

## Revision of Atlantic sharpnose pufferfishes (Tetraodontiformes: Tetraodontidae: *Canthigaster*), with description of three new species

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*Abstract.*—Six species of sharpnose puffers are herein recognized from the Atlantic Ocean, three of which are described as new: *Canthigaster figueiredoi*, n. sp. from the east coast of South America, *Canthigaster jamestyleri*, n. sp. from deep reefs off the southeast coast of the United States and the Gulf of Mexico, and *Canthigaster supramacula*, n. sp. from the west coast of Africa. *Canthigaster capistratus* (Lowe 1839), described from the Madeira Islands and previously considered to be a junior synonym of *C. rostrata* (Bloch, 1786), is revalidated and redescribed; its known distribution extends from the Macaronesian Region to the Mediterranean. *Canthigaster rostrata* (Bloch, 1786), restricted to shallow-water northwestern Atlantic reefs, and *C. sanctaehelenae* (Günther, 1870), endemic to the mid-Atlantic islands of Ascension and St. Helena, also are diagnosed and redescribed. An identification key based on pigment pattern features is provided for all six Atlantic species of *Canthigaster*.

*Resumo.*—Seis espécies do gênero *Canthigaster* (Tetraodontidae: Canthigasterinae) são reconhecidas no Oceano Atlântico, três das quais são descritas como novas: *Canthigaster figueiredoi* sp. n., da costa oriental da América do Sul, *Canthigaster jamestyleri* sp. n., de recifes profundos da costa Sudeste dos Estados Unidos e Golfo do México e, por fim, *Canthigaster supramacula* sp. n., da costa oriental da África. *Canthigaster capistratus* (Lowe 1839), descrita da Ilha da Madeira, é revalidada e redescrita, e sua distribuição conhecida estende-se desde a Região Macaronésica até o Mediterrâneo. *Canthigaster rostrata* (Bloch, 1786), restrita a recifes rasos do Atlântico norte ocidental e *C. sanctaehelenae* (Günther, 1870), endêmica das ilhas meso-Atlânticas de Santa Helena e Ascensão, são também redescritas e diagnosticadas. Uma chave de identificação, baseada em características do padrão de pigmentação, é apresentada para as seis espécies de *Canthigaster* do Oceano Atlântico.

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The subfamily Canthigasterinae (family Tetraodontidae) contains only the genus *Canthigaster* Swainson, 1839, which comprises the tropical and subtropical reef-associated fishes commonly known as sharpnose puffers (Shipp 1974, Tyler 1980). At present, 26 species of *Canthigaster* are recognized in the Indo-Pacific (Allen & Randall 1977, Matsuura 1992). Throughout both sides of the Atlantic and its oceanic

islands, specimens of *Canthigaster* are nearly always referred to a single species, *Canthigaster rostrata* (Bloch, 1786) (e.g., Randall 1996), with only occasional recognition of a separate species, *Canthigaster sanctaehelenae* (Günther, 1870), from Ascension and St. Helena Islands (e.g., Tortonese 1984, Edwards & Glass 1987). However, our analysis indicates that there are at least six Atlantic species of *Canthi-*

*gaster*, three of which are described herein as new.

Pigment pattern is the most important feature used for identification of sharpnose puffers, because there is considerable homogeneity in their external morphology and anatomy (Tyler 1980). As Allen & Randall (1977) remarked, the members of *Canthigaster* are better known for their general lack of characters, rather than for any distinguishing attribute. In addition, the skin of *Canthigaster* species is highly distensible due to the absence of typical overlapping scales, precluding accurate measurements of preserved specimens (Randall & Cea-Egaña 1989). These factors result in an almost complete overlap of morphometric features among all 32 species of sharpnose puffers.

As a consequence of the overall lack of significant intrageneric variation in morphological characters, pigmentation has served as the basis for the discrimination of *Canthigaster* species. However, interpretation of geographical distributions and of variation in pigment characters has varied significantly among authors. For example, whereas Fraser Brunner (1943) recognized 13 *Canthigaster* species in the Indo-Pacific plus two in the Atlantic (*C. rostrata* and *C. sanctaehelenae*), Le Danois (1961) recognized only four species worldwide. In contrast to the latter author, Abe (1949) and Shen & Lin (1974) hypothesized that sharpnose puffers demonstrated a low degree of intraspecific variation in pigmentation features, recognizing six *Canthigaster* species in Japan and eight species in Taiwan. Although some slight intraspecific variation in pigment pattern does exist, at least in some of the species studied herein, no overlap is known to occur in the diagnostic pigmentation characters of species recognized by Allen & Randall (1977) and subsequent workers (Lubbock & Allen 1979, Matsuura 1986, 1992, Edwards & Glass 1987, Randall & Cea-Egaña 1989).

