SL), Mexico; USNM 80598 (2, 129–139 mm SL), Panama; *H. squamipinna* Rocha and Rosa. MZUSP 65676 (3, 128–133 mm SL), Pernambuco; MZUSP 65665 (2, 127–132 mm SL), Pernambuco; AZUSC 4491 (1, 132 mm SL), São Paulo; *H. striatum* (Linnaeus). AZUSC 82203 (1, 147 mm SL), Bahia.

## 3. Results

### 3.1. *Haemulon atlanticus* sp. n.

*Haemulon steindachneri* — Jordan and Swain, 1884: 299–300 [in part, revision].— Courtenay, 1961:86 [in part, revision].— Uyeno et al., 1983:356 [Fishes trawled off Suriname and French Guiana, description].— Cervigón, 1992:335 [in part, description, distribution].— Cervigón, 1993:209 [in part; los peces marinos de Venezuela;

description, illustrated].— Robins and Ray, 1986:180 [in part, description, distribution].— Rocha and Rosa, 1999:448 [identification key].— Lindeman and Toxey, 2002:1545 [in part, description, distribution, illustrated].— Menezes et al., 2003:85 [in part; catalog of marine fishes of the Brazilian coast].— Rocha et al., 2008:921 [in part, Historical biogeography and speciation in the reef fish genus *Haemulon*].— Tavera et al., 2012:6 [in part, Molecular phylogeny].— Marceniuk et al., 2017:40 [identification key, photography, error in Figure 14-F, the correct is figure 14-H].— Tavera et al., 2018:214 [in part, Multilocus phylogeny].

*Holotype*. MPEG 35708, 152 mm SL, Amapá, Brazil, 3°47'N, 50°22'W  
*Paratypes*: MPEG 35753 (2, 143–153 mm SL), 3°47'N, 50°22'W, Amapá; AZUSC 4655 (5, 180–192 mm SL), 23°54'53"S, 46°37'19"W, Caete river, Bragança, Pará; LBP 21368 (1, 192 mm SL), 00°54'54.0"S, 46°38'22.0"W, Furo da ostra, Bragança, Pará; MPEG 33357 1, 211 mm SL, Ajuruteua, Bragança, Pará; MPEG 32859 (1, 201 mm SL), Ajuruteua, Bragança, Pará; MPEG 33240 (1, 186 mm SL), Ajuruteua, Bragança, Pará; MPEG 34530 (3, 192–215 mm SL), Bragança, Pará; MZUSP 68041 (2, 143–165 mm SL), 0°33'0.0"W, 46°35'0.0"W, Pará; LBP 20027 (1, 106 mm SL), Fortaleza, Ceará; LBP 20014 (1, 95 mm SL), 03°41'33.0"S, 38°30'18.0"W, Enseada do Mucuripe, Fortaleza, Ceará; MZUSP 46479 (2, 131–136 mm SL), Fernando de Noronha, Pernambuco; MPEG 34269, 172 mm SL, Jaraguá, Maceió, Alagoas; MPEG 34251 (3, 148–154 mm SL), Jaraguá, Maceió, Alagoas; LBP 23833 (1, 127 mm SL), 13°22'22.1"S, 38°58'43.0"W, Valença, Bahia; MZUSP 68048 (1, 105 mm SL), Salvador, Bahia; MZUSP 51544 (2, 137–156 mm SL), 20°21'0.0"S, 40°15'0.0"W, Ilha dos pacotes, Vila Velha, Espírito Santo; LBP 22158 (2, 123–131 mm SL), 22°56'59.0"S, 43°47'40.0"W, Baía de Guanabara, Rio de Janeiro; LBP 22124 (1, 180 mm SL), 22°56'59.0"S, 43°47'40.0"W, Baía de Guanabara, Rio de Janeiro; MZUSP 68037 (3, 130–155 mm SL), Angra dos Reis, Rio de Janeiro; MZUSP 2438 (1, 159), Ilha Grande, Rio de Janeiro; AZUSC 3307 (3, 86–145 mm SL), 23°27'5"S, 45°2'48"W, Ubatuba, São Paulo; AZUSC 192 (1, 164 mm SL), 24°0'29"S, 46°19'26"W, Guarujá, São Paulo; AZUSC 1977 (1, 204 mm SL), 24°16'49"S, 46°10'37"W, Guarujá, São Paulo; AZUSC 2216 (3, 99–155 mm SL), 23°49'42"S, 45°26'15"W, São Sebastião, São Paulo; AZUSC 447 (1, 164 mm SL), 24°0'35"S, 46°19'30"W, Guarujá, São Paulo; AZUSC 1913 (1, 208 mm SL), 24°7'37"S, 46°31'56"W, Praia Grande, São Paulo; AZUSC 628 (1, 136 mm SL), 24°0'31"S, 46°19'24"W, Guarujá, São Paulo; AZUSC 4453 (2, 119–153 mm SL), 23°54'37"S, 46°23'49"W, Cubatão, São Paulo; AZUSC 4077 (2, 198–214 mm SL), 24°37'8"S, 46°58'58"W, Peruíbe, São Paulo; AZUSC 461 (1, 176 mm SL), 24°0'30"S, 46°19'26"W, Guarujá, São Paulo; AZUSC 2002 (4, 162–214 mm SL), 24°27'43"S, 46°42'56"W, Itanhaém, São Paulo; LBP 21326 (1, 170 mm SL), 23°49'25.0"S, 45°32'11.0"W, São Sebastião, São Paulo; LBP 10058 (2, 184–205 mm SL), 23°51'38.7"S, 46°09'10.5"W, Bertioga, São Paulo; LBP 3537 (2, 118–127 mm SL), 23°26'10.7"S, 45°02'58.9"W, Ubatuba, São Paulo; LBP 20691 (1, 224 mm SL), 25°21'53.0"S, 47°39'11.0"W, Cananéia, São Paulo; LBP 21614 (1, 192 mm SL), 25°10'51.0"S, 47°35'49.0"W, Cananéia, São Paulo; LBP 21359 (1, 180 mm SL), 23°49'25.0"S, 45°32'11.0"W, São Sebastião, São Paulo; MZUSP 68024 (1, 201 mm SL), São Sebastião, São Paulo; MZUSP 2439 (1, 177 mm SL), São Sebastião, São Paulo; MZUSP 1153 (1, 166 mm SL), São Sebastião, São Paulo; LBP 23329 (1, 114 mm SL), 27°07'12.05"S, 48°31'10.17"W, Porto Belo, Santa Catarina; LBP 23404 (1, 125 mm SL), 27°01'27.83"S, 48°34'35.22"W, Balneário Camboriú, Santa Catarina; LBP 23641 (1, 114 mm SL), 27°12'32.88"S, 48°28'11.01"W, Bombinhas, Santa Catarina; MZUSP 49094 (1, 106 mm SL), 27°7'0.0"S, 48°31'0.0"W, Porto Belo, Santa Catarina; ANSP 121585 (15, 55–132 mm SL), Playa Aquica, Peninsula de Araya, Golfo do Cariaco, Estado Sucre, Venezuela; ANSP 105304 (1, 129 mm SL), Quetepe, Golfo do Cariaco, Estado Sucre, Venezuela; ANSP 105164 (2, 91–94 mm SL), Punta Horno, Peninsula de Araya, Estado Sucre, Venezuela; ANSP 121391 (2, 84–102 mm SL), Punta Horno, Peninsula de Araya, Estado Sucre, Venezuela; ANSP 120214 (2, 73 ou 74 mm SL), Estado Sucre, Venezuela; ANSP 104645 (2, 117 mm SL), Laguna Chica,

Península de Araya, Golfo do Cariaco, Estado Sucre, Venezuela.

**Non-type material:** USNM 289563, 1, Colombia (photographic image and X-ray); USNM 361931, 3, Colombia (photographic image and X-ray); USNM 398161, 1, Colombia (photographic image and X-ray); USNM 398162, 1, Colombia (photographic image and X-ray); USNM 389901, 2, Bocas Del Toro, Laguna de Chiriqui, Panama (photographic image and X-ray); USNM 148671, 3, Coco Solo, Panama (photographic image and X-ray).

### 3.1.1. Morphological diagnosis

*Haemulon atlanticus* differs from all congeners of the Western Atlantic by presenting a distinct color pattern composed of a silvery or silver gray body without stripes, with a bluish black bar in the lower anterior part of the operculum, partially hidden by the angle of the preoperculum, and a large rounded and blackish spot at the end of the caudal peduncle and base of the caudal fin. In addition, *H. atlanticus* can be differentiated from: *H. album*, from Florida to Brazil, by having 30.7–40.5% SL of pre-dorsal length (PDL) (vs. 44–48% SL); *H. aurolineatum*, from Chesapeake Bay to Brazil, by containing seven to nine scales above the lateral line (vs. six), 19–24 rakers in the 1<sup>st</sup> branchial arch (vs. 25–28, rarely 24), body silver to silver gray without stripes (vs. white-silver body with two yellow stripes on the dorsolateral side); *H. bonariense* Cuvier, from South Florida and Antilles to southern Venezuela, by having 50–56 scales in the lateral line (vs. 44–49), large mouth with maxillary tip reaching the center of the eye (vs. small mouth with tip of the jaw reaching the anterior border of the eye); *H. boschmae* (Metzelaar), from Mexico to Chinchorro Bank and South American coast of Barranquilla, Colombia to French Guiana, by presenting 31.6–43.9% SL of body height (BH) (vs. 26–30 % SL) and 13.8–21.4% SL of premaxillary length (PL) (vs. 10–13% SL); *H. carbonarium* Poey, from South Florida to Brazil, including the Gulf of Mexico and the entire Caribbean Sea, by having 30.7–40.5% SL of PDL (vs. 40–46% SL, rarely 40), seven to nine scales above the lateral line (vs. six), body silver to silver gray without stripes (vs. silvery gray body dorsally, dark to black ventrally, with at least ten yellowish stripes on the sides of the body); *H. flavolineatum* (Desmarest), from South Carolina to Trinidad, by having 11–16 scales below the lateral line (vs. nine or ten), scales above and below the lateral line with same size (vs. scales below the lateral line twice the size of those above), and body silver to silver gray without stripes (vs. silvery gray body with at least 12 yellowish stripes on the sides of the body); *H. macrostoma* Günther, from South Florida to Suriname, by containing 19–24 rakers in the 1<sup>st</sup> branchial arch (vs. 26–28), 15–17 (rarely 18) pectoral-fin rays (vs. 17), body silver to silver gray without stripes (vs. white-silvery body with dark brown to black stripes), soft dorsal-fin rays relatively larger than spines (vs. soft rays twice the size of spines); *H. melanurum*, from Florida to Brazil, by presenting seven to nine scales above the lateral line (vs. six), spots below the preoperculum and at the end of the caudal peduncle and base of the caudal fin (vs. black spot extending from the upper back and lower back of the dorsal fin joining a horizontal black V at the caudal fin); *H. parra*, from the Gulf of Mexico to Brazil, by having 30.7–40.5% SL of PDL (vs. 41–49% SL), seven to nine scales above the lateral line (vs. six), serrated preoperculum (vs. non-serrated in adults) and scales throughout the body with gray-brown centers (vs. scales with black centers); *H. plumierii*, from Chesapeake Bay to Brazil, by presenting seven to nine scales above the lateral line (vs. five), scales above the lateral line of the same size as below (vs. scales above lateral line greater than those below) and body silver to silver gray without stripes (vs. body and head with blue and yellow stripes); *H. sciurus* (Shaw), from South Carolina to the Guianas, by presenting 30.7–40.5% SL of PDL (vs. 42–46% SL), 19–24 rakers in the 1<sup>st</sup> branchial arch (vs. 26–31), white to gray membranes between the dorsal-fin spines (vs. yellow) and body silver to silver gray without stripes (vs. yellowish-bronze body with blue stripes on the head and body to the base of the caudal fin); *H. squamipinna*, from Fortaleza to Alagoas, by having seven to nine scales above the lateral line (vs. six), 19–24 rakers in the 1<sup>st</sup> branchial arch

(vs. 25–27, rarely 24), and body silver to silver gray without stripes (vs. silvery white body with 10–12 yellow bands); *H. striatum*, from North Carolina to southern Brazil, by presenting 19–24 rakers in the 1<sup>st</sup> branchial arch (vs. 28–34), XII spines in the dorsal fin (vs. XIII) and 15–17 dorsal-fin rays (vs. 13 or 14, rarely 12), oblong and compressed body (vs. elongated body not laterally compressed), and body silver to silver gray without stripes (vs. gray to bluish body dorsally, silvery ventrally, with five yellow stripes along the body); *H. vittatum* (Poey), from northern Florida to Trinidad, by having XII spines in the dorsal fin (vs. IV to XVIII) and 15–17 dorsal-fin rays (vs. ten), 15–17 (rarely 18) rays in the pectoral fin (vs. 19), III spines in the anal fin and eight (rarely nine) soft rays (vs. II, 9), oblong and compressed body (vs. fusiform body, elongate and rounded), operculum without spine (vs. operculum with broad spine and flat at angle posterior), and body silver to silver gray without stripes (vs. blue-green metallic body dorsally, ventrally bluish white, a broad greenish band from the eye to the base of the caudal, plus three brown stripes above).

