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Revision of the circumtropical glasseye fish *Heteropriacanthus cruentatus* (Perciformes: Priacanthidae), with resurrection of two species

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Abstract

The glasseye fish *Heteropriacanthus*, previously known as a monotypic genus, is now divided into three species based on morphological and genetic features. After examination on the type specimens and literature, herein we resurrect two junior binomens, *H. carolinus* (Cuvier, 1829) from the Indo-Pacific Ocean and *H. fulgens* (Lowe, 1838) from the northeastern Atlantic Ocean. *Heteropriacanthus cruentatus* (Lacepède, 1801) is now considered to be restricted to the Atlantic and southwestern Indian oceans. In light of these observations we discuss the evolutionary history of the genus.

Key words: Circumtropical, genetics, *Heteropriacanthus carolinus*, *Heteropriacanthus fulgens,* teleostei, taxonomy

Inroduction

The bigeye family Priacanthidae is a small group of small to mid-sized generally epibenthic fishes that occur in tropical and subtropical seas near coral reefs or rock formations at depths 5 to 400 m or deeper (Starnes, 1988). Members of this family are known to produce sound (Salmon & Winn, 1966).

The family Priacanthidae currently comprises four genera and 19 valid species (Eschmeyer, 2016). Within Priacanthidae, the genus *Heteropriacanthus* is currently recognized as a monotypic genus with a circumtropical distribution (Starnes, 1999). Its common name, glasseye, describes the aspect of the eyes caused by the UV-light absorption properties of the vitreous humor, which are very unique among fishes (Losey *et al*., 2003). Adult glasseyes have solitary habits, hide in caves during the day, and feed mainly at night on larger zooplankton, such as fish and crustacean larvae, pelagic shrimp, octopi, stomatopods, and polychaetes (Randall, 2005).

Heteropriacanthus is characterized by the posterior preopercle lacking scales, being notably striate, and the membranes of the soft dorsal, anal and caudal fins usually having rows of elliptical dark specks. The anterior profile is nearly symmetrical, with the upper end of lower jaw at about the body midline level. The swim bladder is truncate anteriorly and has posterior projections. It is also characterized by a number of characters of squamation, osteology and morphology (Starnes, 1988).

Starnes (1988) stated that "Despite its worldwide distribution, variation in this species is remarkably minimal. Principal components analysis performed on logs of traditional and truss measurements revealed no patterns of variation... Meristic variation, though considerable in such characters as scale counts within regional samples, is negligible between regions. The only consistent regional phenomenon is the lack of dark specks in the median-fin membranes of eastern and mid Atlantic specimens".

Rosenblatt & Waples (1986) reported significant allelic variation (Nei genetic distance = 0.14) between western Atlantic and eastern Pacific samples in allozymes and negligible variation between Hawaiian and eastern Pacific samples. Gaither *et al*. (2015) recently reported 10% divergence in COI sequences between populations in the Caribbean and the Indo-Pacific region, with mixing of lineages off of South Africa.

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Here, we present the results of a range-wide phylogeographic survey of *H. cruentatus* that identified the presence of a third genetic linage in the Tropical Eastern Atlantic. Following the results of the genetic lineages, we then identified differences in body proportions concordant with the observed genetic partitions, and redescribe *Heteropriacanthus* as a complex of three species. *Heteropriacanthus* should no longer be regarded as a monotypic genus of circumtropical distribution.

Methods and materials

Taxonomic methods. Lengths of specimens are given as standard length (SL), measured from the anterior point of the upper lip to the end of hypural plate. Head length (HL) was measured from the front of the upper lip to the posterior end of the opercular membrane. Body depth was measured vertically from the origin of the pelvic fin and mid-portion of trunk. Body width was measured at the posterior portion of gill cover. Snout length was measured from the front of the upper lip to the anterior margin of the orbit. Eye diameter was measured from the fleshy margin to the posterior margin of the orbit. Interorbital width was the narrowest distance between the upper bony margins of the orbit. Upper-jaw length was measured from the front of the upper lip to the posterior end of the maxilla. Dorsal-fin and anal-fin bases were measured from the origin to the end of the fin bases. Fin spines and rays were measured from the base to the tip of the longest ray. Pectoral-fin and pelvic-fin lengths were measured from the insertion to the end of the fin. Caudal-peduncle length is the horizontal distance between the end of the anal-fin base and the posterior end of the hypural plate. Caudal-peduncle height is the narrowest vertical distance between both margins. Caudal-fin length was measured from the end of the hypural plate to the rear end of the fin. Gill-raker counts included rudiments; the raker at the angle was included in the lower limb. Morphometric data presented in the tables are given as percentages of the SL and HL. Terminology generally follows Starnes (1988).

Genetics methods. A detailed phylogeographic survey of *Heteropriacanthus* is presented in a separate article (Fernandez-Silva *et al*., in review). Here we show phylogenetic relationships among *Heteropriacanthus* spp. based on an alignment of 90 COI sequences obtained from specimens collected from the Indian, Pacific and Atlantic oceans, including the NE Atlantic islands of the Canaries and Cape Verde Archipelagos. The alignment is described in detail in Fernandez-Silva *et al*. (in review). We obtained COI sequences of *Cookeolus japonicus*, *Priacanthus hamrur* and *Halichoeres hortulanus* to use as outgroups in the construction of phylogenetic trees, and trimmed all COI sequences to a common length. We constructed Maximum Likelihood (ML) phylogenetic trees with the help of the RaxML web server at http://embnet.vital-it.ch/raxml-bb/ (Varsamos *et al*., 2005). Bootstrap support values were calculated using 1000 replicates.

Results

Family Priacanthidae

Heteropriacanthus Fitch & Crooke, 1984

Heteropriacanthus Fitch & Crooke, 1984:310 (type species: *Labrus cruentatus* Lacepède, 1801; original designation).

Definition. Anterior profile nearly symmetrical, the extremity of lower jaw usually above the midline of body; preopercle posterior to shelf overlying sensory canal without scales and notably striate; soft portions of dorsal and anal fins with 11–13 and 13–14 rays, respectively; pelvic fin short, barely reaching first anal-fin spine or falling short, inserted ventral to pectorals; shelf overlying sensory canal of preopercle not very pronounced, serrate ventrally, smooth posteriorly; preopercular spine broadly triangular, finely serrate, remaining well developed in adults, reaching nearly to the tip of the suboperculum; gill rakers on first arch 21–25; no predorsal bone; membranes of soft dorsal and anal fins and caudal fin usually with rows of elliptical dark specks (may be absent in eastern and central Atlantic specimens). For additional osteological features, see Starnes (1988).

Distribution. Worldwide distribution in three major oceans.

***Heteropriacanthus carolinus* (Cuvier, 1829)**
Pacific glasseye
Figures 1A–E, Tables 1–2

Priacanthus carolinus Cuvier in Cuvier & Valenciennes, 1829:105 (Type locality: Oualan, Caroline Islands, western Pacific; Holotype: MNHN A-0168).
Priacanthus argenteus Cuvier in Cuvier & Valenciennes, 1829:109 (Type locality: Molucca Islands, Indonesia; no types known).
Priacanthus bleekeri Castelnau, 1873:100 (Type locality: Noble Island, Torres Strait, Queensland, Australia; Holotype: MNHN A-3074).

Specimens examined. Holotype. MNHN A-0168 (176.5), Oualan or Strong Island, Caroline Islands, Micronesia, northwestern Pacific Ocean. Other materials listed below.

Nomenclature. The three names above were listed as junior synonyms of *Heteropriacanthus cruentatus* in Starnes (1988). Of them, *Priacanthus carolinus* Cuvier, 1829 takes priority to represent the Indo-Pacific population. Examination of the holotype revealed that it is identical to other specimens examined from the region. It is unlikely that more than one species of *Heteropriacanthus* occurs in the Indo-Pacific region according to the lack of genetic subdivisions (see description of genetic results), although future work may reveal the presence of isolated populations in isolated biogeographic provinces.

Diagnosis. A species of *Heteropriacanthus* with following combination of characters: body depth at pectoral-fin base 2.5–2.9 in SL, at mid-trunk 2.4–2.9 SL; dorsal-fin origin above the bases of the pectoral fins; preopercle with a slightly elongate and blunt spine reaching or beyond the posterior margin of the interopercle; dorsal-fin base (1.7–1.8 in SL) and anal-fin base (2.5–2.8 in SL) relatively short; eye relatively large, eye diameter 2.0–2.6 in HL; interorbital space narrow, its width 3.3–4.1 in HL; head length 1.1–1.3 in body depth; caudal-peduncle length 2.5–3.2 in body depth; pored lateral-line scales 59–78; lateral scale rows 81–96; transversal scales rows 10–12+49–57=60–69.

Description. Mainly based on specimens (n=47) collected from the Pacific Ocean, including the holotype, and specimens from both the eastern and the western Pacific Ocean. Following data are provided for the holotype, followed by range of non-types examined in the present study when different, unless otherwise indicated.

Dorsal-fin rays X, 13; anal-fin rays III, 14; pectoral-fin rays17 (right side)/18 (left side) (17–19). Pored lateral-line scales 66 (59–78); axial scale rows 85 (81–96); scale rows between the origin of the dorsal fin and the lateral line 11 (10–12, mainly 11); scale rows between the lateral line and the origin of the anal fin 52 (49–57). Total gill rakers 24 (21–25), 6 (4–6) on the upper limb and 18 (16–19) on the lower limb.

General profile as shown in Fig. 1. Largest specimen examined 234.0 mm SL. Body relatively narrow, compressed, ovate in lateral profile, dorsal profile flattened along the dorsal fin base, and ventral profile curved. Body depth at mid-trunk 2.5 (2.4–2.9) in SL. When the mouth is closed, the upper end of the lower jaw at about the same level as the midline of body. Body thick, body width 5.4 (5.0–6.2) in SL. Caudal peduncle relatively long, its length 7.4 (6.6–8.6) in SL and 2.7 (2.5–3.2) in body depth; its depth 11.0 (9.9–12.0) in SL.

Head moderately large, its length 2.9 (2.6–3.1) in SL, 1.1 (1.0–1.3) in body depth, with dorsal profile gradually rising to the origin of the dorsal fin. Eye large, eye diameter 2.2 (2.0–2.6) in HL; interorbital space moderately broad, well convex, its width 3.7 (3.3–4.1) in HL; snout short, smaller than the eye, its length 3.2 (3.2–3.9) in HL. Mouth moderately large, strongly oblique; maxilla broad posteriorly and relatively exposed; posterior end of maxilla below the anterior half of eye; lower jaw upturned, strongly projecting. Upper jaw length 2.0 (1.9–2.0) in HL.