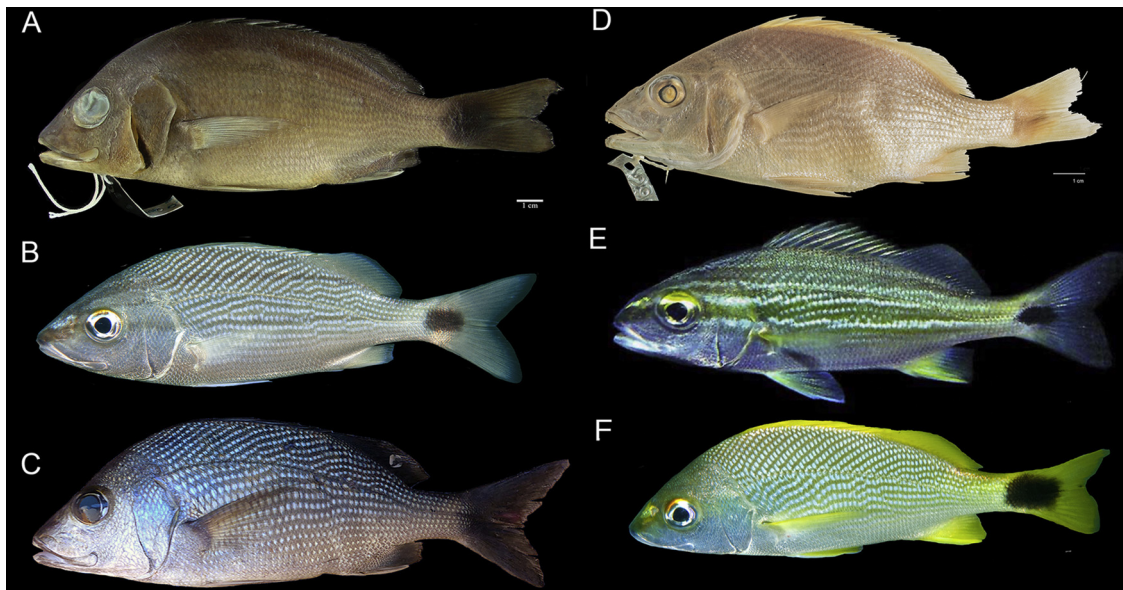
*Haemulon atlanticus* differs from its eastern Pacific congeners as follows: from *H. flaviguttatum* Gill, from Southern California to Peru, by having 19–24 rakers in the 1<sup>st</sup> branchial arch (vs. 26–31), eight (rarely nine) soft rays in the anal fin (vs. 10 or 11), large mouth with maxilla reaching the center of the eye (vs. small mouth, with maxilla reaching the anterior border of the eye); from *H. maculicauda* (Gill), from southern Baja California to northern Peru, by the scales on the sides of the body with grayish/silver centers forming oblique lines to the axis of the body (vs. scales with white and black centers forming longitudinal stripes parallel to the axis of the body), dorsal and anal fin yellow (vs. gray); from *H. scudderii*, from Southern Baja and Central Gulf of California to Ecuador, by presenting seven to nine scales above the lateral line (vs. five or six), scales all over the body with gray-brown centers (vs. black spots on each scale); from *H. sexfasciatum*, from Baja California to Ecuador, by containing eight (rarely nine) anal fin soft rays (vs. nine or ten), body silver to silver gray without bars (vs. six or seven bars in the dorsolateral surface of the body) and head without spots (vs. dark spots on the side of the head); from *H. steindachneri*, from the Gulf of California to northern Peru, by presenting an anal fin usually with eight rays (vs. usually nine rays); 13–15 scales below the lateral line, rarely 12 (vs. 12 scales below the lateral line, rarely 13), posterior margin of the maxilla robust with a smoothly angled end (vs. smaller maxilla with moderately convex extremity), a spot on the preoperculum, broad and robust, with no definite shape (vs. narrow spot, with anterior extremity tuned and posterior straight, resembling a triangle) (Fig. 2).

### 3.1.2. Molecular diagnosis

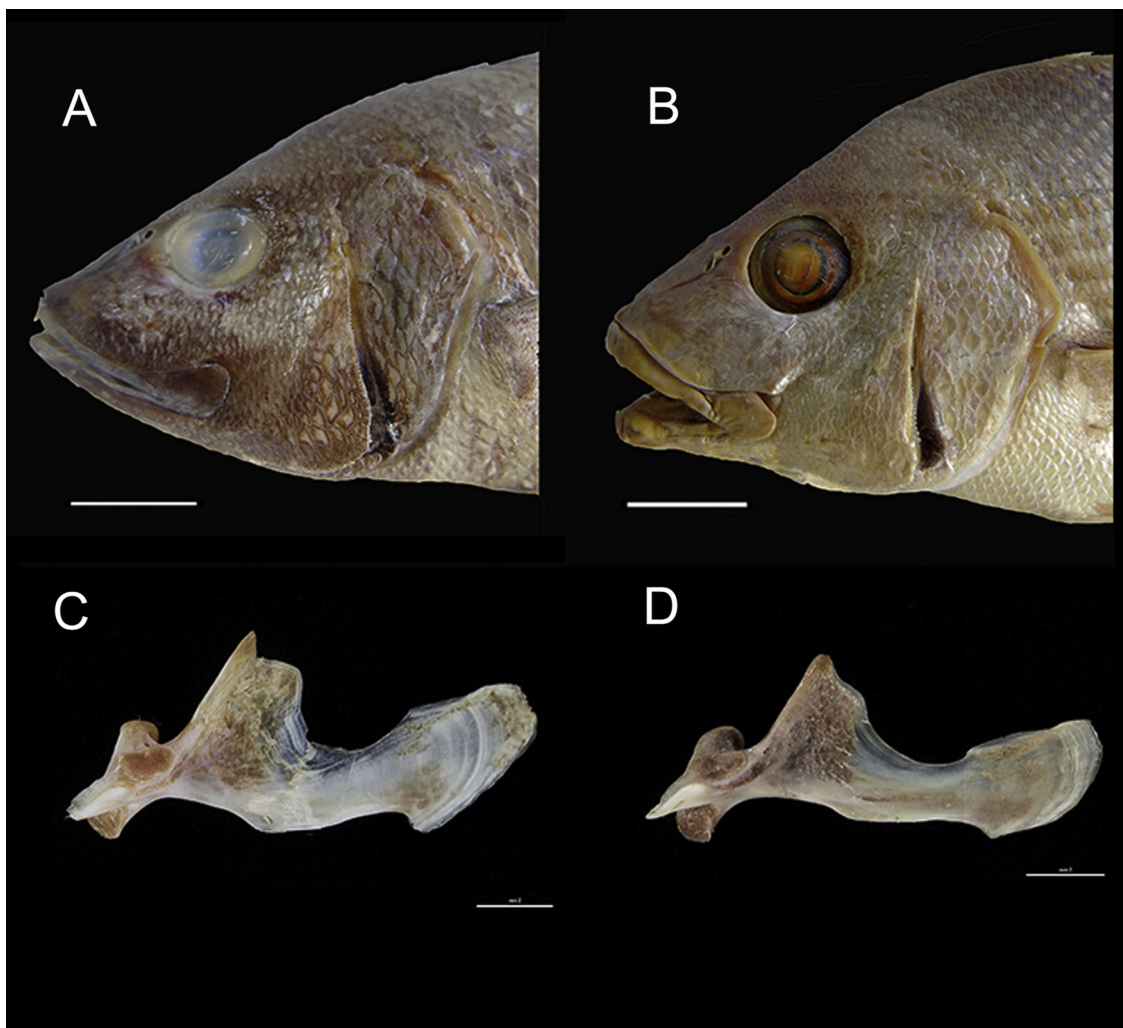
*Haemulon atlanticus* forms a distinct group (Fig. 3) with genetic distance (K2P) from other representatives ranging from 7.4% (*H. steindachneri*) to 15.5% (*H. melanurum*) (Table 3). The COI haplotypes of *H. atlanticus* differ from their congeners by 35 (*H. steindachneri*) to 68 bases (*H. melanurum*) (Table 4). The molecular separation of *H. atlanticus* and *H. steindachneri* is corroborated by the species delimitation analysis, as well as in the haplotype network (see Supplement I Appendix A). In addition, two distinct molecular lineages were recognized in *H. atlanticus* along the Atlantic coast, one comprised of specimens from Amapá on the coast of Brazil and the Caribbean coast and the other from additional coastal areas of Brazil (see Supplement I Appendix A). Although these lineages are differentiated by two exclusive COI mutations (see haplotype network in Supplement I Appendix A), the genetic distance between them is very small ( $0.013 \pm 0.005$ ). The GMYC and bPTP analyses recognized these two lineages as distinct species; however, the ABGD analysis did not support this recognition (see Supplement I Appendix A), and no morphological differences were found to separate them.

### 3.1.3. Description

Morphometric data in Table 1 and meristic data in Table 2. Body



**Fig. 1.** Body of *Haemulon atlanticus* and *Haemulon steindachneri* in lateral view. (A) *Haemulon atlanticus* holotype, MPEG 35708, 152 mm SL. (B) *Haemulon atlanticus* juvenile, by Luiz Rocha. (C) *Haemulon atlanticus* fresh specimen, MPEG 35708, 189 mm TL. (D) *Haemulon steindachneri* syntype, USNM 29226, by Sandra Raredon. (E) *Haemulon steindachneri* juvenile, by Gerald R. Allen. (F) *Haemulon steindachneri* fresh specimen, by Luiz Rocha.



**Fig. 2.** Head and maxilla of *Haemulon atlanticus* and *H. steindachneri* in lateral view. (A) *Haemulon atlanticus* 192 mm SL, Pará (MPEG 34530). (B) *H. steindachneri*, 191 mm SL, Mexico (SU 2825). (C) Right jaw of *Haemulon atlanticus*, 172 mm SL, Alagoas, Brazil (MPEG 34269). (D) Right jaw of *H. steindachneri*, 178 mm SL, Mexico, Panama (USNM 404497).