Nostrils close to each other, located close to the eye at its upper margin; anterior nostril small and rounded, with a posterior fleshy rim covering the entire nostril when fully folded anteriorly; posterior nostril a transverse slit, its height about a fourth of the eye diameter. Dentary, premaxilla, vomer and palatine with small conical teeth.

Opercle with a flat, blunt triangular spine at the center of the posterior margin, with 2–4 fine serrae on the tip (some with a blunt tip). Fine serrae on posterior and lower margins of the preopercle, those on the lower margin slightly stronger than those on the posterior margin, both meeting at an angle and forming a flat; blunt elongate spine, its tip reaching or over the posterior margin of the interopercle or subopercle. One additional finely serrate ridge above the lower margin of the preopercle, ending near the tip of the preopercular spine. Lower part of the posterior margins of the subopercle and the posterior margin of the interopercle smooth or with very weak

serration, mostly covered by membranes. A deep notch on the posterior portion of the interopercle covered by the preopercular spine; a narrow gap between the subopercle and interopercle.

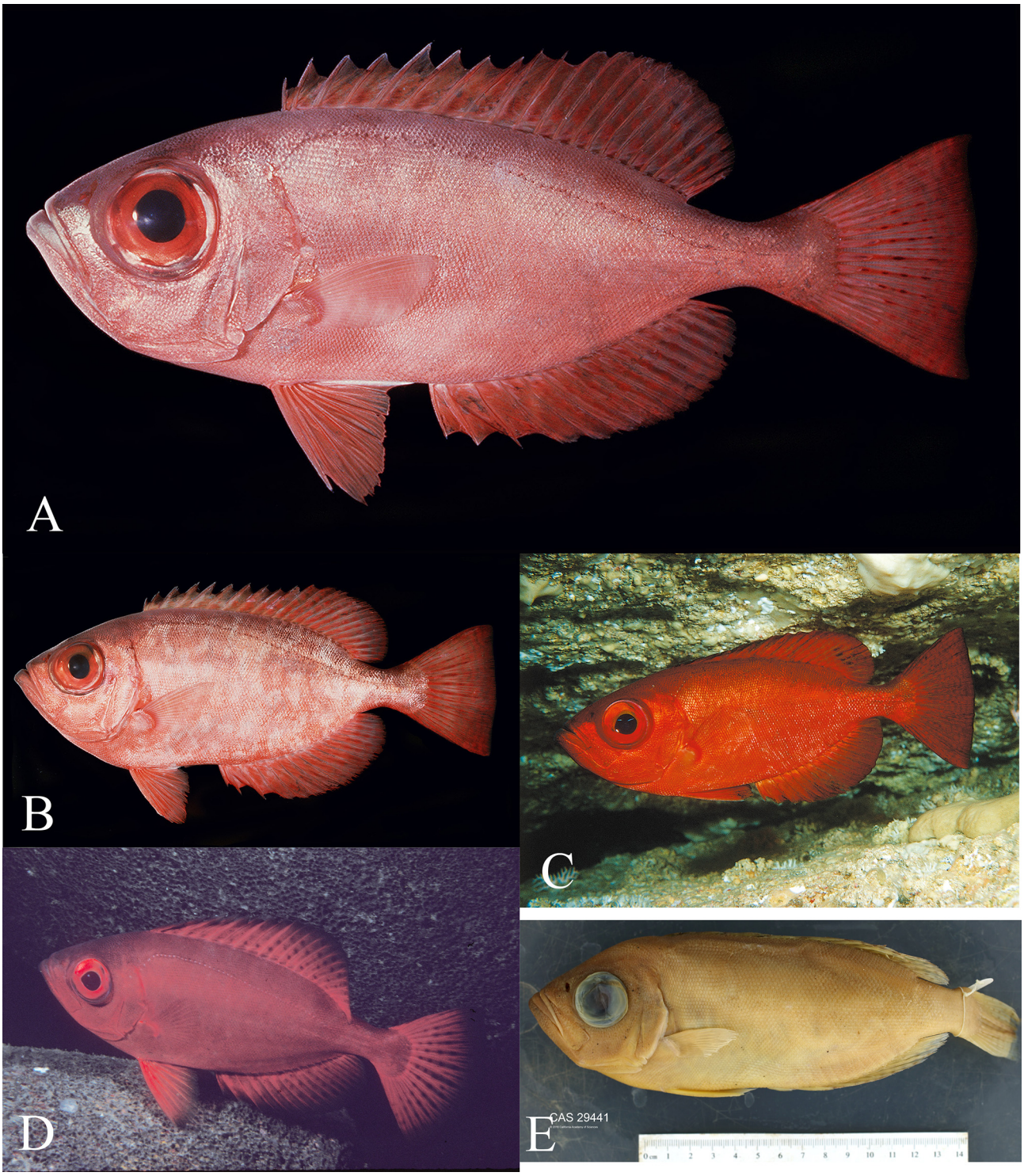

FIGURE 1. *Heteropriacanthus carolinus* (Cuvier, 1829). A. Easter Island, 20.9 cm SL (Photo: J.E. Randall). B. Lord Howe, 15.8 cm SL (J.E. Randall). C. Ogasawara (Photo: J.E. Randall). D. Hawai‘i (J.E. Randall). E. preserved specimen, CAS 29441, the Philippines (D. Catania).

One continuous long-based dorsal fin originating above the upper end of the gill slit, its base 1.8 (1.7–1.8) in SL; spines of the dorsal fin gradually longer, the last spine the longest; first dorsal-fin spine short, its length 6.7 (4.2–7.7) in HL; second dorsal-fin spine 3.9 (3.0–5.0) in HL; last dorsal-fin spine (10th) 2.3 (2.1–2.7) in HL; longest dorsal-fin rays (usually middle rays) 1.9 (1.6–2.2) in HL. Pectoral fin relatively short and broadly pointed,

its length 2.0 (1.6–2.0) in HL, base oblique with upper end beneath the origin of the dorsal fin. Pelvic fin moderately long, inserted beneath or slightly anterior to the pectoral fin, attached to the belly by a broad membrane along and beyond the entire length of the innermost ray, the membranes ending on either side of the anus; pelvic-fin rays ranging from not reaching the origin of the anal-fin to reaching the base of the first anal-fin spine. One continuous long-based anal fin originating beneath the 6th or 7th dorsal-fin spine, its base 2.7 (2.5–2.8) in SL; anal-fin spines relatively strong compared to the spines on the dorsal fin; first anal-fin spine 4.4 (3.2–4.6) in HL; third anal-fin spine 2.9 (2.2–2.9) in HL; longest anal-fin ray (usually middle rays) 1.8–3.6 in HL (broken in the holotype). Soft portions of the dorsal and anal fins broadly rounded. Caudal fin truncate or slightly rounded, its length 3.5–4.5 in HL (broken in the holotype). Anus right next to the anal fin.

Small modified cycloid or spinous scales on almost the entire body (see Remarks below), absent from all fins, the posterior portion of preopercle, and branchistegal rays, except for the base of the caudal fin. Thick granule-like scales on the mandible, chin, gular, chest, and abdomen; enlarged scales along either side of the dorsal and the anal fins. Scales on lateral body cycloid or spiny with 7–30 fine spinules on the posterior margin. Lateral line originating at the upper end of the supracleithra, rising immediately in the following few scale rows to form a curve, then roughly following the upper profile, gradually descending to the body axis at the caudal peduncle, and ending at the caudal fin. Lateral-line scales with a simple central tube and two short posterior branches, one directed upward and one directed downward.

Coloration. When alive or fresh (Figs. 1A–D), body bright red with bright, silver patches usually present. Many black dots on the posterior portions of the dorsal and anal fins and most of the caudal fin. All fins with black margins. Preserved specimens (Fig. 1E) uniformly creamy white, some blackish bands maybe present on lateral body; many blackish elliptical dots on posterior portions of the dorsal and anal fins and most of the caudal fin. All fins with blackish margins.

Etymology. The specific name was derived from the type locality, the Caroline Islands in Micronesia.

Distribution. Widespread in the Indian and Pacific Oceans. Specimens examined were collected off of Madagascar, Indonesia, Japan, Taiwan, the Philippines, Solomon Islands, Palau, Micronesia, Hawai'i, and Galapagos Islands. Additional localities confirmed by genetic analyses are Johnston Atoll, American Samoa, Gambier, Tonga, Fiji, Cook Islands, Society Islands, Marquesas, Rapa Nui, Indonesia, South Africa, Mauritius, and Mozambique. Usually photographed or collected from shallow water not deeper than 100 meters.

Remarks. *Heteropriacanthus carolinus* shares nearly identical morphology to the Atlantic congener *H. cruentatus*, but with 11% divergence in COI sequences. Both have similar body proportions and overlapping meristic values. It has generally a broader range of morphometric and meristic values than *H. cruentatus* and on average, the first 7 dorsal-fin spines are longer than in *H. cruentatus* (Table 1, Fig. 2A). In addition, the body is somewhat more slender in *H. carolinus* than in *H. cruentatus* (Fig. 2B).

A genetic survey of the Eastern Pacific population of *Heteropriacanthus* revealed that specimens from Clipperton, Cocos I., Panama, Galapagos and Revillagigedo Is. are of the same genetic clade as *H. carolinus*, which also indicated population-level differences with the Central Pacific (Lessios & Robertson, 2006).

While examining specimens collected from worldwide locations, we found some variation, mainly pertaining to the squamation and morphology of spines. Many of these differences may be attributed to individual variation or growth-related changes.

Most specimens have a truncated caudal fin, but some specimens from Hawai'i and Fiji examined by us have upper and/or lower rays longer than median rays.

Scales on the lateral body were mostly spiny in most specimens examined. The holotype (MNHN A.168) has weakly spiny scales on lateral body. However, some specimens from the Galapagos Islands (CAS 3692), French Polynesia, Micronesia and Palau have almost entirely cycloid scales on the lateral body.

Hawaiian specimens have a long preopercular spine that projects beyond the posterior margin of the subopercle and interopercle; the posterior margin of the operculum and the posterior part of the lower margin of the interopercle are either smooth or weakly serrated; opercular spine has 3 fine serrae at the posterior tip. Hawaiian specimens also have higher counts of pored lateral-line scales (70–78) and lateral scale rows (94–96). These morphological differences are concordant with population-level genetic differentiation identified in Hawaiian specimens (Fernandez-Silva *et al*., in review).