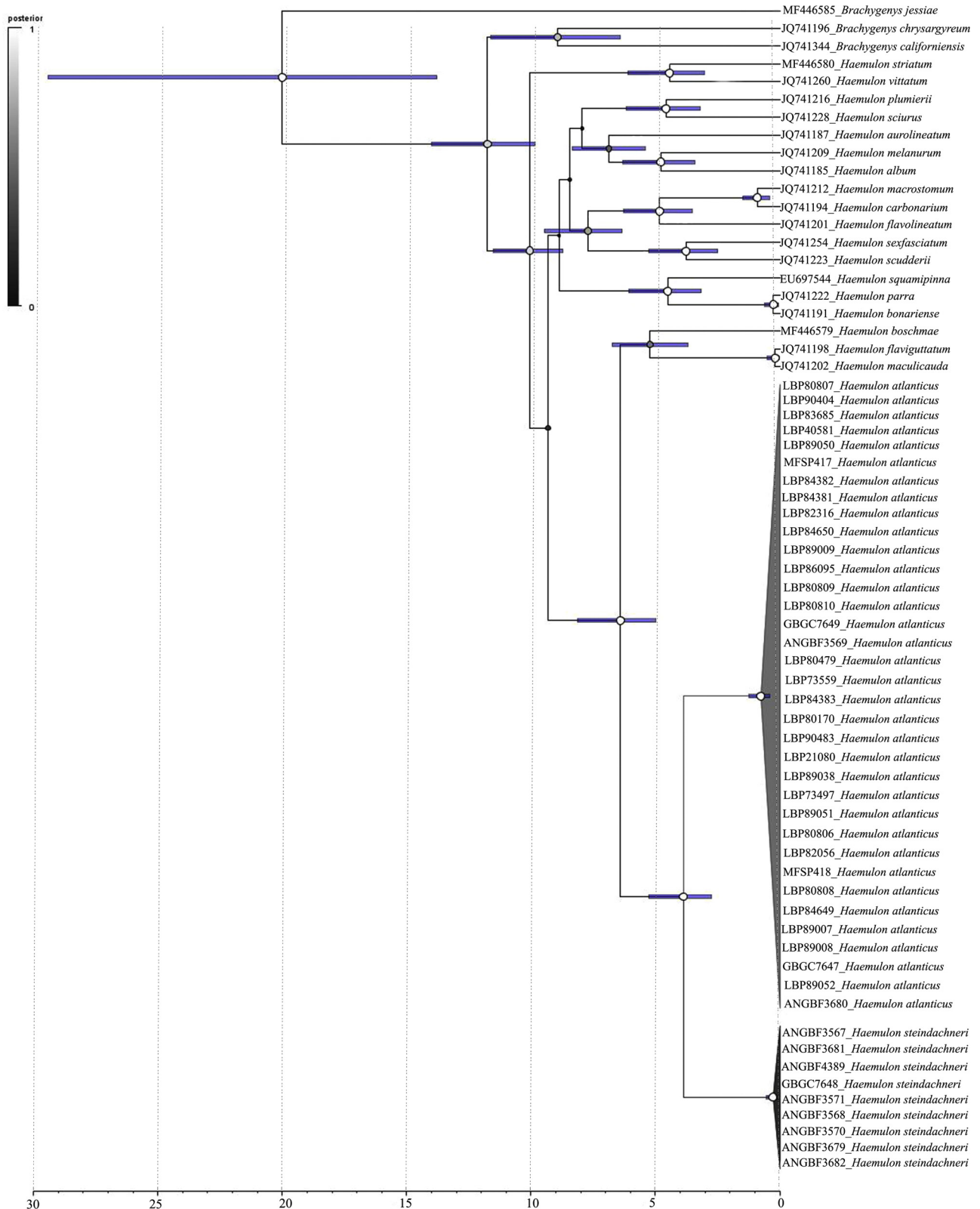


Fig. 3. Time-calibrated tree of New World *Haemulon* obtained from COI data. White circles indicate 0.75–1 posterior probability.

elongated, compressed laterally, greatest height at vertical through origin of dorsal fin. Dorsal profile of body convex from end of snout to base of first ray of dorsal fin, posterolaterally inclined at dorsal-fin base, approximately straight from last ray of dorsal to caudal peduncle. Ventral profile of body straight from anterior end of maxilla to base of pelvic fin, slightly convex from this point to origin of anal fin,

posterodorsally inclined at base of anal fin and approximately straight from last ray of anal to origin of inferior branch of caudal fin. Head pointy longer than high. Pointed snout, with length about one third of length of head. Eye large, ellipsoid, slightly before the middle of the head length. Small nostrils located laterally on head, anterior broadly teardrop-shaped and posterior oval, about half size of first; posterior

**Table 1**  
Measures of *Haemulon atlanticus* and *H. steindachneri* expressed as percentages of the standard length.

	<i>Haemulon atlanticus</i>				<i>Haemulon steindachneri</i>		
	N	Holotype	Amplitude	Average	N	Amplitude	Average
Standard length	101	152	55–224	-	12	98–201	-
Body height	101	39.5	31.6–43.9	36.5	12	32.8–38.0	35.1
Body width	101	19.2	9.8–21.3	16.7	12	12.3–18.7	15.1
Height of caudal peduncle	101	11.2	8.9–12.3	10.7	12	7.8–11.2	10.1
Width of caudal peduncle	101	3.7	2.7–5.6	3.6	12	2.8–4.1	3.5
Length of caudal peduncle	101	18.4	15.5–23.0	18.2	12	15.8–21.4	19.0
Distance between the snout and the pelvic fin	101	39.6	34.1–43.0	37.9	12	33.1–41.4	37.0
Length of the pelvic fin	101	21.9	18.0–24.3	20.4	12	17.8–21.0	19.8
Dorsal fin height	101	15.9	12.1–20.7	14.9	12	13.2–15.6	14.6
Pectoral fin length	101	29.4	22.2–32.8	27.0	12	22.8–29.5	26.8
Anal fin height	101	13.7	10.2–19.9	14.9	12	13.5–17.6	15.9
Pre-pectoral length	101	34.5	31.5–40.4	35.2	12	31.0–38.3	33.8
Pre-dorsal length	101	36.2	30.7–40.5	35.9	12	31.4–37.0	34.8
Pre-anal length	101	72.7	62.4–79.1	70.1	12	67.9–72.5	70.0
Head length	101	34.1	31.2–41.2	35.3	12	30.6–37.2	33.7
Head height	101	38.3	29.1–41.2	34.5	12	29.8–35.5	33.2
Interorbital distance	101	8.6	6.1–10.0	8.3	12	7.8–9.6	8.7
Post-orbital length	101	15.2	10.2–16.7	14.3	12	10.1–15.4	13.6
Snout length	101	12.6	8.4–15.1	12.1	12	9.8–13.7	11.5
Diameter of the orbit	101	10.1	8.6–17.2	10.7	12	8.6–10.9	9.4
Dorsal fin base length	101	56.6	45.7–58.5	52.3	12	49.4–57.0	52.4
Anal fin base length	101	14.2	11.8–17.2	14.1	12	12.6–15.2	13.8
Mouth width	101	13.3	8.4–15.4	12.6	12	9.1–14.5	11.9
Premaxillary length	101	18.4	13.8–21.4	18.0	12	14.4–19.2	16.5
Premaxillary width	101	2.9	2.4–4.3	3.2	12	2.4–3.3	3.0
Length of the lower lobe of the caudal fin	101	23.3	17.4–29.2	23.1	12	18.5–23.5	21.8
Length of upper lobe of caudal fin	101	26.3	16.8–26.5	21.3	12	17.6–22.8	21.0

**Table 2**  
Meristic data of *Haemulon atlanticus* and *H. steindachneri*. Holotype represented by \*.

<b>Lateral-line scales</b>	<b>50</b>	<b>51</b>	<b>52</b>	<b>53</b>	<b>54</b>	<b>55</b>	<b>56</b>
<i>Haemulon atlanticus</i>	3	3	33	20*	11	8	5
<i>H. steindachneri</i>	1	2	5	4			
<b>Longitudinal series of scales above the lateral line</b>	<b>7</b>	<b>8</b>	<b>9</b>				
<i>Haemulon atlanticus</i>	5	53	26*				
<i>H. steindachneri</i>	3	9					
<b>Longitudinal series of scales below the lateral line</b>	<b>11</b>	<b>12</b>	<b>13</b>	<b>14</b>	<b>15</b>	<b>16</b>	
<i>Haemulon atlanticus</i>	1	3	29	33	13*	4	
<i>H. steindachneri</i>		9	3				
<b>Dorsal-fin rays</b>	<b>XII</b>			<b>15</b>	<b>16</b>	<b>17</b>	
<i>Haemulon atlanticus</i>	85			34	47	4*	
<i>H. steindachneri</i>	12				11	1	
<b>Anal-fin rays</b>	<b>III</b>			<b>8</b>	<b>9</b>		
<i>Haemulon atlanticus</i>	85			59*	26		
<i>H. steindachneri</i>	12				12		
<b>Pectoral-fin rays</b>	<b>15</b>	<b>16</b>	<b>17</b>	<b>18</b>			
<i>Haemulon atlanticus</i>	5	48*	28	3			
<i>H. steindachneri</i>		2	10				
<b>1<sup>st</sup> Branchial Arch</b>	<b>19</b>	<b>20</b>	<b>21</b>	<b>22</b>	<b>23</b>	<b>24</b>	<b>24</b>
<i>Haemulon atlanticus</i>	1	2	6	10	21*	28	13
<i>H. steindachneri</i>	1	1	1	2	3	1	2
<b>2<sup>nd</sup> Branchial Arch</b>	<b>14</b>	<b>15</b>	<b>16</b>	<b>17</b>	<b>18</b>	<b>19</b>	
<i>Haemulon atlanticus</i>		10*	17	18	35	5	
<i>H. steindachneri</i>	1	2	3	5	1		

nostril in front and slightly above horizontal line of center of eye, anterior nostril just above horizontal of inferior margin of eye. Large mouth, posterior margin of robust maxilla with slightly angled extremity, situated vertically through center of orbit; fleshy and thick lips; upper lip slightly beyond tip of jaw. Conical teeth, in narrow band on each jaw, extended outer series. Chin with two pores and median groove. Short and thin gill rakers on first branchial arch.

Operculum without spine, covered with five or six vertical lines of ctenoid scales. Pre-operculum with slightly concave and serrated

posterior margin. Ctenoid scales (rough to touch), small or moderate, extending over head (except in front of snout, lips and chin) to caudal fin; longitudinal scales above oblique lateral line along axis of body; those below in horizontal series. Lateral line continuous gently curved posteriorly, following dorsal contour of body and becoming straight on peduncle. Soft rays of dorsal and anal fin densely scaled almost to edge of fin. Base of pectoral fin scaled.

Dorsal fin with small notch in middle; origin at vertical through posterior margin of operculum; high, strong spines, fourth more prominent, about one-third greater than soft rays; spines XII, rays 15 or 16 (rarely 17\*), first ray unbranched, branched remnants. Anal fin origin below base of 3rd or 4th ray of dorsal fin; spines III, rays eight\* or Nine, all branched; spines strong, second most prominent; long soft rays, first ray almost reaching tip of first spine. Caudal fin emarginated to forked, lobes approximately equal in size; principal rays ten + eight, upper and lower rays unbranched. Pectoral fins moderately long, not reaching or reaching tip of pelvic fin, fifth ray longest; rays 15(5), 16(48\*), or 17(28) (rarely 18); first ray shorter, unbranched, second ray about two times longer, unbranched, remaining rays branched. Origin of pelvic fins below lower base of pectoral fins, at vertical through base of 2nd or 3rd dorsal spine; first ray longest (second equal to first); spines I, rays five, all branched. Caudal peduncle longer than high.

Lateral line scales 50(3), 51(3), 52(33), 53(20\*), 54(11), 55(8), or 56(5); scales above lateral line to base of first dorsal fin spine eight or nine\* (rarely seven); scales below lateral line to first spine of anal fin 12(3), 13(29), 14(33), 15(13\*), or 16(4) (rarely 11); rakers on first branchial arch 19(1), 20(2), 21(6), 22(10), 23(21\*), or 24(13); rakers on second branchial arch 15(10\*), 16(17), 17(18), 18(35), or 19(5) (Table 2).

Supraneurals 3. Vertebrae 11 + 15. First pterygophore of dorsal fin inserted above second neural spine; last pterygophore of dorsal fin inserted in front of neural spine of 19th vertebra. First pterygophore of anal fin inserted below first hemal spine; last pterygophore of anal fin inserted in front of sixth hemal spine. Caudal skeleton with one ural center; five autogenic hypurals; three epurals; 17 (nine + eight) major caudal rays, with simple procurent rays (see Supplement II Appendix

**Table 3**Genetic distance K2P obtained among *Haemulon* clusters. Interspecific distance below the diagonal. Standard error above diagonal.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1. <i>Haemulon atlanticus</i>	0.005	0.012	0.017	0.016	0.015	0.017	0.019	0.015	0.019	0.017	0.015	0.020	0.016	0.019	0.019	0.019	0.017	0.018	0.017	0.019
2. <i>H. steindachneri</i>	0.074	0.002	0.017	0.016	0.018	0.018	0.018	0.013	0.017	0.018	0.014	0.019	0.018	0.016	0.018	0.018	0.015	0.019	0.017	0.017
3. <i>H. album</i>	0.122	0.125	0.002	0.017	0.016	0.018	0.017	0.016	0.016	0.017	0.016	0.015	0.016	0.018	0.016	0.017	0.015	0.019	0.017	0.017
4. <i>H. aurolineatum</i>	0.116	0.106	0.117	0.002	0.016	0.017	0.018	0.016	0.016	0.018	0.016	0.016	0.017	0.017	0.015	0.017	0.016	0.018	0.017	0.019
5. <i>H. bonariense</i>	0.107	0.130	0.107	0.112	0.000	0.018	0.017	0.017	0.017	0.018	0.017	0.017	0.004	0.018	0.017	0.017	0.015	0.014	0.017	0.020
6. <i>H. boschmae</i>	0.122	0.129	0.137	0.121	0.135	0.000	0.018	0.015	0.019	0.019	0.014	0.019	0.018	0.018	0.018	0.019	0.018	0.019	0.018	0.020
7. <i>H. carbonarium</i>	0.136	0.123	0.117	0.130	0.127	0.133	0.000	0.018	0.015	0.007	0.018	0.018	0.018	0.018	0.018	0.017	0.015	0.020	0.018	0.018
8. <i>H. flaviguttatum</i>	0.096	0.077	0.114	0.106	0.128	0.099	0.130	0.004	0.017	0.019	0.003	0.016	0.018	0.015	0.017	0.016	0.014	0.018	0.016	0.018
9. <i>H. flavolineatum</i>	0.139	0.115	0.118	0.107	0.122	0.148	0.088	0.130	0.000	0.015	0.017	0.017	0.018	0.018	0.019	0.017	0.016	0.020	0.018	0.021
10. <i>H. macrostoma</i>	0.123	0.123	0.120	0.130	0.135	0.138	0.024	0.142	0.090	0.000	0.019	0.020	0.018	0.018	0.019	0.019	0.017	0.021	0.020	0.020
11. <i>H. maculicauda</i>	0.096	0.082	0.109	0.108	0.125	0.099	0.133	0.004	0.133	0.142	0.006	0.016	0.018	0.016	0.017	0.016	0.014	0.018	0.016	0.018
12. <i>H. melanurum</i>	0.155	0.138	0.091	0.108	0.120	0.150	0.140	0.113	0.113	0.157	0.111	0.000	0.017	0.017	0.018	0.017	0.016	0.020	0.017	0.018
13. <i>H. parra</i>	0.109	0.132	0.110	0.120	0.006	0.143	0.130	0.136	0.130	0.132	0.133	0.122	0.002	0.019	0.017	0.017	0.015	0.014	0.016	0.019
14. <i>H. plumierii</i>	0.133	0.100	0.125	0.124	0.131	0.132	0.128	0.101	0.128	0.133	0.106	0.124	0.134	0.011	0.014	0.016	0.016	0.020	0.016	0.019
15. <i>H. sciurus</i>	0.132	0.119	0.111	0.098	0.122	0.134	0.127	0.119	0.141	0.135	0.116	0.129	0.125	0.079	0.002	0.017	0.017	0.019	0.015	0.019
16. <i>H. scudderii</i>	0.138	0.126	0.116	0.129	0.120	0.156	0.127	0.103	0.128	0.140	0.101	0.114	0.123	0.101	0.114	0.002	0.012	0.016	0.017	0.018
17. <i>H. sexfasciatum</i>	0.117	0.098	0.101	0.113	0.100	0.139	0.107	0.091	0.109	0.117	0.088	0.113	0.102	0.100	0.113	0.062	0.000	0.017	0.015	0.017
18. <i>H. squamipina</i>	0.131	0.127	0.139	0.125	0.081	0.141	0.148	0.134	0.148	0.159	0.131	0.141	0.088	0.147	0.139	0.115	0.120	0.000	0.018	0.018
19. <i>H. striatum</i>	0.122	0.115	0.118	0.115	0.115	0.133	0.138	0.113	0.133	0.148	0.116	0.118	0.112	0.111	0.103	0.123	0.108	0.125	0.002	0.015
20. <i>H. vittatum</i>	0.145	0.128	0.118	0.147	0.149	0.157	0.132	0.136	0.165	0.150	0.139	0.139	0.146	0.137	0.142	0.129	0.124	0.133	0.089	0.000

A).

### 3.1.4. Coloration in life

Body gray dorsally, silver to dark gray ventrally; scales with gray/silver centers, forming oblique lines along rows of scales; head dark gray at top of snout to vertical passage through pre-operculum border, light gray/silver in infraorbital region; distinct blackish spot on lower anterior part of operculum, partially covered by pre-operculum angle. Dark, large, distinct and rounded spot at end of caudal peduncle and at base of caudal fin. Dorsal and anal fins gray with lighter tonality on interradial membranes; pectoral and pelvic fins gray to yellowish; dark caudal fin. Juveniles with three dark stripes on the sides of the body; one above the eye to end of dorsal-fin base; the middle one being a short stripe from the top of eye along the upper operculum; and a brownish mid-lateral stripe starting from the snout, through the eye to near the end of the caudal-fin base (Fig. 1).

### 3.1.5. Coloration of preserved specimens

Upper dorsal and lateral surface of body relatively light brown or gray. Ventral surface of body pale yellowish-brown. Distinct blackish spot on lower anterior part of operculum, partially hidden by pre-operculum angle. Dark, large, distinct and rounded spot at end of caudal peduncle and at base of caudal fin.

### 3.1.6. Distribution and habitat

*Haemulon atlanticus* occurs on the western Atlantic coast of Costa Rica to Santa Catarina-Brazil (Fig. 4), inhabiting estuarine and coastal marine waters up to 30 m deep. The species is associated with coral reefs and can be found on sand and rubble substrates.

### 3.1.7. Etymology

The specific epithet “atlanticus” is related to the distribution of the species from the western Atlantic coast. A noun in apposition.

### 3.1.8. Remarks

*Haemulon steindachneri* was described by Jordan and Gilbert (1882), as *Diabasis steindachneri*, based on specimens collected on the Pacific coast. The same authors, when reviewing the type material of *H. caudimacula* Cuvier (Type locality: Acapulco, Rio de Janeiro, Rio Grande do Sul, Maranhão), recognized that *H. caudimacula* represents a junior synonym of *H. parra*, showing that *H. caudimacula* was erroneously identified as synonym of *H. steindachneri* because it contained 15

dorsal-fin rays (vs. 16) and seven anal-fin rays (vs. 8) (Jordan and Gilbert, 1882).

Hong (1977) was the first author to discuss possible differences among populations of *H. steindachneri*, comparing specimens from the Eastern Pacific with specimens examined by Courtenay (1961) in the Western Atlantic. According to Hong (1977), the Atlantic and Pacific specimens are similar except for the length of the snout and length of the maxillary jaw that were 1 to 2% SL larger in the Atlantic specimens. These differences were not found in the present study; however, differences in the shape of the maxillary margin of these pairs of species were found.

Regarding nominal species available for the Western Atlantic, we consider that *Haemulon atlanticus* is not related to *Haemulon fur* Poey, by possessing a silver to silver gray body without stripes (vs. steel gray body with golden yellow bands); *H. helenae* Boulenger, by containing III spines in the anal fin and eight (rarely nine) soft rays (vs. III, 12); *H. hians* Haly, by having a silver to silver gray body without stripes (vs. longitudinally striped body); *H. jaguanum* Poey, by having a large rounded blackish spot at the end of the caudal peduncle and base of the tail fin (vs. spot in the caudal absent); *H. melanopterum* Ranzani, by presenting 15–17 rays in dorsal fin (vs. 10–12); *H. modestum* Tschudi, by containing III spines in anal fin and eight (rarely nine) soft rays (vs. IV, 13); *H. schranki* Agassiz, by presenting 15–17 rays in dorsal fin (vs. 18); *H. serrula* (Cuvier), by having 15–17 rays in dorsal fin (vs. 13) and *H. similis* Castelnau, by possessing a silver to silver gray body without stripes (vs. body with yellow longitudinal bands).

It is need to be clarified that the designation of the Atlantic forms of the *H. steindachneri* species complex (*sensu* Lindeman and Toxey, 2002), as *H. bonariense* (Fig. 5). Recognized by having a great similarity with *H. canna* Cuvier, *H. bonariense* was described based on a specimen collected in the vicinity of Buenos Aires. Being recognized as a valid specie for the Caribbean (Parenti, 2019), Courtenay (1961: 104), as first reviser, selected *H. bonariense* as nominal species over *H. canna*. However, Moura (2003; unpub. PhD. thesis), recognized *H. bonariense* as the name available for the Atlantic *H. steindachneri*, without justifying his decision. Even considering that the nominal specie could be recognized as *nomem dubium*, by having been established based on specimen collected from the proximities of Buenos Aires, Argentina, where there are no records for any species of the genus *Haemulon* as well as the presence of 14 rays in the dorsal fin (vs. 15 or 16, rarely 17 in *H. atlanticus*, *H. steindachneri* and *H. bonariense*), characteristic of morphology not observed in any representative of the genus. In that way, based on

**Table 4**  
Nucleotide differences observed in the COI gene among the analyzed specimens.

	5	6	8	11	14	17	20	23	26	29	35	41	44	47	50	53	56	77	83	86	89	95	98	107	110	111	113	119	125	128	131	134	137	
<i>Haemulon atlanticus</i>	C	C	T	G	C	T	A	C	T	C	T	T	G	T	G	C	A	G	T	C	C	G	T	A	C	G	T	A	C	A	G	C	T	
<i>H. steindachneri</i>	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	A	.	.	.	.	.	.	.	G	.	.	.	
<i>H. album</i>	.	.	.	T	.	.	G	C	.	.	.	.	.	.	A	.	.	A	.	.	.	T	.	.	T	.	C	.	.	.	A	.	.	
<i>H. aurolineatum</i>	.	.	G	A	.	C	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	A	.	T	.	C	.	.	G	.	T	.	
<i>H. bonariense</i>	.	.	G	.	.	C	G	.	.	.	.	.	C	.	.	.	.	.	.	.	.	T	.	G	.	.	.	.	.	G	.	.	.	
<i>H. boschmae</i>	.	.	A	.	.	G	C	T	.	.	.	.	.	.	.	.	.	.	.	.	.	T	A	.	.	.	.	.	.	A	.	.	.	
<i>H. carbonarium</i>	T	.	A	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	G	C	A	.	.	
<i>H. flaviguttatum</i>	.	.	C	.	.	C	G	T	.	.	.	.	.	.	.	.	.	.	.	.	.	T	A	.	T	.	.	.	.	.	.	.	C	
<i>H. flavolineatum</i>	.	.	G	.	.	G	.	.	.	.	.	A	.	.	.	G	.	.	.	.	T	A	.	T	.	C	G	.	G	C	A	.		
<i>H. macrostoma</i>	T	.	A	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	G	C	A	.	.	
<i>H. maculicauda</i>	.	.	.	.	C	G	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	A	.	T	.	.	.	.	.	.	.	C	
<i>H. melanurum</i>	.	.	G	.	.	C	G	T	.	.	A	A	.	.	.	.	.	.	.	.	T	T	A	.	T	.	C	.	T	G	.	T	.	
<i>H. parra</i>	.	.	G	.	.	C	G	.	.	.	.	C	.	.	.	.	.	.	.	.	T	.	G	.	.	.	.	.	T	G	.	.	.	
<i>H. plumierii</i>	.	.	C	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	T	A	.	.	.	.	T	G	.	.	C	
<i>H. sciurus</i>	.	.	G	A	.	C	G	.	.	.	.	.	.	.	A	.	.	C	.	.	T	.	.	.	.	.	C	.	T	G	A	.	.	
<i>H. scudderii</i>	.	.	A	.	.	C	.	T	.	.	.	.	.	.	.	.	.	.	.	.	T	A	C	.	.	.	C	.	T	.	.	.	C	
<i>H. sexfasciatum</i>	.	.	A	.	.	C	G	T	.	.	C	.	.	.	.	.	.	.	.	.	T	A	.	.	.	.	.	.	T	G	.	.	C	
<i>H. squamipinna</i>	.	T	G	.	.	C	G	.	.	.	.	.	.	.	.	T	.	.	.	.	T	A	.	.	.	A	C	.	.	.	.	.	.	
<i>H. striatum</i>	.	.	G	.	.	C	G	.	.	C	C	.	.	.	.	.	G	.	C	.	T	A	.	T	.	C	.	.	G	.	.	.	.	
<i>H. vittatum</i>	.	.	A	.	T	C	G	.	.	C	.	.	.	.	A	.	.	.	.	.	T	A	C	.	.	.	C	.	.	.	.	.	T	.