Fiji specimens have smooth margins on the subopercle and interopercle, a blunt spine on the opercle and a strong preopercular spine extending slightly beyond the margins of the subopercle and interopercle.

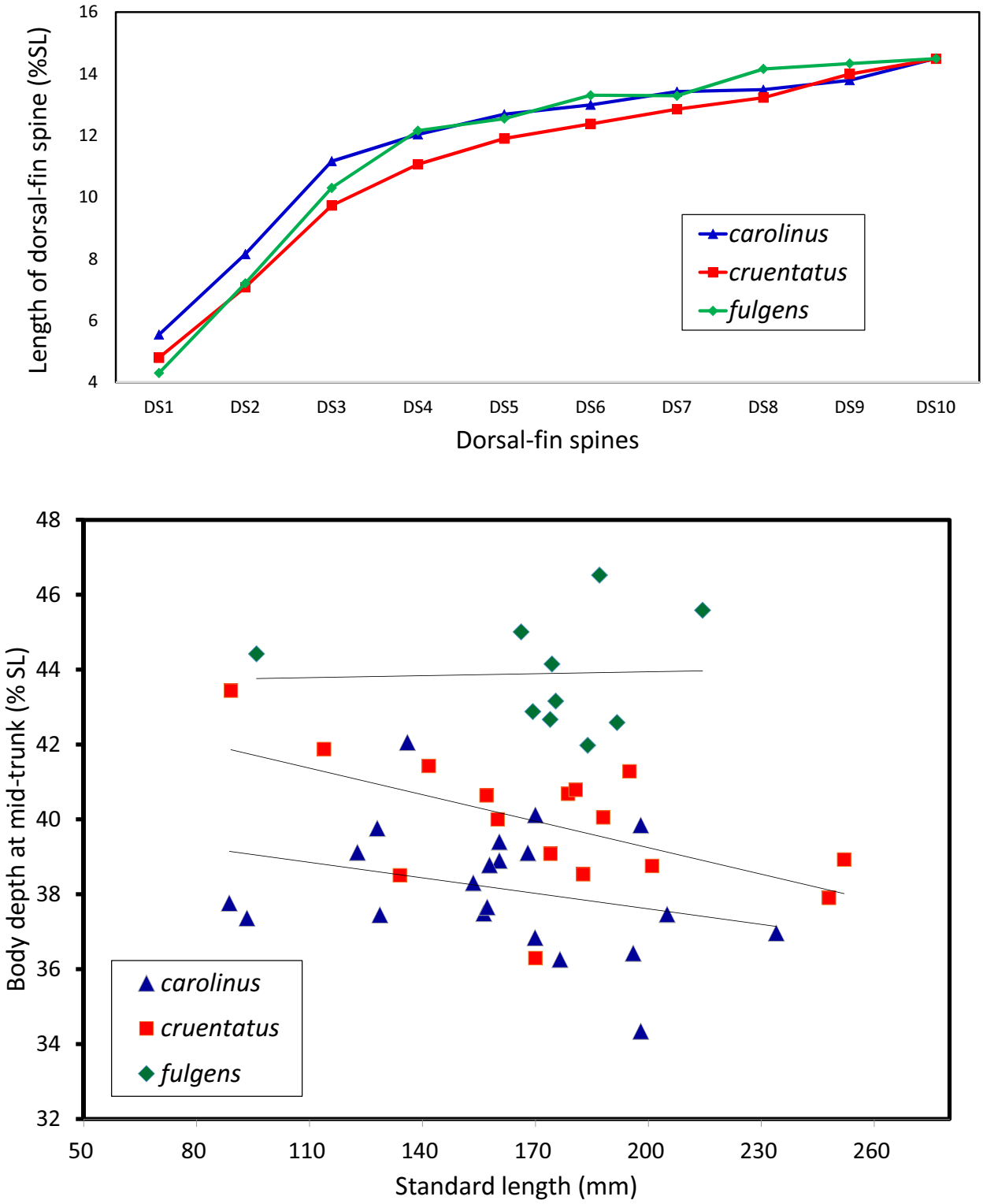

FIGURE 2. A. Comparison of length of the all dorsal-fin spines as percentage of head length (mean values) among the three *Heteropriacanthus* species. B. Comparison of body depth at mid-trunk as percentage of standard length among the three *Heteropriacanthus* species.

TABLE 1. Morphometric data of the three *Heteropriacanthus* spp. in this study. P=pectoral-fin; D=dorsal-fin; C=caudal-fin; A=anal-fin; V=pelvic fin.

	H. carolinus		*H. cruentatus*		*H. fulgens*	
	Holotype	n=18	Neotype	n=16	Neotype	n=10
Standard length (mm)	176.5	88.7–196.0	157.0	89.1–252.0	174.4	95.9–214.4
%SL		Mean (range)		Mean (range)		Mean (range)
Head length	34.0	33.7 (32.0–38.1)	32.4	32.9 (31.8–34.3)	32.0	32.6 (31.6–34.5)
Body depth at P base	36.0	37.6 (34.1–40.5)	40.0	38.5 (31.2–40.4)	42.3	42.3 (41.1–43.7)
Body depth at mid-trunk	36.3	38.3 (34.3–42.1)	40.6	39.8 (36.3–41.9)	44.2	44.1 (42.7–46.5)
Body width	18.5	17.6 (16.1–19.8)	18.2	17.5 (16.0–19.0)	16.9	17.4 (16.7–18.2)
Predorsal length	32.4	32.5 (30.7–34.8)	31.6	31.8 (31.2–33.0)	32.9	31.8 (30.0–33.2)
Prepectoral length	34.0	33.1 (31.9–34.7)	33.3	33.7 (32.8–34.6)	32.4	32.5 (31.5–33.2)
Prepelvic length	37.2	38.0 (36.3–39.9)	39.3	39.2 (38.6–40.2)	38.9	39.0 (37.4–40.8)
Caudal-peduncle length	13.6	13.3 (11.6–15.0)	16.5	14.4 (13.0–16.5)	12.5	13.1 (11.9–14.4)
Caudal-peduncle depth	9.1	9.3 (8.3–10.1)	9.4	9.4 (8.5–10.5)	10.0	10.3 (9.9–11.1)
D base	56.7	57.3 (55.7–59.9)	57.4	57.1 (54.0–59.5)	60.2	60.9 (59.7–64.4)
A base	37.3	38.2 (36.3–40.6)	37.4	37.4 (35.0–39.7)	39.9	40.5 (39.0–42.6)
C length	--	25.6 (22.2–28.5)	22.9	24.2 (22.7–27.0)	25.6	25.2 (23.3–27.8)
%HL						
Snout length	31.0	28.8 (25.4–31.4)	31.9	29.9 (27.3–33.7)	9.1	29.1 (26.4–31.3)
Orbital diameter	46.3	43.1 (38.5–50.5)	39.4	43.3 (39.2–51.3)	12.7	39.7 (38.6–41.7)
Interorbital width	26.8	27.3 (24.3–30.0)	28.3	28.0 (25.7–29.8)	9.7	31.8 (30.3–33.4)
Upper-jaw	50.5	51.7 (49.5–53.4)	50.4	51.4 (48.9–53.0)	16.7	50.5 (49.2–52.3)
1st D spine	15.0	16.9 (13.0–23.7)	16.9	14.5 (9.8–17.4)	2.0	13.2 (6.3–16.8)
2nd D spine	25.7	24.8 (20.1–33.8)	18.7	21.3 (18.2–23.9)	7.9	22.1 (18.7–24.6)
3rd D spine	35.3	33.8 (26.6–41.1)	31.3	29.5 (26.0–33.9)	10.7	31.6 (23.8–37.3)
4th D spine	37.0	36.4 (29.4–44.5)	36.0	33.6 (30.2–37.3)	11.4	37.2 (33.0–40.5)
5th D spine	41.3	38.3 (31.2–44.5)	38.4	36.1 (33.6–38.4)	11.4	38.4 (33.3–46.7)
6th D spine	42.0	39.2 (33.2–45.7)	40.9	37.4 (35.2–40.9)	11.7	40.8 (36.4–49.3)
7th D spine	41.0	40.3 (34.9–44.5)	45.1	39.1 (36.2–45.1)	13.0	40.7 (37.5–43.2)
8th D spine	43.0	40.4 (33.9–46.3)	42.9	40.3 (33.5–43.9)	13.0	43.2 (40.5–45.6)
9th D spine	42.2	41.5 (35.4–49.0)	45.9	42.6 (36.2–48.0)	13.8	43.9 (42.4–45.2)
10th D spine	43.2	43.5 (37.0–48.1)	48.2	44.1 (36.2–48.2)	13.9	44.4 (41.8–49.0)
Longest D ray	52.2	53.1 (45.7–61.3)	50.0	50.7 (42.3–62.2)	19.2	57.9 (53.1–62.7)
1st A spine	22.8	25.6 (21.9–31.0)	23.8	24.0 (20.1–26.2)	7.6	26.7 (23.8–30.0)
2nd A spine	30.3	30.9 (25.0–35.2)	29.9	28.6 (24.8–32.0)	9.9	32.2 (26.9–35.3)
3rd A spine	35.0	39.1 (34.9–45.7)	41.1	37.7 (32.7–42.3)	11.9	40.1 (36.7–44.5)
Longest A ray	--	48.5 (28.2–55.4)	49.6	48.4 (44.3–52.6)	17.7	54.4 (48.5–60.7)
P length	49.5	57.3 (49.5–61.2)	57.9	57.4 (53.0–62.7)	19.8	59.0 (55.1–61.8)
Pelvic fin spine	60.7	57.8 (46.5–68.9)	63.6	58.3 (53.8–63.6)	19.3	60.0 (51.3–66.8)
Longest V ray	58.7	67.4 (58.1–75.3)	67.1	64.9 (60.2–69.5)	22.8	71.1 (65.9–76.2)

Palau specimens have a short preopercular spine that extends to the margins of the subopercle and interopercle; posterior margin of preopercle serrated, but sometimes with some smooth parts; both inner and outer margins have the lower preopercle serrated.

One specimen collected from Micronesia (CAS 68844) has a very narrow body, only 34% SL; entire body covered by cycloid scales; enlarged scales along the dorsal- and anal- fin bases with a pointed posterior spine; preopercular spine short, reaching margins of subopercle and interopercle; margins of subopercle and interopercle smooth; upper margin of lower preopercle smooth; and posterior margin of preopercle finely serrated.

One specimen from French Polynesia (MNHN 1997-1817) has X, 11 dorsal-fin rays and II, 14 anal-fin rays, all of which may be attributed to individual variation as other specimens we examined from same region have normal fin ray numbers.

TABLE 2. Meristic data of the three *Heteropriacanthus* species in this study.

	H. carolinus		*H. cruentatus*		*H. fulgens*	
	Holotype	n=21	Neotype	n=14	Neotype	n=10
Dorsal-fin rays	X, 13	X, 13 (1 with X, 14)	X,13	X,13	X,13	X, 13
Anal-fin rays	III, 14	III, 14 (1 with III, 13)	III, 14	III, 14	III, 14	III, 14 (1 with 13)
Pectoral-fin rays	17;18	17–19	18;18	17–19	19;19	17–19
Caudal-fin rays	16	16	16	16	16	16
Pored lateral-line scales	66;66	59–78	60;62	58–69	65;62	60–65
Axial scale rows	85	81–96	85;87	77–96	85;87	83–89
Transverse scales rows above lateral line	11	10–12	12	10–13	12	12–15
Transverse scale rows between lateral line and origin of anal fin (anterior)	52	49–57	51	48–53	47	47–51
Transverse scale rows between lateral line and origin of anal fin (posterior)	41	37–45	41	37–43	39	39–40
Gill rakers on first gill arch	6+18	4–6+16–19 =21–25	6+17	5–6+16–18 =22–24	6+18	5–6+18–19 =23–24
Circumpeduncular scale rows	42	42–49	39	38–44	40	39–44
Enlarged scales on dorsal-fin base	43	41–52	47	40–51	49	44–51
Enlarged scales on anal-fin base	21	20–28	29	28–30	28	23–29

Heteropriacanthus cruentatus **(Lacepède, 1801)**

Atlantic glasseye

Figure 3; Tables 1–2

Labrus cruentatus Lacepède, 1801:452, 522, pl. 2, fig. 3 (Type locality: General area south of Scotts Head, Dominica, Lesser Antilles, Western Atlantic; Neotype: USNM 285473, designated by Starnes, 1988).

Anthias boops Forster in Bloch & Schneider, 1801:308 (Type locality: Atlantic near St. Helena; no types known, based on description and drawing of *Perca boops*).

Priacanthus cepedianus Desmarest, 1823:169 (Type locality: Havana, Cuba; Holotype: MNHN A-3075).

Priacanthus bonariensis Cuvier in Cuvier & Valenciennes, 1829:105 (Type locality: Buenos Aires, Argentina; no types known).

Specimen examined. Neotype: USNM 285473 (157 mm), general area south of Scotts Head, Dominica, Lesser Antilles, Western Atlantic, 26 Oct. 1964. Other specimens are listed below.

Diagnosis. A species of *Heteropriacanthus* with following combination of characters: body depth at pectoral fin base 2.5–3.2 in SL, at mid-trunk 2.4–2.8 SL; dorsal-fin origin above the bases of the pectoral fins; preopercle

with a short triangular spine not or just reaching the posterior margin of the subopercle and interopercle; dorsal-fin base (1.7–1.9 in SL) and anal-fin base (2.5–2.9 in SL) relatively short; eye relatively large, eye diameter 2.0–2.6 in HL; interorbital space narrow, its width 3.3–3.9 in HL; head length 1.1–1.3 in body depth; caudal-peduncle length 2.5–3.1 in body depth; pored lateral-line scales 59–69; lateral scale rows 77–96; transversal scales rows 10–13+47–53=58–66.

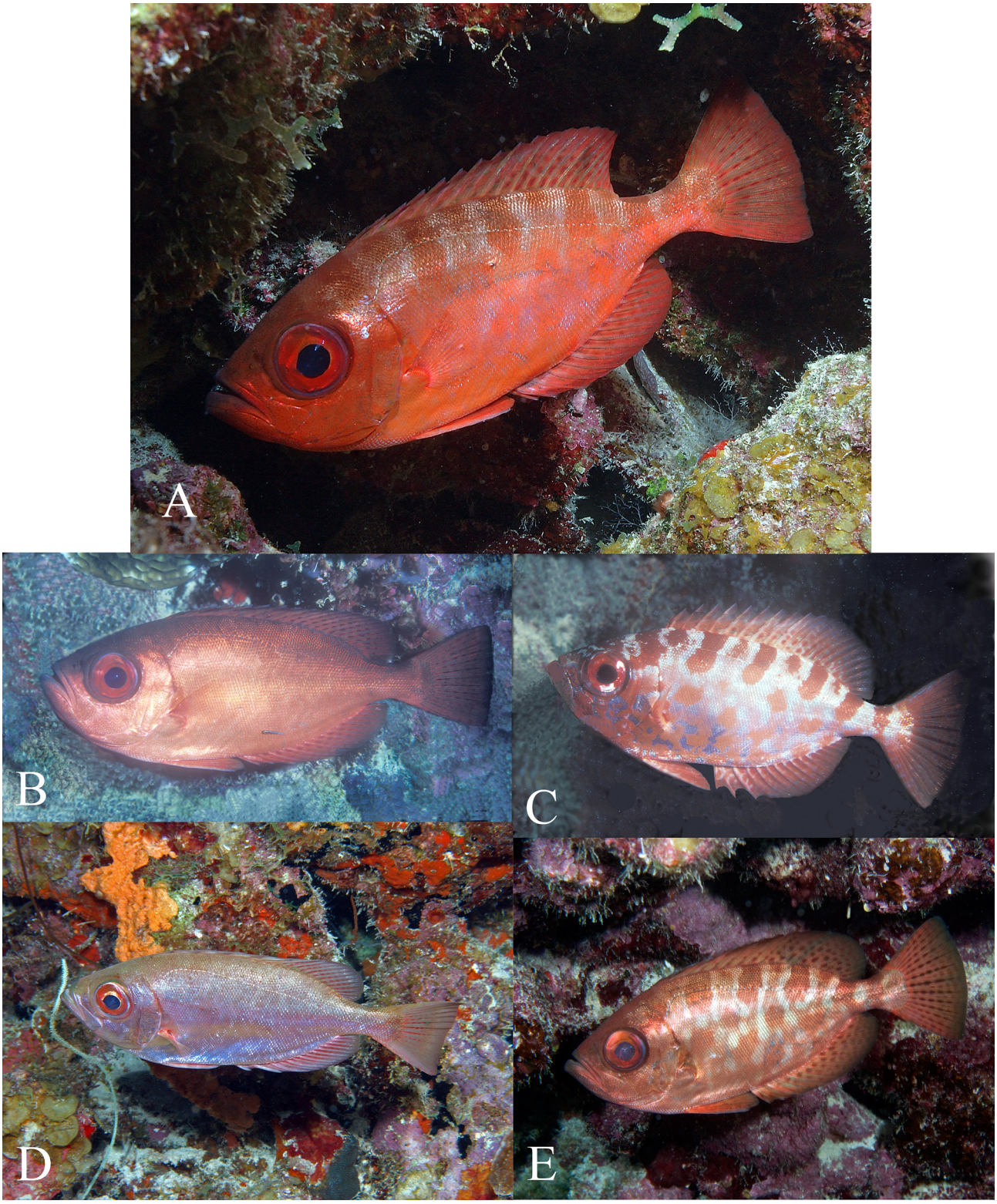

FIGURE 3. *Heteropriacanthus cruentatus* (Lacepède, 1801). A. Curaçao (Photo: R. Myers). B. Saint Croix (J.E. Randall). C. Saint Croix (Photo: J.E. Randall). D. Curaçao. (R. Myers). E. Florida (R. Myers). F. Florida (R. Myers). G. preserved specimen, Jamaica (D. Catania). H. preserved specimen, Havana, Cuba (D. Catania).

FIGURE 3. (Continued)

Description. Mainly based on specimens (n=15) collected from the western and central Atlantic Ocean, including the neotype. The following data are provided for the neotype, followed by range of non-types examined in the present study, except where indicated otherwise.

Dorsal-fin rays X, 13; anal-fin rays III, 14; pectoral-fin rays 18 (17–19). Pored lateral-line scales 60/62 (58–69); axial scale rows 85 (right side)/87 (left side) (77–96); scale rows between origin of dorsal fin and lateral line 12 (10–13); scale rows between lateral line and origin of anal fin 51 (47–52). Total gill rakers 23 (22–24), 6 (5–6) on upper limb and 17 (16–18) on lower limb.

General profile as shown in Fig. 3. Largest specimen 252.0 mm SL. Body relatively narrow, compressed, ovate in lateral profile, dorsal profile flattened along dorsal fin base; and ventral profile curved. Body depth at pectoral-fin base 2.5 (2.5–3.2) in SL, at middle portion of trunk 2.5 (2.4–2.8) in SL. When the mouth is closed, upper end of the lower jaw at about the level of the midline of the body. Body thick, body width 5.5 (5.3–6.2) in SL. Caudal peduncle relatively long, its length 6.1 (6.1–7.7) in SL and 2.8 (2.5–3.1) in body depth; its depth 10.7 (9.6–11.8) in SL.

Head moderately large, its length 3.1 (2.9–3.1) in SL, 1.3 (1.1–1.3) in body depth, with dorsal profile gradually rising to the origin of the dorsal fin. Eye large, eye diameter 2.5 (2.0–2.6) in HL; interorbital space moderately broad, strongly convex, its width 3.5 (3.4–3.9) in HL; snout short, smaller than eye, its length 3.1 (3.0–3.7) in HL. Mouth moderately large, strongly oblique; maxilla broad posteriorly and relatively exposed; posterior end of maxilla below the anterior half of the eye; lower jaw upturned, strongly projecting. Upper jaw length 2.0 (1.9–2.0) in HL.

Nostrils close to each other, situated close to the eye at its upper margin; anterior nostril small and rounded, with a posterior fleshy rim covering the entire nostril when fully folded anteriorly; posterior nostril a transverse slit, its height about a fourth of the eye diameter. Dentary, premaxilla, vomer and palatine with small conical teeth.

Opercle with a flat, blunt triangular spine at the center of the posterior margin, with 2–4 fine serrae at its tip (some with a blunt tip). Fine serration on posterior and lower margins of the preopercle, serrae on the lower margin slightly stronger than those on the posterior margin, both margins meeting at angle and forming a flat; blunt elongate spine, its tip reaching or over the posterior margin of the interopercle or subopercle. One additional finely serrate ridge above the lower margin of the preopercle, ending near the tip of the preopercular spine. Lower part of the posterior margins of the subopercle and the posterior margin of the interopercle smooth or with very weak serration, mostly covered by membranes. A deep notch on posterior portion of the interopercle covered by the preopercle spine; a narrow gap between the subopercle and the interopercle.