	134	137	140	143	149	152	155	158	161	170	176	179	182	185	188	194	197	200	203	206	209	212	215	218	221	224
<i>Haemulon atlanticus</i>	C	T	G	A	C	A	A	T	C	T	C	T	C	C	C	C	T	C	T	T	A	G	A	G	C	
<i>H. steindachneri</i>	.	.	.	.	G	.	G	.	.	.	.	C	T	.	T	.	.	.	.	.	.	.	.	.	.	T
<i>H. album</i>	.	.	A	.	.	.	G	.	.	T	C	T	.	T	.	.	C	.	C	.	G	C	.	A	.	
<i>H. aurolineatum</i>	T	.	.	.	A	.	G	C	T	.	.	T	A	T	T	.	T	C	.	C	.	C	.	A	T	
<i>H. bonariense</i>	.	.	.	.	.	.	G	.	.	.	.	C	.	T	T	.	T	A	C	.	.	.	T	A	.	
<i>H. boschmae</i>	.	.	.	G	.	.	G	C	.	.	.	C	T	G	T	T	.	A	.	C	.	.	.	.	T	
<i>H. carbonarium</i>	A	.	.	.	.	.	G	.	.	G	C	.	.	T	A	.	C	.	C	.	.	.	.	A	.	
<i>H. flaviguttatum</i>	.	C	.	.	.	.	G	C	T	.	.	C	T	.	T	T	.	.	C	.	.	.	.	.	T	
<i>H. flavolineatum</i>	A	.	.	.	T	C	G	C	.	C	T	C	.	.	T	.	.	.	C	.	.	.	.	A	.	
<i>H. macrostoma</i>	A	.	.	.	.	.	G	.	.	G	C	.	.	T	A	.	C	.	C	.	.	.	.	A	.	
<i>H. maculicauda</i>	.	C	.	.	.	.	G	C	T	.	.	C	T	.	T	T	.	.	C	.	.	.	.	.	T	
<i>H. melanurum</i>	T	.	A	.	.	.	G	C	.	.	C	.	.	T	T	T	C	.	C	C	.	.	.	A	.	
<i>H. parra</i>	.	.	.	.	.	.	G	.	.	.	C	.	.	T	.	T	.	A	C	.	.	.	.	T	A	.
<i>H. plumierii</i>	.	C	.	.	.	.	G	.	.	.	C	T	.	T	T	.	.	.	.	.	.	.	T	.	T	
<i>H. sciurus</i>	.	.	.	.	.	.	G	.	.	.	C	T	C	T	T	.	.	.	C	.	.	C	.	.	T	
<i>H. scudderii</i>	.	C	.	.	.	G	G	.	.	.	C	.	.	T	T	.	.	.	C	.	.	A	.	.	.	
<i>H. sexfasciatum</i>	.	C	.	.	.	.	G	.	.	.	C	T	.	T	.	.	.	.	C	.	.	.	.	.	.	
<i>H. squamipinna</i>	.	.	.	.	.	.	G	.	.	.	C	.	C	.	.	.	.	T	C	.	.	.	T	A	G	
<i>H. striatum</i>	.	.	.	.	.	.	G	.	.	.	C	T	.	T	T	T	C	.	C	.	.	A	.	.	G	
<i>H. vittatum</i>	T	.	.	.	G	.	G	.	.	.	C	T	.	.	.	.	.	C	.	.	.	.	.	.	A	

	227	230	233	236	239	242	245	48	251	254	257	258	260	263	266	269	270	272	275	278	281	284	287	290	293	296	
<i>Haemulon atlanticus</i>	G	T	C	A	A	A	T	T	C	C	T	C	G	T	G	T	C	G	A	C	C	G	G	G	T	T	
<i>H. steindachneri</i>	A	.	A	G	.	.	.	C	.	.	.	.	.	C	A	.	.	.	.	.	.	.	A	.	.	.	
<i>H. album</i>	.	.	A	T	G	G	.	.	.	.	.	.	.	.	.	C	T	.	.	T	.	A	.	A	.	C	
<i>H. aurolineatum</i>	.	.	G	T	.	.	.	T	.	.	.	.	A	.	.	.	.	.	.	.	.	.	A	A	.	.	
<i>H. bonariense</i>	.	.	G	T	.	.	.	.	T	.	.	.	A	.	.	C	.	.	.	A	.	A	.	C	A	C	
<i>H. boschmae</i>	A	A	G	.	.	.	.	.	.	.	.	.	A	C	.	.	.	.	A	G	T	.	A	.	A	C	C
<i>H. carbonarium</i>	A	.	G	T	G	.	C	G	.	.	T	A	.	A	.	.	.	.	T	T	A	A	C	.	C		
<i>H. flaviguttatum</i>	.	.	A	G	G	.	.	C	.	.	.	.	A	.	.	.	A	.	T	.	.	.	.	.	C		
<i>H. flavolineatum</i>	.	.	T	T	.	.	A	.	.	T	A	C	A	.	.	A	.	A	.	T	.	.	A	C	.	C	
<i>H. macrostoma</i>	A	.	G	T	.	.	C	G	.	.	T	.	.	A	.	.	.	.	T	T	.	A	C	.	C		
<i>H. maculicauda</i>	.	.	A	G	G	.	.	C	.	.	.	.	A	.	.	C	.	A	.	T	.	.	.	.	C		
<i>H. melanurum</i>	.	.	A	T	G	G	.	C	.	.	.	.	A	C	.	C	T	.	T	.	A	.	A	.	C		
<i>H. parra</i>	.	.	G	T	.	.	.	.	.	T	.	.	.	.	.	C	.	.	.	.	.	A	.	C	A	C	
<i>H. plumierii</i>	.	C	A	T	G	G	.	.	.	.	.	.	A	C	A	.	.	A	.	T	T	.	A	A	.	C	
<i>H. sciurus</i>	.	C	G	G	G	.	.	.	.	.	.	.	A	G	T	C	.	.	.	.	T	.	A	A	.	C	
<i>H. scudderii</i>	.	.	G	T	G	.	.	C	.	T	C	T	A	.	A	C	.	A	G	.	.	A	A	.	.		
<i>H. sexfasciatum</i>	.	.	G	T	.	.	.	C	.	.	.	T	A	.	A	C	.	.	.	T	.	C	A	A	.	.	
<i>H. squamipinna</i>	A	.	G	T	.	.	.	C	.	T	C	.	A	.	A	C	.	C	.	.	.	A	.	A	A	C	
<i>H. striatum</i>	.	.	G	T	.	.	.	C	T	.	.	.	.	A	.	.	.	.	.	.	.	A	.	A	C	C	
<i>H. vittatum</i>	A	.	G	T	G	G	.	.	C	.	.	.	.	A	.	.	.	.	.	.	.	A	.	A	.	C	

	299	302	305	308	311	314	318	320	323	326	329	332	335	341	344	347	350	353	359	362	365	368	371	374	377	380
<i>Haemulon atlanticus</i>	T	A	C	C	C	T	T	A	A	T	T	A	A	T	A	C	C	C	T	A	A	C	T	C	A	A
<i>H. steindachneri</i>	.	.	.	.	.	.	.	.	.	.	C	.	.	.	G	T	.	.	.	.	.	.	.	.	G	G
<i>H. album</i>	.	.	T	.	.	C	.	.	.	.	.	C	.	.	C	G	.	.	.	.	G	T	.	.	G	G
<i>H. aurolineatum</i>	.	.	.	.	.	C	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	T	G	G
<i>H. bonariense</i>	G	.	T	.	.	C	.	.	.	.	C	C	.	C	G	.	.	.	.	.	.	.	.	.	G	.
<i>H. boschmae</i>	.	.	.	.	.	C	.	.	G	.	C	.	G	.	.	.	.	.	.	G	.	T	.	.	G	.

(continued on next page)

Table 4 (continued)