One continuous long-based dorsal fin originating above the upper end of the gill slit, its base 1.7 (1.7–1.9) in SL; spinous portion of the dorsal fin gradually longer, the last spine the longest; first dorsal-fin spine short, its length 5.9 (5.7–10.2) in HL; second dorsal-fin spine 5.3 (4.2–5.5) in HL; last dorsal-fin spine (10th) 2.1 (2.1–2.8) in HL; longest dorsal-fin rays (usually middle rays) 2.0 (1.6–2.4) in HL. Pectoral fin relatively short and broadly pointed, its length 1.7 (1.6–1.9) in HL, base oblique, with the upper end beneath the origin of the dorsal fin. Pelvic fin moderately long, inserted beneath or slightly anterior to the pectoral fin, adnate, attached to belly by a broad membrane along and beyond the entire length of the innermost ray, the membranes ending on either side of the anus; pelvic-fin rays ranging from not reaching the origin of the anal-fin to reaching the base of the first anal-fin spine.

One continuous long-based anal fin originating beneath 6th or 7th dorsal-fin spine, its base 2.7 (2.5–2.9) in SL; anal-fin spines relatively strong compared to the spines on the dorsal fin; first anal-fin spine 4.2 (3.8–5.0) in HL; third anal-fin spine 2.4 (2.4–3.1) in HL; longest anal-fin ray (usually middle rays) 2.0 (1.9–2.3) in HL. Soft portions of the dorsal and the anal fins broadly rounded. Caudal fin truncate or slightly rounded, its length 4.4 (3.7–4.4) in HL. Anus right next to the anal fin.

Small modified cycloid or spinous scales on almost the entire body (see Remarks below), absent from all fins, the posterior portion of the preopercle, and branchistegal rays, except for the base of the caudal fin. Thick granule-like scales on the mandible, chin, gular, chest, and abdomen; enlarged scales along either side of dorsal and anal fins. Scales on lateral body cycloid or with 20–30 fine ctenii on posterior margin. Lateral line originating at upper end of the supracleithra, rising immediately in the following few scale rows to form a curve, then roughly following the upper profile and gradually descending to the body axis at the caudal peduncle, ending at the caudal fin. Lateral-line scales with a simple central tube and two short posterior branches, one directed upward and one directed downward.

Coloration. When alive (Figs. 3A–F), body either with red patches on silver background or bright silver reticulations on red background; all fins generally with bright red color and black margins; small deep brown or blackish spots on posterior portions of dorsal and anal fins and the middle portion of the caudal fin. Preserved specimens (Figs. 3G–H) uniformly creamy white sometimes with some blackish bands present; many blackish dots on the posterior portions of dorsal and anal fins and most of the caudal fin. All fins with blackish margins.

Distribution. Widespread in western and south central Atlantic Ocean, specimens examined from off of Florida, Panama, Mexico, Cuba, Jamaica, Curaçao, and Saint Helena. Records confirmed by DNA analyses from Belize and Bahamas (Fig. 5). Most specimens were collected from shallow waters not deeper than 100 m.

Remarks. The present species is extremely similar to its Indo-Pacific congener *H. carolinus* in general appearance, morphometrics, meristics and coloration, and much more similar to *H. carolinus* than to its NE Atlantic sibling *H. fulgens*. However, the first 7 dorsal-fin spines are generally shorter than in *H. carolinus*, as reflected by the relatively small mean values (Table 1, Fig. 2A). Although not remarkably different, the preopercular spine is generally a short triangle, not or just reaching the margins of the subopercle and interopercle. The scales on the lateral body are mostly spiny, with the exception of some specimens that have almost entirely cycloid scales.

Moreover, this species can be easily separated from *H. fulgens* in having a relatively narrow body (Fig. 2B).

Specimens of *Heteropriacanthus* collected from the Indian Ocean off South Africa were assigned to the same genetic clade as specimens of *H. cruentatus* from the Western Atlantic Ocean (Gaither *et al*., 2015, Fernandez-Silva *et al*., in review). Thus, the taxonomic delineation of the Western Indian Ocean populations warrants further study.

***Heteropricanthus fulgens* (Lowe, 1838)**
Figures 4–5; Tables 1–2
Bright glasseye

Priacanthus fulgens Lowe, 1838:174, tab. II (Type locality: Madeira; no type know).

Neotype (herein designated). CAS 239122 (174.4), out of CAS 238003, Canary Islands, La Palma, 19 Sept 2014, Nieves González.

Nomenclature. Hureau (1973, 1990) listed *Serranus rufus* Bowdich, 1825 as junior synonym of *Priacanthus cruentatus*, although it was not treated in Starnes (1988). Judging from the elements of the pectoral (16), anal (II, 9) and caudal fin (19, branched) in the original description, the name can be excluded from *Heteropriacanthus*, which has P. 17–19, A. III,13–14 and C. 16 (including two unbranched rays), respectively. The closest similar priacanthid species is *Pristigenys alta* (Gill, 1862), which occurs only in the western Atlantic and has never been recorded from the eastern Atlantic (based on the records of Fishbase (www.fishbase.org)). Thus, we exclude the name from the synonymy.

The most senior available name with type locality from the NE Atlantic is *Priacanthus fulgens* Lowe, 1838. Although Hureau (1973, 1990) included this name as a junior synonym of *Priacanthus arenatus* Cuvier, 1829, Starnes (1988) stated "...There apparently is no type extant but the description and good illustration clearly are referable to *cruentatus* based on preopercular spine, fin configurations and pigmentation." We concur.

Moreover, from the illustration (Fig. 4A), the fish has a relatively deep body (ca. 43%), deep caudal peduncle (10%), and a slightly posterior origin of the dorsal fin right above the pectoral fin base, which is identical to specimens examined by us.

As there is no type known and the only known specimen collected from off Madeira is a small fish (AMNH 16871), a neotype (CAS 239122, Fig. 4B) collected from an adjacent region, the Canary Islands, is designated in order to fix the diagnostic characters.

Diagnosis. A species of *Heteropriacanthus* with the following combination of characters: a relatively deep and oval body, body depth at pectoral fin base 2.3–2.4 in SL, at mid-trunk 2.1–2.3 in SL; dorsal-fin origin above or slightly anterior to the pectoral fin base; preopercle with a short, pointed triangular spine not or nearly reaching the posterior margin of the interopercle; dorsal-fin base (1.6–1.7 in SL) and anal-fin base (2.3–2.6 in SL) relatively long; eye small, eye diameter 2.4–2.6 in HL; interorbital space broad, its width 3.0–3.3% HL; HL 1.2–1.5 in body depth; caudal-peduncle length 3.0–3.8 in body depth; pored lateral-line scales 60–65; lateral scale rows along body axis 85–89; transversal scales rows 12–15+47–51=59–66.

Description. Morphometric and meristic data are provided in Tables 1–2. The following data are given for the neotype, followed by five additional specimens (CAS 238003 and MNHN 2006-0980), except otherwise indicated. Dorsal-fin rays X, 13; anal-fin rays III, 14 (1 with III, 13); pectoral-fin rays 17–19. Pored lateral-line scales 85 (right side)/87 (left side) (83–89); scale rows between origin of dorsal fin and lateral line 12 or 13 (1 with 15); scale rows between lateral line and origin of anal fin 47–51. Total gill rakers 23–24, 5–6 on upper limb, 18–19 on lower limb.

General profile as shown in Figs. 4–5. Largest specimen 214.4 mm SL. Body relatively deep, compressed, ovate in lateral profile, dorsal and ventral profile broadly curved. Body depth at middle portion of trunk 2.3 (2.1–2.3, n=11) in SL. When mouth closed, upper end of the lower jaw about at level with midline of the body (above the body axis in some specimens). Body thick, body width 5.9 (5.5–6.0) in SL. Caudal peduncle relatively short, its length 8.0 (6.9–8.4, n=10) in SL and 3.5 (3.1–3.8, n=10) in body depth, its depth 10.0 (9.0–10.1, n=10) in SL.

Head moderately large, its length 3.1 (2.9–3.2) in SL, 1.4 (1.2–1.5, n=9) in body depth, with dorsal profile strongly rising to the origin of the dorsal fin. Eye large, eye diameter 2.5 (2.4–2.6) in HL, but relatively small compared to its congeners; interorbital space moderately broad, its width 3.3 (3.0–3.3) in HL, relatively broad compared to its congeners; snout short, smaller than the eye, its length 3.5 (3.2–3.8) in HL. Mouth moderately large, strongly oblique; maxilla broad posteriorly and relatively exposed; posterior end of maxilla below the anterior half of eye; lower jaw upturned, strongly projecting. Upper jaw length 1.9 (1.9–2.0) in HL.

Nostrils close to each other, located close to the eye at its upper margin; anterior nostril small and rounded, with a posterior fleshy rim just covering the entire nostril when fully folded anteriorly; posterior nostril a transverse slit, its height about a fourth of the eye diameter. Dentary, premaxilla, vomer and palatine with small conical teeth.

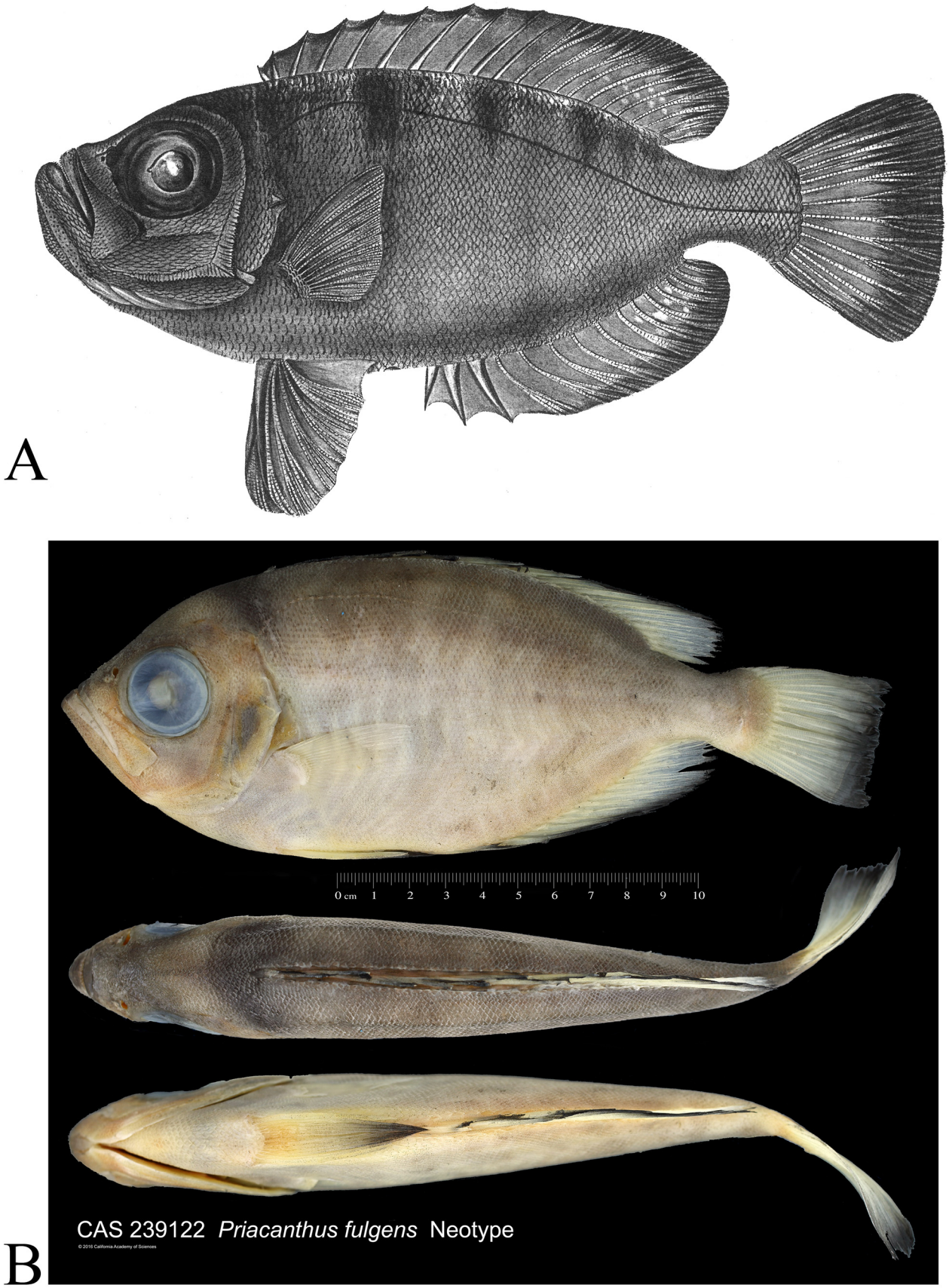

FIGURE 4. A. Original drawing of *Priacanthus fulgens* Lowe, 1838, from Madeira. B. Neotype of *Heteopriacanthus fulgens*, CAS 239122 (Photo: D. Catania).

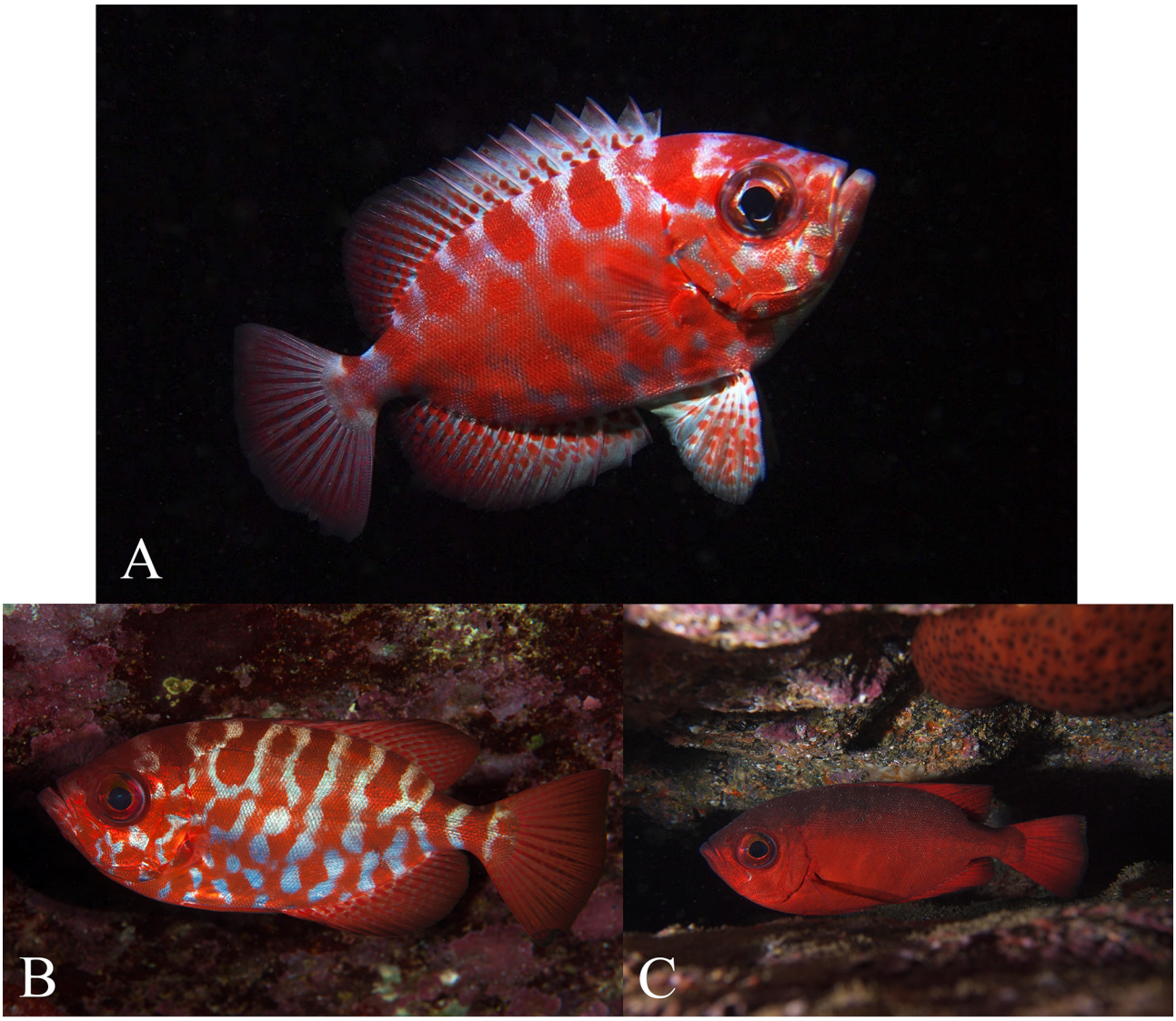

FIGURE 5. Underwater photographs of 3 different individuals of *Heteropriacanthus fulgens*, all taken from Gran Canaria (Photo: V. Nuñez).

Opercle with a flat blunt triangular spine at middle position of posterior margin, with 2–4 fine serrae at its posterior tip (some with a blunt spine). Fine serrae on posterior and lower margins of preopercle, those on lower margin slightly stronger than those on posterior margin, both meeting at an angle and forming a flat, pointed, triangular spine, its tip not reaching the posterior margin of the interopercle or subopercle (nearly reaching the margins in some specimens). One additional finely serrate ridge above the lower margin of the preopercle, ending near the tip of the preopercular spine. Lower part of posterior margins of the subopercle and posterior margin of the interopercle with very weak serrae, mostly covered by membranes. A deep notch on the posterior portion of interopercle just covered by the preopercle spine; a narrow notch between the subopercle and interopercle.

One continuous long-based dorsal fin originating above the upper end of the gill slit, its base 1.7 (1.6–1.7) in SL; spinous position of dorsal fin gradually longer, the last spine of each fin longest; first dorsal-fin spine short, its length 15.9 (5.9–15.9) in HL; second dorsal-fin spine 4.1 (4.1–5.4) in HL; last dorsal-fin spine (10th) 2.3 (2.0–2.4) in HL; longest dorsal-fin rays (usually middle rays) 1.7 (1.6–1.9) in HL. Pectoral fin relatively short and broadly pointed, its length 1.6 (1.6–1.8) in HL, base oblique with upper end beneath second dorsal-fin spine (some beneath the origin of the dorsal fin). Pelvic fin moderately long, inserted beneath the pectoral fin (sometimes slightly anterior to the pectoral fin), adnate, attached to the belly by a broad membrane along and beyond the entire length of the innermost ray, the membranes ending on either side of the anus; pelvic-fin rays reaching the base of the 2nd anal-fin spine (some reaching the 3rd dorsal-fin spine). One continuous long-based anal fin originating beneath the

7th dorsal-fin spine (some beneath the 6th dorsal-fin spine), its base 2.5 (2.3–2.6) in SL; anal-fin spines relatively strong compared to spines on the dorsal fin; first anal-fin spine 4.2 (3.3–4.2) in HL; third anal-fin spine 2.7 (2.2–2.7) in HL; longest anal-fin ray (usually middle rays) 1.8 (1.6–2.1) in HL. Soft portions of dorsal and anal fins broadly rounded. Caudal fin truncate or slightly rounded, its length 3.9 (3.6–4.3) in HL. Anus right next to the anal fin.

Small modified spinous scales on almost the entire body, absent from all fins, posterior portion of the preopercle, and branchistegal rays, except for the base of the caudal fin. Thick granule-like scales on mandible, chin, gular, chest, and abdomen; enlarged scales along either side of dorsal and anal fins. Scales on lateral body with 23–28 fine spinules on posterior margin (up to 31 in other specimens). Lateral line originating at the upper end of the supracleithra, rising immediately in the following few scale rows to form a curve, then roughly following the upper profile and gradually descending to the body axis at the caudal peduncle, ending at the caudal fin. Lateral-line scales with a simple central tube and two short posterior branches, one directed upwards and one directed downwards.

Coloration. When alive (Fig. 5), body mixed with bright red and silver colors, either forming red patches on silver background or bright silver reticulations on red background; all fins generally with bright red color and black margins; bases of dorsal and anal fins always with silver color; small deep brown or blackish spots on the posterior portions of the dorsal and anal fins and the middle portion of the caudal fin. Preserved specimens (Fig. 4B) with head and dorsal half brownish to blackish, ventral half paler. About 6 darker blotches crossing dorsal region, the first one is solid-colored, right before the dorsal fin; the second to sixth evenly distributed on the dorsal portion of the body. Dorsal and anal fins with narrow black margins; pelvic and caudal fins with broad black margins; and many small black spots on posterior portions of dorsal, anal and caudal fins.

Etymology. The specific name is from the Latin *fulgens*, meaning shining or glittering, which might refer to the silver white reticulate pattern on the body when alive.

Distribution. Known from the northeastern Atlantic Ocean off of the Canary Islands and Madeira. Record confirmed by genetic analyses from Cape Verde Islands, where the species was photographed in shallow water near a reef cave. One lot of specimens examined was collected at a depth of 20.4 m.