	299	302	305	308	311	314	318	320	323	326	329	332	335	341	344	347	350	353	359	362	365	368	371	374	377	380	
<i>H. carbonarium</i>	.	.	T	.	.	C	.	.	.	.	C	.	G	.	G	.	.	.	C	.	G	T	.	T	G	G	
<i>H. flaviguttatum</i>	.	.	.	.	.	C	.	.	.	.	C	.	G	.	.	.	.	.	.	.	.	T	.	.	G	.	
<i>H. flavolineatum</i>	C	.	T	.	.	C	.	.	.	.	G	.	.	.	G	.	.	.	C	.	.	T	.	.	G	G	
<i>H. macrostoma</i>	.	.	T	.	.	C	.	.	.	.	.	.	G	.	G	.	.	.	C	.	G	T	.	.	G	G	
<i>H. maculicauda</i>	.	.	.	.	.	C	.	.	.	.	C	.	G	.	.	.	.	.	.	.	.	T	.	.	G	.	
<i>H. melanurum</i>	.	.	T	.	.	C	.	.	T	.	C	.	.	.	.	.	.	T	C	.	.	.	.	C	.	G	G
<i>H. parra</i>	G	.	T	.	.	C	.	.	.	.	C	C	.	C	G	.	.	.	.	.	.	.	.	.	.	G	.
<i>H. plumierii</i>	.	.	T	.	.	.	.	.	.	.	.	.	.	C	G	T	T	.	C	.	.	T	.	.	.	G	.
<i>H. sciurus</i>	.	.	.	T	.	.	.	.	.	.	C	G	.	C	G	.	.	.	C	.	.	T	.	T	G	G	
<i>H. scudderii</i>	.	.	T	.	.	C	C	.	G	C	.	C	C	C	G	.	T	.	C	.	G	T	.	.	G	.	
<i>H. sexfasciatum</i>	A	.	T	.	.	C	.	.	G	C	G	.	G	G	.	T	.	.	.	.	G	T	.	.	G	.	
<i>H. squamipinna</i>	G	.	T	.	.	A	C	G	.	.	C	.	.	C	G	.	.	T	.	T	.	.	.	.	G	.	
<i>H. striatum</i>	.	.	.	.	.	.	G	.	.	.	C	G	.	G	G	.	.	.	.	G	.	T	.	.	.	.	
<i>H. vittatum</i>	.	G	T	.	T	C	.	G	G	G	C	G	.	G	G	.	.	.	C	G	G	.	.	T	G	.	
	383	386	389	392	395	398	401	404	407	410	411	413	416	419	422	425	428	431	434	437	440	443	446	449	452	455	
<i>Haemulon atlanticus</i>	T	T	C	C	G	A	C	G	C	C	C	G	C	A	A	A	T	C	C	T	C	T	T	T	T	A	
<i>H. steindachneri</i>	.	.	.	.	.	G	.	A	T	G	.	A	.	.	.	.	C	.	.	.	.	C	.	.	C	G	
<i>H. album</i>	.	C	T	.	.	G	.	.	.	G	.	.	.	.	.	.	C	.	T	.	.	G	C	.	.	G	
<i>H. aurolineatum</i>	C	C	T	.	.	.	A	.	A	T	A	T	.	.	.	.	C	.	.	.	.	A	C	.	.	G	
<i>H. bonariense</i>	.	C	T	.	T	.	.	.	T	.	.	T	G	.	.	.	G	.	.	C	.	G	C	.	.	.	
<i>H. boschmae</i>	C	.	.	.	A	.	T	A	.	.	.	A	T	G	.	.	C	T	.	C	T	.	A	.	.	G	
<i>H. carbonarium</i>	C	C	T	.	.	C	.	.	.	.	.	C	.	.	.	.	C	T	T	.	T	.	A	C	A	G	
<i>H. flaviguttatum</i>	.	.	.	.	.	G	.	A	T	.	.	A	.	.	.	.	.	.	.	T	.	.	C	.	.	C	G
<i>H. flavolineatum</i>	C	C	T	.	.	G	.	.	.	A	.	.	.	.	.	C	C	T	.	.	T	A	C	.	.	G	
<i>H. macrostoma</i>	C	C	T	.	.	.	.	.	.	.	.	C	.	.	.	.	C	T	T	.	T	.	A	C	A	G	
<i>H. maculicauda</i>	.	.	.	.	.	G	.	A	T	.	.	A	.	.	.	.	.	.	.	T	.	.	.	.	C	G	
<i>H. melanurum</i>	.	C	T	.	.	G	.	A	.	G	.	.	T	.	G	C	C	.	A	.	.	A	C	.	.	G	
<i>H. parra</i>	.	C	T	.	T	.	.	.	T	.	.	T	G	.	.	G	.	.	C	.	G	C	C	.	.	.	
<i>H. plumierii</i>	.	C	T	.	C	G	T	A	.	.	.	A	.	G	G	.	C	.	T	.	T	A	C	.	.	C	
<i>H. sciurus</i>	.	C	T	.	A	.	T	A	.	.	.	.	.	G	.	.	C	.	T	.	.	A	.	.	.	C	
<i>H. scudderii</i>	.	C	T	.	.	G	.	A	T	.	.	.	.	.	G	C	.	A	.	.	A	C	.	.	.	G	
<i>H. sexfasciatum</i>	C	.	T	.	.	G	.	.	T	.	.	.	.	.	.	C	.	A	.	.	G	C	.	.	.	G	
<i>H. squamipinna</i>	.	C	T	T	.	.	A	T	.	.	A	T	G	.	.	C	T	.	.	.	G	.	.	.	.	T	
<i>H. striatum</i>	.	C	T	.	C	G	.	A	.	.	.	.	.	C	.	C	.	C	.	T	.	T	A	.	C	.	
<i>H. vittatum</i>	.	C	T	T	C	G	.	.	T	.	.	A	.	C	.	C	C	.	T	.	T	A	.	C	C	.	
	458	461	464	467	470	473	476	479	482	485	488	491	494	497	500	501	503	505	506	507	509	510	512				
<i>Haemulon atlanticus</i>	C	.	C	A	A	C	A	T	C	T	A	G	C	C	A	C	C	A	A	C	C	G	A	T			
<i>H. steindachneri</i>	.	.	.	.	.	G	.	T	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C			
<i>H. album</i>	.	.	.	.	T	G	G	.	C	.	.	.	.	.	T	.	.	.	.	.	.	.	A	.	C		
<i>H. aurolineatum</i>	.	.	.	C	T	G	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	C		
<i>H. bonariense</i>	.	.	C	.	.	G	C	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	A	.	C		
<i>H. boschmae</i>	.	.	.	.	T	.	.	.	C	.	.	.	T	.	.	.	.	.	.	.	T	.	A	.	.		
<i>H. carbonarium</i>	.	.	C	T	.	G	C	.	.	.	.	T	.	.	.	.	.	.	.	.	T	.	.	.	C		
<i>H. flaviguttatum</i>	T	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	A	.	.		
<i>H. flavolineatum</i>	.	.	C	T	.	G	.	.	.	.	.	A	T	.	.	G	.	.	T	.	.	.	.	C	C		
<i>H. macrostoma</i>	.	T	C	T	.	G	C	.	.	.	.	T	.	.	.	.	.	.	.	.	T	.	.	.	C		
<i>H. maculicauda</i>	T	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	A	.	.		
<i>H. melanurum</i>	.	.	.	.	T	G	G	.	.	.	.	.	.	.	T	.	.	.	.	T	.	A	A	.	C		
<i>H. parra</i>	.	.	C	.	.	G	C	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	A	.	C		
<i>H. plumierii</i>	.	T	.	.	.	G	A	.	.	G	.	.	T	.	.	.	.	.	.	.	.	.	A	.	C		
<i>H. sciurus</i>	.	.	.	G	.	G	.	T	.	G	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.		
<i>H. scudderii</i>	.	.	.	.	.	G	.	.	.	G	.	G	T	G	.	.	.	.	.	.	T	.	A	.	.		
<i>H. sexfasciatum</i>	.	.	.	.	.	G	.	T	.	.	.	.	T	G	.	.	.	.	.	.	.	.	A	.	C		
<i>H. squamipinna</i>	.	.	T	.	.	G	C	.	.	.	.	A	G	.	.	.	.	.	.	.	T	.	A	.	C		
<i>H. striatum</i>	.	.	.	.	.	G	.	.	.	.	.	T	T	.	.	.	.	.	.	.	T	.	A	.	C		
<i>H. vittatum</i>	.	.	.	.	T	G	.	.	.	.	A	T	T	.	.	.	G	.	.	T	.	A	.	C			

examination of the type specimen (Fig. 5c), we recognize that the name *H. bonariense* does not apply to the forms here designated as *H. atlanticus*. Our decision is sustained by the presence of distinctly larger scales, observed in *H. bonariense* holotype (Fig. 5c) (vs. notoriously smaller scales in *H. atlanticus* (Fig. 5d)), condition that determines the presence of a smaller number of scales on the lateral line (about 43) in the *H. bonariense* holotype (45–48 in non-type specimens of *H. bonariense*), against 50–56 in *H. atlanticus* and 50–53 in *H. steindachneri*. Additionally, we consider that *H. bonariense* holotype, as well as non-type specimens, have a relatively smaller mouth in relation to *H. atlanticus* (Fig. 5), while the *H. bonariense* holotype maxilla has a convex end (vs. maxilla with angled end in *H. atlanticus*, Fig. 5).

### 3.2. *Haemulon steindachneri* (Jordan and Gilbert, 1882)

*Haemulon steindachneri* (Jordan and Swain, 1884) [Redescription]. — Hong, 1977:496 [in part, revision]. — Allen and Robertson, 1994:149 [Fishes of the tropical eastern Pacific, description; photograph]. — Bussing and López, 1994:120 [in part; description; illustrated]. — McKay and Schneider, 1995:1157 [in part; identification key; description; illustrated]. — De La Cruz Agüero et al., 1997:183 [in part, Catalogo de los peces marinos de Baja California Sur]. — Chirichigno and Vélez, 1998:375 [in part; identification key; distribution, Mexico to Peru]. — Castro-Aguirre et al., 1999:338 [in part, identification key; distribution, Panama to Brazil in Atlantic and

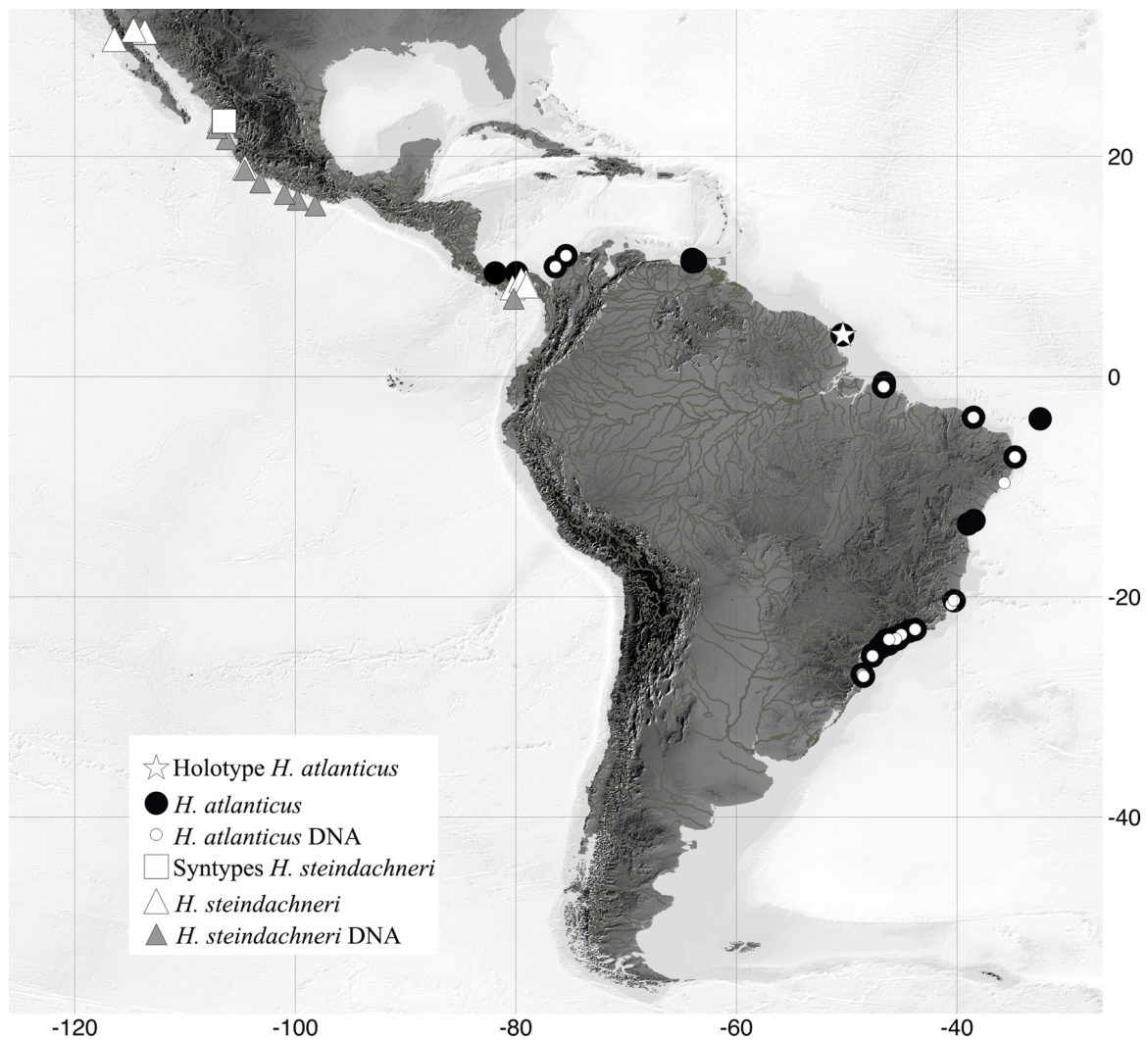


Fig. 4. Map of the locations of *Haemulon atlanticus* and *H. steindachneri* reviewed.

California Gulf to Panama in Pacific]. — Rocha et al., 2008:921 [in part, Historical biogeography and speciation in the reef fish genus *Haemulon*]. — Tavera et al., 2012:6 [in part, Molecular phylogeny]. —

Galván-Villa et al., 2016:147 [in part, checklist]. — Tavera et al., 2018:214 [in part, Multilocus phylogeny]. — González-Murcia et al., 2019:304 [in part, ichthyology collection at the Natural History

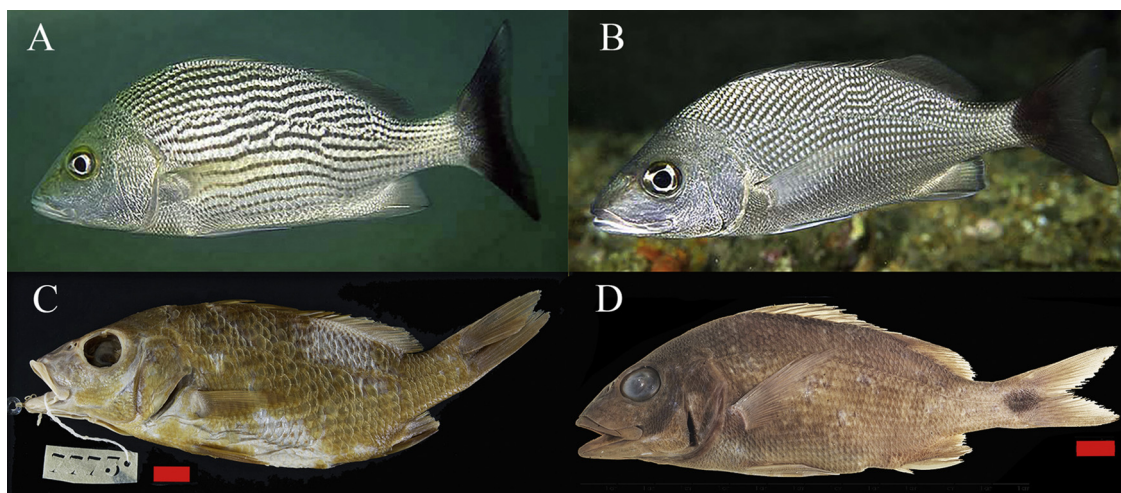


Fig. 5. Body in lateral view. (A) Live specimen of *Haemulon bonariense* from Isla Margarita, Venezuela, Luiz Rocha. (B) Live specimen of *Haemulon atlanticus* from Isla Margarita, Venezuela, Luiz Rocha. (C) Holotype of *Haemulon bonariense* (MNHN 0000-7773) from Buenos Aires, Argentina. (D) Non-type specimen of *Haemulon atlanticus* (USNM 361931), from Colombia.

Museum of El Salvador].

*Diabasissteindachneri* Jordan and Gilbert, 1882:322 [original description; type locality: Panama, Mazatlán. Syntypes: BMNH 1895.5.27.55—57 (3) Mazatlán; USNM 28172 (1), 29226 (1), 29305 (1, not found in 1980), 29387 (?), 29634 (1, lost), 29759 (1), 29778 (1), 29795 (0).

*Syntypes*: USNM 28172 (1, 175 mm SL), Mazatlan, Sinaloa, Mexico (photographic image and X-ray); USNM 29226 (1, 196 mm SL), Mazatlan, Sinaloa, Mexico (photographic image and X-ray); USNM 29759 (1, 160 mm SL), Mazatlan, Sinaloa, Mexico (photographic image and X-ray); USNM 29778 (1, 164 mm SL), Mazatlan, Sinaloa, Mexico (photographic image and X-ray); USNM 29795 (1, 160 mm SL), Mazatlan, Sinaloa, Mexico (photographic image and X-ray).

*Additional material*: LACM 9476.1 (1, 115 mm SL), Rancho El Tule, Gulf of California, Mexico (photographic image and X-ray); LACM 30383.2 (2, 187—194 mm SL), Cabo San Lucas, Mexico (photographic image and X-ray); LACM 32155.2 (1, 170 mm SL), Point Mita, Mexico (photographic image and X-ray); LACM 34079.2 (2, 206—214 mm SL), Gulf of California, Mexico (photographic image and X-ray); LACM 35744.23 (1, 193 mm SL), Guaymas, Gulf of California, Mexico (photographic image and X-ray); LACM 35745.13 (1, 154 mm SL), Guaymas, Gulf of California, Mexico (photographic image and X-ray); LACM 38.098.1 (1, 157 mm SL), Magdalena Bay, Mexico (photographic image and X-ray); MZUSP 79692 (1, 172 mm SL), Cabe San Lucas, Mexico; SU 2825 (1, 191 mm SL), Gulf of California, Sonora, Mexico; SU 2858 (1, 121 mm SL), Sinaloa, Mazatlan, Mexico; SU 55462 (1, 198 mm SL), Manzanillo, Colima, Mexico; LACM 30723.3 (2, 169—184 mm SL), Gulf of Nicoya, Puntarena, Costa Rica (photographic image and X-ray); LACM 32499.17 (1, 65 mm SL), Punta Santa Helena, Costa Rica (photographic image and X-ray); LACM 35493.5 (1, 103 mm SL), Gulf of Nicoya, Costa Rica (photographic image and X-ray); ANSP 86216 (1, 174 mm SL), Pearl Island, Panama; CAS 234330 (1, 150 mm SL), Taboguila, Panama; SU 6879 (3, 133—164 mm SL), Panama; USNM 398152 (1, 137 mm SL), Mexico; USNM 396688 (1, 98 mm SL), Panama; USNM 404497 (1, 178 mm SL), Sonora, Mexico.

### 3.2.1. Morphological diagnosis

*Haemulon steindachneri* differs from its eastern Pacific congeners as follows: from *H. flaviguttatum*, by presenting 19–24 rakers in the 1<sup>st</sup> branchial arch (vs. 26–31), nine soft rays in the anal fin (vs. 10 or 11), large mouth with maxillary tip reaching the center of the eye (vs. small mouth, with maxillary end reaching the anterior border of the eye); from *H. maculicauda*, by the scales on the sides of the body having grayish/silver centers forming oblique lines to the axis of the body (vs. scales with white and black centers forming longitudinal stripes parallel to the axis of the body); dorsal and anal fin yellow (vs. gray); from *H. scudderii*, by presenting 31.4–37.0% SL of PDL (vs. 38–45% SL), seven or eight scales above the lateral line (vs. five or six), nine soft rays in the anal fin (vs. seven or eight) and scales all over the body with gray-brown centers (vs. black spots on each scale); from *H. sexfasciatum*, by presenting 31.4–37.0% SL of PDL (vs. 40–46% SL), silver to silvery gray body without bars (vs. six or seven bars on the dorsolateral surface of the body) and head without spots (vs. dark spots on the side of the head).

*Haemulon steindachneri* differs from its western Atlantic congeners as follows: *H. album*, by presenting 31.4–37.0% SL of PDL (vs. 44–48% SL), 9.8–13.7% SL of snout length (SnL) (vs. 14–17% SL), 12 or 13 scales below the lateral line (vs. 14); *H. aurolineatum*, by containing seven or eight scales above the lateral line (vs. six), 19–24 rakers in the 1<sup>st</sup> branchial arch (vs. 25–28, rarely 24), body silver to silver gray without stripes (vs. silvery-white body with two yellow stripes on the dorso-lateral portion); *H. bonariense*, by having 50–53 scales in the lateral line (vs. 44–49), large mouth with jaw end reaching the center of the eye (vs. small mouth, with jaw end reaching the anterior edge of the eye); *H. boschmae*, by presenting 32.8–38.9% SL of BH (vs. 26–30% SL), and 14.4–19.2% SL of PL (vs. 10–13% SL), and XII spines in the dorsal

fin (vs. XIII or XIV), 16 or 17 rays in the dorsal fin (vs. 11–15) and seven or eight scales above the lateral line (vs. five or six); *H. carbonarium*, by presenting 31.4–37.0% SL of PDL (vs. 40–46% SL, rarely 40), 9.8–13.7% SL of SnL (vs. 14–17% SL), body silver to silver gray without stripes (vs. body dorsally silvery gray, dark to black ventrally, with at least ten yellowish stripes on the sides of the body); *H. flavolineatum*, by possessing 16 or 17 dorsal-fin rays (vs. 14 or 15), 12 or 13 scales below the lateral line (vs. nine or ten), scales above and below the lateral line of the same size (vs. scales below lateral line two times the size of those above), and body silver to silver gray without stripes (vs. silvery gray body with at least 12 yellowish stripes on the sides of the body); *H. macrostoma*, by containing 19–24 rakers in the 1<sup>st</sup> branchial arch (vs. 26–28), 16 or 17 (rarely 18) rays in the pectoral fin (vs. 18, rarely 17), body silver to silver gray without stripes (vs. white-silvery body with dark brown to black stripes), soft dorsal-fin rays relatively larger than spines (vs. soft rays twice the size of spines); *H. melanurum*, by presenting seven or eight scales above the lateral line (vs. six), spots below the pre-operculum, at the end of the caudal peduncle and at the caudal-fin base (vs. black spot extending from the upper back and lower dorsal fin joining a horizontal black V at the caudal fin); *H. parra*, by presenting 31.4–37.0% SL of PDL (vs. 41–49% SL), seven or eight scales above the lateral line (vs. six), pre-operculum serrated (vs. non-serrated in adults) and scales throughout the body with gray-brown centers (vs. scales with black centers); *H. plumierii*, by presenting 31.4–37.0% SL of PDL (vs. 39–48% SL), seven or eight scales above the lateral line (vs. five), scales above the lateral line of the same size as below (vs. scales above the lateral line larger than those below) and silver to silver gray body without stripes (vs. body and head with blue and yellow stripes); *H. sciurus*, by presenting 31.4–37.0% SL of PDL (vs. 42–46% SL), 19–24 rakers in the 1<sup>st</sup> branchial arch (vs. 26–31), membranes between the dorsal-fin spines white to gray (vs. yellow) and silver to silver gray body without stripes (vs. yellowish-bronze body with blue stripes on the head and body to the base of the caudal fin); *H. atlanticus*, by presenting anal fin usually with nine rays (vs. usually eight rays); 12 scales below the lateral line, rarely 13 (vs. 13–15 scales below the lateral line, rarely 12), posterior margin of the maxilla with moderately convex extremity (vs. maxilla robust with anterior gently angulated), narrow spot on the pre-operculum, with anterior extremity tuned and posterior straight, resembling a triangle (vs. broad and robust spot, with no definite shape (Fig. 2); *H. squamipinna*, by having seven or eight scales above the lateral line (vs. six), 19–24 rakers in the 1<sup>st</sup> branchial arch (vs. 24–27, rarely 24) and silver to silver gray body without stripes (vs. silvery white body with 10–12 yellow bands); *H. striatum*, by presenting 19–24 rakers in the 1<sup>st</sup> branchial arch (vs. 28–34), XII spines in the dorsal fin (vs. XIII) and 16 or 17 rays in the dorsal fin (vs. 12–14), body oblong and compressed (vs. elongated body not laterally compressed) and silver to silver gray body without stripes (vs. gray to bluish body dorsally, silvery ventrally, with five yellow stripes along the body); *H. vittatum*, by presenting XII spines in the dorsal fin (vs. IV to XVIII) and 16 or 17 rays in the dorsal fin (vs. ten), 16 or 17 (rarely 18) rays in the pectoral fin (vs. 19); III spines in the anal fin (vs. II), oblong and compressed body (vs. fusiform body, elongate and rounded), operculum without spine (vs. operculum with broad and flat spine in posterior angle) and silver to silver gray body without stripes (vs. blue-green metallic body dorsally, ventrally bluish white, a broad greenish band from the eye to the base of the caudal, plus three brown stripes above).

### 3.2.2. Molecular diagnosis

*Haemulon steindachneri* forms a distinct group (Fig. 3) with genetic distance (K2P) from other *Haemulon* representatives ranging from 7.4% (*H. atlanticus*) to 13.8% (*H. melanurum*) (Table 3). The COI haplotypes of *H. steindachneri* differ from their congeners by 35 (*H. atlanticus*) to 64 bases (*H. flavolineatum* and *H. melanurum*) (Table 4). The molecular separation of *H. steindachneri* and *H. atlanticus* is corroborated by the species delimitation analysis, as well as the haplotype network (see Supplement I Appendix A).

### 3.2.3. Redescription

Morphometric data in Table 1, meristic data in Table 2. Body elongated, compressed laterally, greatest height under vertical through dorsal-fin origin. Dorsal profile of body convex from tip of snout to base of first ray of dorsal fin, posterolaterally inclined at dorsal-fin base, approximately straight from last ray of dorsal to caudal peduncle. Ventral profile of body straight from anterior end of maxilla to base of pelvic fin, slightly convex from this point to anal-fin origin, posterodorsally inclined at base of anal fin and approximately straight from last ray of anal to origin of lower lobe of caudal fin. Head pointy longer than high. Snout pointed about one-third length of head. Eye large, ellipsoid, slightly before the middle of the head length. Small nostrils located laterally on head, anterior broadly teardrop-shaped and posterior oval, about half size of first; posterior nostril in front of and slightly above horizontal line through center of eye, anterior nostril just above horizontal through lower margin of eye. Mouth large; posterior margin of maxilla with moderately convex extremity, located at vertical through center of orbit; fleshy and thick lips, upper lip slightly beyond tip of jaw. Teeth conical, in narrow band on each jaw, extended outer series. Chin with two pores and median groove. Gill rakers on first branchial arch short and thin.

Operculum without spine, covered with five or six vertical lines of ctenoid scales. Pre-operculum with slightly concave and serrated posterior margin. Scales ctenoid (rough to touch), small or moderate, extending over head (except in front of snout, lips and chin) to caudal fin; longitudinal scales oblique above lateral line along axis of body; those below in horizontal series. Lateral line continuous gently curved posteriorly, following dorsal contour of body, becoming straight on peduncle. Soft rays of dorsal and anal fin densely scaled almost to edge of fin. Pectoral fin scaled at base.