Remarks. Materials were either photographs examined by the authors or by colleagues in various collections, and/or x-ray films examined by the authors. The confirmed distribution for *H. fulgens* based on specimens examined is the Canary Islands and Madeira, and based on genetic analyses is the Canary Islands and Cape Verde Islands. The species can be distinguished from both congeners by the relatively deep and round body profile, stout caudal peduncle and differing COI gene sequence.

Two characteristics shown in the original drawing (Fig. 4A) are not quite consistent with the specimens we examined. One of the diagnostic characters of *Heteropriacanthus* is the symmetry of the head with the upper end of lower jaw at approximately the same level as the body axis (Starnes, 1988), however, the original drawing shows the upper end of lower jaw at the level of the upper third of the body. Indeed, some specimens and photographs we examined (at least 5 individuals) had the upper end of lower jaw above the body axis. Thus, the diagnostic character for the genus should be modified accordingly, though near symmetry is diagnostic relative to confamilials.

The preopecular spine in the original drawing does not reach the posterior margins of the subopercle and interopercle, with the posterior notch of the interopercle exposed. Photographs of two specimens (MNHN 56157, 16159) have a similar morphology when their mouths are fully opened and gill covers are expended laterally. Most specimens we examined had spines covering the posterior concave of interopercle and with their tips not far away from the margins (when gill cover not expanded). The very short peropercular spine may be attributable to individual variation or to imprecise depiction in the drawing.

Genetics results

We prepared an alignment with 90 sequences of a 562 bp-segment of the COI gene (Table 3). Phylogenetic trees based on Maximum-Likelihood inference (Fig. 6) revealed the presence of three well-supported clades (bootstrap values ≥ 82). The first clade was composed exclusively of haplotypes from the Indo-Pacific region, with representative sequences of 48 fishes collected in waters of Hawai‘i, French Polynesia, Tonga, Fiji, Cook Islands, American Samoa, Japan, Taiwan, Indonesia, Madagascar, Mauritius, Mozambique and South Africa, and thus this

group geographically encompasses the locale of the type of *H. carolinus*. The second clade is largely distributed in the Tropical West Atlantic, with 22 sequences from Curaçao, Belize, Bahamas and the Caribbean coast of Mexico represented in our tree, plus a sequence of a single specimen obtained Western Indian Ocean off South Africa. As such, the geographic range of this second clade includes populations assignable to *H. cruentatus* of the West Atlantic and also raises the need for future taxonomic work in the Western Indian Ocean. The third genetic clade is exclusive to the northeastern Atlantic archipelagoes, with 19 representative sequences collected in various locations in the Canary Islands and Cape Verde, corresponding to the distributional range of *H. fulgens*.

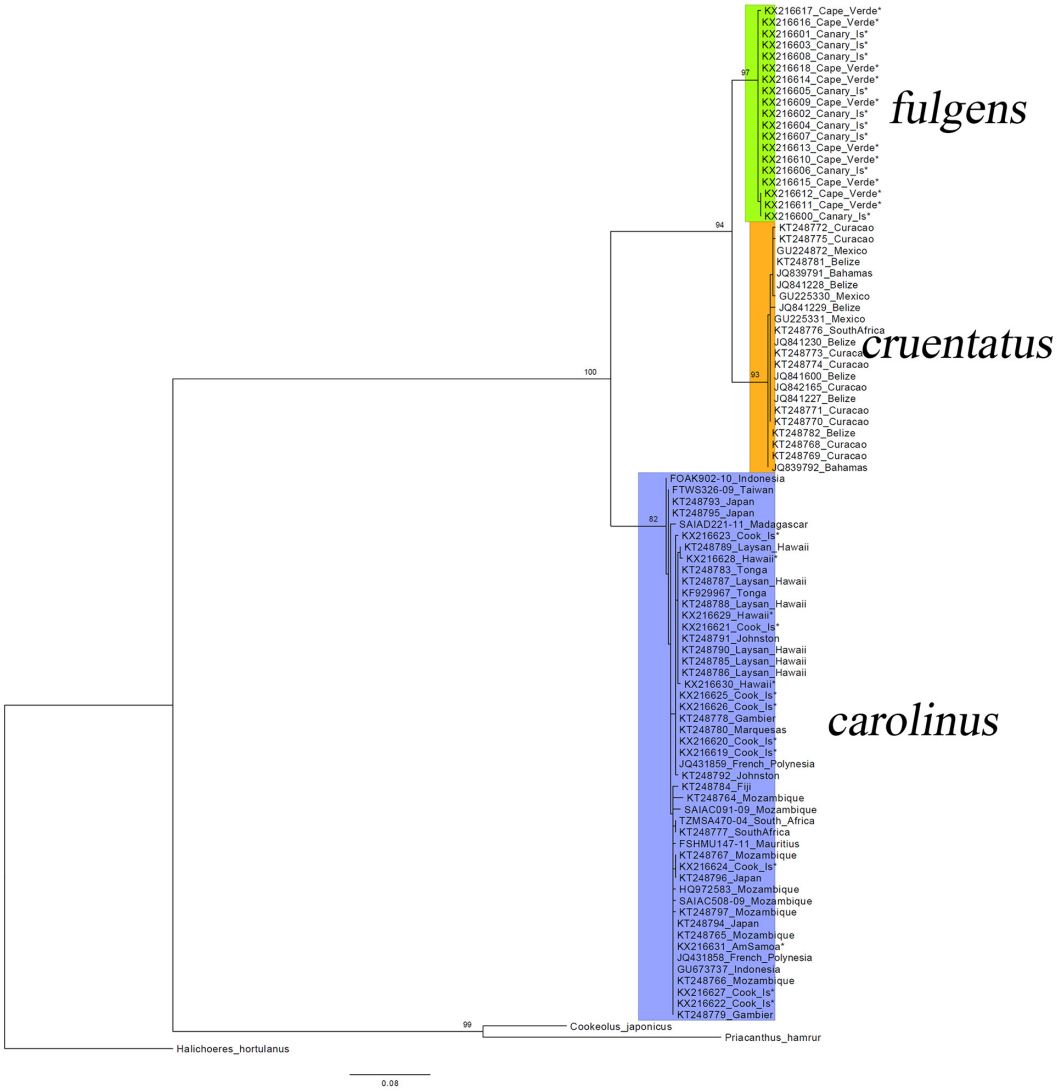

FIGURE 6. Phylogenetic tree (Maximum-Likelihood) showing relationships among COI haplotypes obtained from *Heteropriacanthus* spp. collected from across the range and three outgroups. In green, the eastern Atlantic clade (*H. fulgens*), in orange, the West Atlantic clade (*H. cruentatus*) and in blue, the Indo-Pacific clade (*H. carolinus*). Branch tips indicate the Genbank Acc. Nr. of the COI haplotype and sampling location of each fish specimen used to construct the tree. The nodes show posterior probabilities. Branch lengths are according to estimated divergence time.

TABLE 3. Specimens and locations included in the genetic analyses. Sequences from BOLD that were listed as *Heteropriacanthus* but were similar to other species in the family were excluded from the analyses, sequences that were listed as Perciforms in BOLD but formed bins with *Heteropriacanthus* were included. Mexico samples are from the Caribbean. * indicates sequences that had Ns and were changed to a consensus base for analyses. N/A: not available.

COI Sequence ID (S7 sequence ID if different)	Sequencing / Field / Tissue / Specimen ID	Sampling Localite	Sequence Source	Genbank Accession Nr.		Tissue Source
				COI	*S7*	
HCU39	Hcr_Praia1 / HCU019	Praia, Cape Verde	this study	KX216609	N/A	BANGEMAC
HCU40	Hcr_Praia2 / HCU020	Praia, Cape Verde	this study	KX216610	N/A	BANGEMAC
HCU41	Hcr_Praia3 / HCU021	Praia, Cape Verde	this study	KX216611	N/A	BANGEMAC
HCU42	Hcr_Praia4 / HCU022	Praia, Cape Verde	this study	KX216612	N/A	BANGEMAC
HCU43	Hcr_Praia5 / HCU023	Praia, Cape Verde	this study	KX216613	N/A	BANGEMAC
HCU44	Hcr_Praia6 / HCU024	Praia, Cape Verde	this study	KX216614	N/A	BANGEMAC
HCU45	Hcr_Praia7 / HCU025	Praia, Cape Verde	this study	KX216615	N/A	BANGEMAC
HCU46	Hcr_Praia8 / HCU026	Praia, Cape Verde	this study	KX216616	N/A	BANGEMAC
HCU47	Hcr_Praia9 / HCU027	Praia, Cape Verde	this study	KX216617	N/A	BANGEMAC
HCU48	Hcr_Praia10 / HCU028	Praia, Cape Verde	this study	KX216618	N/A	BANGEMAC
HCU50	Pme002	Maui, Hawaii	this study	KX216628	N/A	CAS
HCU52	Pme004	Maui, Hawaii	this study	KX216629	N/A	CAS
HCU53	Pme005	Maui, Hawaii	this study	KX216630	N/A	CAS
HCU54	Pha033	Rarotonga, Cook Islands	this study	KX216619	N/A	CAS
HCU55	Pha034	Rarotonga, Cook Islands	this study	KX216620	N/A	CAS
HCU56	Pha035	Rarotonga, Cook Islands	this study	KX216621	N/A	CAS
HCU57	Pha036	Rarotonga, Cook Islands	this study	KX216622	N/A	CAS
HCU58	Pha037	Rarotonga, Cook Islands	this study	KX216623	N/A	CAS
HCU59	Pha038	Rarotonga, Cook Islands	this study	KX216624	N/A	CAS
HCU60	Pha039	Rarotonga, Cook Islands	this study	KX216625	N/A	CAS
HCU61	Pha040	Rarotonga, Cook Islands	this study	KX216626	N/A	CAS
HCU62	Pha041	Rarotonga, Cook Islands	this study	KX216627	N/A	CAS
HCU63	Pbl001	American Samoa	this study	KX216631	N/A	CAS
HCRU003_CC	HCRU003_CC	Gran Canaria, Canary Islands	this study	KX216607	XXXX	BANGEMAC
HCRU004_CC	HCRU004_CC	Gran Canaria, Canary Islands	this study	KX216606	XXXX	BANGEMAC
HCRU005_CC	HCRU005_CC	Gran Canaria, Canary Islands	this study	N/A	XXXX	BANGEMAC
HCRU006_CC	HCRU006_CC	Gran Canaria, Canary Islands	this study	KX216600	XXXX	BANGEMAC
HCRU007_CC	HCRU007_CC	Gran Canaria, Canary Islands	this study	KX216605	XXXX	BANGEMAC
HCRU008_CC	HCRU008_CC	Gran Canaria, Canary Islands	this study	KX216608	XXXX	BANGEMAC
HCRU011_CP	HCRU011_CP	La Palma, Canary Islands	this study	KX216603	N/A	BANGEMAC
HCRU012_CP	HCRU012_CP	La Palma, Canary Islands	this study	KX216602	XXXX	BANGEMAC
HCRU013_CP	HCRU013_CP	La Palma, Canary Islands	this study	KX216604	XXXX	BANGEMAC
HCRU014_CP	HCRU014_CP	La Palma, Canary Islands	this study	KX216601	N/A	BANGEMAC

……*continued on the next page*

TABLE 3. (Continued)

COI Sequence ID (S7 sequence ID if different)	Sequencing / Field / Tissue / Specimen ID	Sampling Localite	Sequence Source	Genbank Accession Nr.		Tissue Source
				COI	*S7*	
HCU01	CUR107	Curaçao	Gaither et al.	KT248768	KT248798	CAS
HCU02	CUR108	Curaçao	Gaither et al.	KT248769	KT248799	CAS
HCU03	CUR109	Curaçao	Gaither et al.	KT248770	KT248800	CAS
HCU04	CUR110	Curaçao	Gaither et al.	KT248771	KT248801	CAS
HCU05	CUR111	Curaçao	Gaither et al.	KT248772	KT248802	CAS
HCU06	CUR112	Curaçao	Gaither et al.	KT248773	KT248803	CAS
HCU07	CUR113	Curaçao	Gaither et al.	KT248774	KT248804	CAS
HCU08	CUR114	Curaçao	Gaither et al.	KT248775	KT248805	CAS
HCU12	76058	South Africa	Gaither et al.	KT248776	KT248806	SAIAB
HCU13	TM11-373	South Africa	Gaither et al.	KT248777	KT248809	SAIAB
HCU16	GAM-734	Gambier, FP	Gaither et al.	KT248778	KT248810	NMNH Paris
HCU17	Gam-735	Gambier, FP	Gaither et al.	KT248779	KT248811	NMNH Paris
HCU18	Marq-164	Marquesas, FP	Gaither et al.	KT248780	KT248812	NMNH Paris
HCU19	KU-115	Belize	Gaither et al.	KT248781	KT248808	UKNHM
HCU20	KU-295	Belize	Gaither et al.	KT248782	KT248807	UKNHM
HCU21	KU-787	Tonga	Gaither et al.	KT248783	KT248813	UKNHM
HCU23	KU-4924	Fiji	Gaither et al.	KT248784	KT248814	UKNHM
HCU27	NW13_128/Hcr014	Laysan Atoll, HI	Gaither et al.	KT248785	KT248815	CAS
HCU28	NW13_129/Hcr015	Laysan Atoll, HI	Gaither et al.	KT248786	KT248816	CAS
HCU29	NW13_148/Hcr016	Laysan Atoll, HI	Gaither et al.	KT248787	KT248817	CAS
HCU30	NW13_149/Hcr017	Laysan Atoll, HI	Gaither et al.	KT248788	KT248818	CAS
HCU31	NW13_151/Hcr018	Laysan Atoll, HI	Gaither et al.	KT248789	KT248819	CAS
HCU32	NW13_152/Hcr019	Laysan Atoll, HI	Gaither et al.	KT248790	KT248820	CAS
HCU33	NW13_578/Hcr020	Johnston Atoll	Gaither et al.	KT248791	KT248821	CAS
HCU34	NW13_579/Hcr021	Johnston Atoll	Gaither et al.	KT248792	KT248822	CAS
HCU35	KUR-006	Shikoku, Japan	Gaither et al.	KT248793	KT248823	CAS
HCU36	KUR-007	Shikoku, Japan	Gaither et al.	KT248794	KT248824	CAS
HCU37	KUR-008	Shikoku, Japan	Gaither et al.	KT248795	KT248825	CAS
HCU38	KU-372	Shikoku, Japan	Gaither et al.	KT248796	KT248826	CAS
MM14-213 (MB9702)	MM14-213	Mozambique Ch.	Gaither et al.	N/A	KT248827	SAIAB
MB9715 (MB9703)	MM14-214	Mozambique Ch.	Gaither et al.	KT248797	KT248828	SAIAB
MB9799 (MB9704)	MM14-215	Mozambique Ch.	Gaither et al.	KT248767	KT248829	SAIAB

……*continued on the next page*

TABLE 3. (Continued)

COI Sequence ID (S7 sequence ID if different)	Sequencing / Field / Tissue / Specimen ID	Sampling Localite	Sequence Source	Genbank Accession Nr.		Tissue Source
				COI	*S7*	
*SAIAC090-09 (MB9705)	ACEP08-728	Mozambique Ch.	Gaither et al.	KT248764	KT248830	SAIAB
*SAIAC089-09 (MB9706)	ACEP08-727	Mozambique Ch.	Gaither et al.	KT248766	KT248831	SAIAB
*SAIAC091-09 (MB9707)	ACEP08-729	Mozambique Ch.	BOLD / Gaither et al.	SAIAC091-09	KT248832	SAIAB
SAIAC263-09	ACEP-08-814	Mozambique Ch.	Gaither et al.	KT248765	N/A	SAIAB
BOLD ID	**Species ID in BOLD**	**Collection Location**		**Genbank Accesssion**		
BAHA145-08	*H. cruentatus*	Bahamas	BOLD	JQ839792	N/A	
BAHA255-08	*H. cruentatus*	Bahamas	BOLD	JQ839791	N/A	
BZLWD475-08	*H. cruentatus*	Belize	BOLD	JQ841229	N/A	
BZLWD476-08	*H. cruentatus*	Belize	BOLD	JQ841228	N/A	
BZLWD618-08	*H. cruentatus*	Belize	BOLD	JQ841230	N/A	
BZLWD619-08	*H. cruentatus*	Belize	BOLD	JQ841227	N/A	
BZLWE001-08	*H. cruentatus*	Belize	BOLD	JQ841600	N/A	
*CURA360-09	*H. cruentatus*	Curaçao	BOLD	JQ842165	N/A	
MBFA638-07	*H. cruentatus*	Moorea	BOLD	JQ431859	N/A	
MBFA639-07	*H. cruentatus*	Moorea	BOLD	JQ431858	N/A	
MEFM463-06	*H. cruentatus*	Mexico	BOLD	GU225331	N/A	
MEFM464-06	*H. cruentatus*	Mexico	BOLD	GU225330	N/A	
*MFLII544-07	*H. cruentatus*	Mexico	BOLD	GU224872	N/A	
*TZMSA470-04	*H. cruentatus*	South Africa	BOLD	not in Genbank	N/A	
FOAJ852-09	Perciformes	Indonesia	BOLD	GU673737	N/A	
FOAK902-10	Perciformes	Indonesia	BOLD	not in Genbank	N/A	
FSHMU147-11	Perciformes	Mauritius	BOLD	not in Genbank	N/A	
FTWS326-09	Perciformes	Taiwan	BOLD	FTWS326-09	N/A	
SAIAC507-09	Perciformes	Mozambique	BOLD	HQ972583	N/A	
SAIAC508-09	Perciformes	Mozambique	BOLD	not in Genbank	N/A	
SAIAD221-11	Perciformes	Madagascar	BOLD	not in Genbank	N/A	
UKFBK098-08	Perciformes	Tonga	BOLD	KF929967	N/A	

The corrected average pairwise sequence divergence between the Indo-Pacific (*H. carolinus*) and West Atlantic lineages (*H. cruentatus*) was *d* = 11.0 % (Tamura & Nei, 1993), between the Indo-Pacific (*H. carolinus*) and the East Atlantic (*H. fulgens*) *d* =11.4 %, and between the East Atlantic (*H. fulgens*) and West Atlantic (*H. cruentatus*) lineages *d* = 4.2 %. These values are much higher than the genetic divergence within each lineage (Indo-Pacific: 0.6%; West Atlantic: 0.2%; East Atlantic: 0.1%). The levels of divergence among *Heteropriacanthus* spp. here reported are comparable to the levels of interspecific sequence divergence typically reported among sister species of reef fishes (reviewed by Lessios, 2008).

Specimens examined. *Heteropriacanthus carolinus* (Cuvier, 1829): CAS 3692 (205 mm), Galapagos. CAS 29441 (179.4 mm), Philippines. CAS 55014 (24, 64.4–126.6 mm), CAS 68844 (198 mm), Micronesia. CAS 55025 (3, 122.7–156.3 mm), CAS 60367 (160.4 mm), CAS 60368 (157.2 mm), Palau. CAS 222201 (160.4 mm), Fiji. CAS 209879 (2, 128.7–136 mm), CAS 209890 (157.8 mm), CAS-SU 13372 (169.9 mm), Hawai'i. MNHN 1997-1817 (196 mm), MNHN 24351 (234 mm), MNHN 2008-0834 (93.4 mm), MNHN 2008-0837 (88.7 mm), French Polynesia. USNM 380484 (170 mm), Solomon Is. USNM 412592 (128 mm), Philippines. USNM 424192 (168 mm), USNM 409164 (198 mm), French Polynesia. USNM 82931 (188 mm), Fiji Island. USNM 84251 (170 mm), Philippines. ***Heteropriacanthus cruentatus* (Lacepède, 1801)**: CAS-SU 1596 (89.1 mm), Brazil. CAS-SU 4876 (182.7 mm), Jamaica. CAS 18418 (178.7 mm), Cuba. CAS 55012 (134 mm), Caribbean Sea. CAS 55053 (248 mm), CAS 55054 (252 mm), Mexico. CAS 236603 (2, 113.9–180.7 mm), CAS 236575 (195 mm), Curaçao. MNHN A.0166 (2, 174–201 mm), St. Helena. MNHN A.3062. MNHN A.3063. MNHN 2002-1112 (141.7 mm). USNM 167884. USNM 414585 (160 mm). ***Heteropriacanthus fulgens* (Lowe, 1838)**: AMNH 16871 (95.9 mm), Madeira. AMNH 56157 (191.7 mm), AMNH 56158 (214.4 mm), AMNH 56159 (183.9), CAS 238003 (4, 166.2–175.4 mm), Canary Islands. MNHN 2006-0980 (187 mm), 28°49'1.2"N, 14°37'1.2"E. NCSM 33491 (195 mm), purchased in a fish market in Santa Cruz de Tenerife, Canary Islands. UF 117500 (3, 190–200 mm), Canary Islands, 20.4 m.

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