Dorsal fin with small notch in middle, origin at vertical through posterior margin of operculum; high, with strong spines, fourth spine more prominent, about one-third greater than soft rays; spines XII, rays 15 or 16 (rarely 17\*), first ray unbranched, branched remnants. Anal-fin origin below base of 3rd or 4th rays of dorsal fin; spines III, rays nine, all branched; spines strong, second most prominent; long soft rays, first ray almost reaching tip of first spine. Caudal fin emarginated to forked, lobes approximately equal size; principal rays ten + eight, upper and lower rays unbranched. Pectoral fins moderately long, not reaching or reaching tip of pelvic fin, fifth ray longest; rays 17(10) (rarely 16); first ray shorter, unbranched, second ray about two times longer, unbranched, remaining rays branched. Pelvic-fins origin below lower base of pectoral fins, at vertical through base of 2nd or 3rd dorsal spine; first ray longest (second equal to first); spines I, rays five, all branched. Caudal peduncle longer than high.

Lateral line scales 50(1), 51(2), 52(5), 53(4); scales above lateral line to base of first dorsal-fin spine, seven to nine; scales below lateral line to first spine of anal fin 12(9) or 13(3); rakers on first branchial arch 19(1), 20(1), 21(1), 22(2), 23(3) or 24(2); rakers on second branchial arch 14(1), 15(2), 16(3), 17(5) or 18(1) (Table 2).

Supraneurals 3. Vertebrae 11 + 15. First pterygophore of dorsal fin inserted above second neural spine and last pterygophore of dorsal fin inserted in front of neural spine of 19th vertebra. First pterygophore of anal fin inserted below first hemal spine and last pterygophore of anal fin inserted in front of sixth hemal spine. Caudal skeleton with one ural center; five autogenic hypurals; three epurals; 17 (nine + eight) major caudal rays, with simple procurvent rays (see Supplement II Appendix A).

### 3.2.4. Coloration in life

Body gray dorsally, silver to dark gray ventrally; scales with gray/silver centers, forming oblique lines along rows of scales; head dark gray from top of snout to vertical through pre-operculum border, light gray/silver in infraorbital region; distinct blackish spot on lower anterior part of operculum, partially covered by pre-operculum angle; dark, large, distinct and rounded spot at end of caudal peduncle and at base

of caudal fin. Dorsal and anal fins gray with lighter tonality on inter-radial membranes; pectoral and pelvic fins gray to yellowish; dark caudal fin. Juveniles with two to three diffuse brownish stripes on the dorsolateral side; a black spot at base of caudal fin (Fig. 1).

### 3.2.5. Coloration of preserved specimens

Upper dorsal and lateral surface of body relatively light brown or gray. Ventral surface of body pale yellowish-brown. Distinct blackish spot on lower anterior part of operculum, partially hidden by pre-operculum angle; dark, large, distinct, and rounded spot at end of caudal peduncle and base of caudal fin.

### 3.2.6. Distribution and habitat

*Haemulon steindachneri* occurs in the eastern Pacific between the Gulf of California and Peru (Fig. 4), inhabiting estuarine and coastal marine waters up to 30 m deep. The species is associated with coral reefs and can be found over sand and rubble.

### 3.2.7. Remarks

Jordan and Gilbert (1882) described *Haemulon steindachneri* as *Diabasis steindachneri* Jordan and Gilbert, 1882, based on two specimens collected in Panama and six specimens collected in Mazatlan, Mexico, from the Pacific. Jordan and Swain (1884) reviewed *D. steindachneri*, altering the generic nomenclature, since the name *Diabasis* Desmarest was pre-occupied in Coleoptera. The examination of the type specimens indicated that *H. steindachneri* is a valid species of *Haemulon* (Fig. 1), based on a bluish black bar in the lower anterior part of the operculum, partially hidden by the angle of the pre-operculum, a large blackish rounded spot at the end of the caudal peduncle and the base of the caudal fin, and the posterior margin of the maxilla with moderately convex extremity.

According to Courtenay (1961), specimens of *H. steindachneri sensu lato* present a large black spot below the margin of the pre-operculum and a black spot at the base of the caudal fin, whereas Hong (1977), when comparing their *H. steindachneri* data from the Atlantic and the Pacific with data from Courtenay (1961), suggested that the specimens from both oceans were similar except for the snout length and upper jaw length, which were 1 to 2% SL larger in the Atlantic specimens. This difference was not observed in the present work.

## 4. Discussion

The examination of the morphology of all *Haemulon* species confirmed that both *H. atlanticus* and *H. steindachneri* are distinct from all other congeners by presenting a distinct color pattern composed of a silvery or silver gray body without stripes, with a bluish black bar in the lower anterior part of the operculum, partially hidden by the angle of the pre-operculum, and a large rounded and blackish spot at the end of the caudal peduncle and base of the caudal fin. Although *H. atlanticus* and *H. steindachneri* present great morphology similarities, we consider them distinct species due to the following differences found: anal fin usually with eight rays in *H. atlanticus* (vs. usually nine rays in *H. steindachneri*); 13–15 scales below the lateral line, rarely 12 in *H. atlanticus* (vs. 12 scales below the lateral line, rarely 13 in *H. steindachneri*), posterior margin of the maxilla robust with a smoothly angled end in *H. atlanticus* (vs. smaller maxilla with moderately convex extremity in *H. steindachneri*), a spot on the pre-operculum, broad and robust, with no definite shape in *H. atlanticus* (vs. narrow spot, with anterior extremity tuned and posterior straight, resembling a triangle in *H. steindachneri*) (Fig. 2). Agreeing with these results, our molecular analyses shows that *H. atlanticus* forms a distinct group from *H. steindachneri* by presenting 7.4% of genetic distance and 35 different bases in COI haplotypes.

Despite the differences found between *H. atlanticus* and *H. steindachneri*, they still have a conserved morphology, being considered very morphologically similar. Based only on the morphological criteria, *H.*

*atlanticus* and *H. steindachneri* were often recognized as a single species. The identification of cryptic species, as these showed in this study, is of fundamental importance to the understanding of diverse evolutionary, biogeographic and ecological processes (Bickford et al., 2007; Pfenninger and Schwenk, 2007). Cryptic species are common among metazoans and can be found in all types of biogeographic zones (Bickford et al., 2007; Pfenninger and Schwenk, 2007). Many studies have demonstrated that molecular techniques supplementing traditional taxonomy are efficient for the identification of these enigmatic lineages (Neusser et al., 2011; Jörgen and Schrödl, 2013; Souza et al., 2017), hypothesis confirmed in the present paper.

Our molecular analyses showed that the genetic distance (K2P) between *H. atlanticus* and other species of the genus varies from 7.4% (between *H. steindachneri*) and 15.5%, which is similar to the divergences of other trans-isthmian twin pairs, such as those in the genus *Chromis* (Pomacentridae, 3.1–3.5 million years ago), and *Chaetodon* (Chaetodontidae, 3.4 Ma), whose divergences vary from 9.35% to 10.40% when using the K2P model (Coates et al., 1992; Bermingham et al., 1997; Domingues et al., 2005). The divergence time estimated from our data,  $3.2 \pm 0.7$  mya, is compatible with the final data of closure of the Panama Isthmus (Fig. 3). Divergence rates such as those found between the *H. atlanticus* and *H. steindachneri* pairs are related to trans-isthmian species that have a greater affinity with coastal and estuarine waters; this prediction correlates with the geological history of the isthmus closure, where the only connections between the Caribbean and the eastern Pacific prior to the final closure were probably coastal areas with estuarine conditions (Knowlton et al., 1993; Coates and Obando, 1996; Tringali et al., 1999; Bernardi and Lape, 2005). Both *H. atlanticus* and *H. steindachneri* occur in coastal areas and are often found in low salinity waters (Raz-Guzman and Huidobro, 2002), with juveniles in shallow areas and rocky shores, and are recognized as crucial to maintaining the integrity of these ecosystems (Furia, 1996; Rocha, 1997).

As previously stated, there is substantial evidence that the rise of the Isthmus of Panama influenced the speciation of *H. steindachneri* and *H. atlanticus*. The cessation of the uplift of the isthmus occurred about 3 million years ago at the end of the Pliocene (O'Dea et al., 2016). Tavera et al. (2012; 2018; Tavera and Wainwright, 2019), in their molecular analyses of the Haemulidae, estimated that the separation of the lineages of *H. steindachneri* occurred during this period. Our analyses provided a similar divergence time (Fig. 3), corroborating the hypothesis that the Isthmus of Panama was responsible for the allopatric speciation between the species pairs *H. atlanticus* and *H. steindachneri*.

Additionally, the molecular analysis of this work revealed the presence of a possible emergent species in the Atlantic coast from Amapá and Caribbean. A similar result was found by Rocha et al. (2008), where the mitochondrial DNA presented a 0.7% sequence divergence between the Brazilian and the Venezuelan populations. Although these lineages from the Brazilian and Caribbean coast are differentiated by two exclusive COI mutations and by the GMYC and bPTP analysis (see haplotype network in Supplement I Appendix A), the genetic distance between them is very small ( $0.013 \pm 0.005$ ) and the ABGD and morphological analysis did not support this recognition. Given those results, we consider the two Atlantic lineages of *H. atlanticus* to be an example of gray zone, where alternative species concepts come into conflict (De Queiroz, 2007).

The Amazon river barrier influences significantly the reef habitats between Brazil and the Caribbean Coast by having a 2300 km of muddy coastline, which separates its reef fauna (Rocha, 2003; Rocha et al., 2005; 2008). In spite of this, Menezes et al. (2003) showed that the majority of species found in Brazil also occurred in the Caribbean coast. This situation can be explained by the absence of any major physical barriers between these two regions (Marceniuk et al., 2019). For the provinces of the Greater Caribbean, variations in shelf environments could be responsible for the substantial differences in its faunas (Robertson and Cramer, 2014). Similarly, the differentiation

encountered on the Brazilian coast fauna may be caused by the considerable heterogeneity of its environments (Silva et al., 2016). Considering the variations in their environments, further taxonomic reviews of the marine-estuarine fish fauna of the Brazilian and the Caribbean coasts are necessary to better understand how the biogeographic patterns are changing the species in these areas.

## Acknowledgements

The authors thank the following people: Sandra Raredon (USNM), Luiz Rocha (CAS), and Rick Feeney (LACM) for their availability to send photos and x-rays of the material; J. Pflinger (MNHN) and J. Astarloa (UNMDP) for the images and counts of the *Haemulon bonariense* holotype; Professor L. Nassar (UFRA) for allowing us to use his laboratory to take x-rays from our specimens; Professor J. Sales (UFPA), A. Akama (MPEG), and R. Caires (MZUSP) for information through personal communication, criticisms and critical reading; N. N. C. D. Cerqueira and R. Batista for technical assistance; M. Dopazo, D. Carvalho, and M. Mendonça for their criticisms and suggestions. We are grateful to the Laboratory of Molecular Biology of *Museu Paraense Emílio Goeldi* (MPEG) (Financiadora de Estudos e Projetos (FINEP), Brazil, grant 'Parque analítico do MPEG: análise das transformações da Amazonia e seus reflexos na sociobiodiversidade e na paisagem' (# 0118003100)) and the 'Laboratório de Biologia e Genética de Peixes' from São Paulo State University for allowing the realization of the molecular techniques of this work at their spaces. We thank Kelsey Barnhill, native English speaker, for corrections to the manuscript. COC is grateful for the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Brazil, for granting a scholarship, finance code 001; to the Postgraduate Program in Biodiversity and Evolution (PPGBE) of MPEG. BWB thanks the Conselho Nacional de Desenvolvimento Científico e Tecnológico - CNPq, Brazil, (grant process numbers 300940/2015-7 and 302497/2018-8) and FINEP (process 01 17 005600). APM is grateful for the Programa de Capacitação Institucional (MCTIC/CNPq, Process 444338/2018-7 and 300675/2019-4). CO thanks the financial support from Fundação de Amparo à Pesquisa do Estado de São Paulo - FAPESP, Brazil, (grants 2016/09204-6, 2014/26508-3) and CNPq (grant process 306054/2006-0).

## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.zool.2020.125782>.

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