With the exception of *C. sanctaehelenae*, all other Atlantic sharpnose puffers have

long been referred to *C. rostrata* (e.g., Jordan & Edwards 1886, but see LeDanois 1961). However, after examination of pigmentation characters that have not been used previously for species identification in this group, a complex of six Atlantic *Canthigaster* allospecies, including three undescribed species, can be recognized. The objectives of this paper are to describe these three species, revise the three Atlantic species previously named, and provide a key for the six valid Atlantic species.

### Methods

Methods of counting and measuring specimens follow Allen & Randall (1977). Museum acronyms follow Leviton et al. (1985), with the addition of LIRP (Laboratório de Ictiologia de Ribeirão Preto, Universidade de São Paulo, Brazil). In descriptions of new species, which are based solely on the holotypes and all paratypes, the ranges for counts and proportional measurements are presented first, followed by values for the holotype, neotype, or syntypes in parentheses. Individual species accounts focus primarily on pigment pattern characteristics because we found, as did Allen & Randall (1977), that pigment pattern characters are the most useful features for separating species. Specimens of 24 species of *Canthigaster* from the Indo-Pacific region also were examined and are listed under "Comparative material examined". Abbreviations: SL, standard length; HL, head length.

### General Morphology of Atlantic *Canthigaster*

Fin-ray counts and measurements for the six Atlantic species are given in Tables 1–6. Body moderately deep and compressed, greatest body depth, when not inflated, located at a vertical through middle of pectoral fin. Dorsal profile of head slightly convex to straight from margin of lip to vertical through pupil; strongly convex from that point to dorsal-fin origin; straight to slightly

convex and posteroventrally slanted along base of dorsal fin; straight to slightly concave from posterior termination of dorsal fin to base of caudal fin. Dorsal portion of body rounded transversely above pectoral fin, with movable ridge of skin along mid-dorsal line, less rounded transversely posteriorly. Ventral profile of head straight to slightly concave. Ventral profile of body straight when not inflated to strongly convex when inflated; straight to slightly convex and posterodorsally slanted along anal-fin base; straight to slightly concave along caudal peduncle. Head markedly pointed in lateral profile, snout conical, and mouth terminal. Single minute nostril on each side of snout, with circular opening and set in short inconspicuous tube. Eye of moderate size. Gill openings small, ending ventrally at about level of midportion of pectoral-fin base. Teeth fused into premaxillae and dentaries as beak-like jaws, convex in outer view and separated by a median suture. Teeth white. Head and body with scattered tiny prickles consisting of modified scales. Lateral line only visible using microscope. Dorsal-fin margin slightly rounded. Dorsal fin situated on posterior half of body, originating at vertical through beginning of posteriormost third of standard length. Pectoral fin moderately developed, its posterior margin straight to slightly rounded. Pelvic fins and associated internal skeleton absent. Anal fin originating immediately posterior to vertical through posterior termination of dorsal-fin base, ventral margin slightly rounded. Caudal-fin margin slightly rounded.

*Canthigaster figueiredoi*, new species

Fig. 1A, Tables 1, 2

*Canthigaster rostrata* (not of Bloch, 1786).—Mago-Leccia, 1970:122 in part (listed for Venezuela).—Carvalho-Filho, 1994:248 (diagnosis, distribution, notes on biology, illustration based on Caribbean specimens).—Ferreira et al., 1995: 225 (listed).—Figueiredo & Menezes,

2000:69 (diagnosis, key, illustration, distribution, notes on biology).—Szpilman, 2000:288 (listed for Brazil).

*Canthigaster* sp.—Carvalho-Filho, 1999: 248 (diagnosis, illustration, color photograph, distribution, notes on biology).—Rocha & Rosa, 2001:992 (listed for north-eastern Brazil)

*Holotype*.—MZUSP 45608 (72.9 mm SL), Alcatrazes Archipelago (24°06', 45°42'W), São Paulo State, Brazil, 28 Apr 1993, R. L. Moura.

*Paratypes* (14 specimens, 48.8–78.8 mm SL, all from Brazil).—MZUSP 53044 (1, 62.2 mm SL), Manoel Luís Reefs (00°52'S, 44°15'W), Maranhão State, 1 Jul 1998, R. L. Moura & R. B. Francini-Filho; MZUSP 53032 (2, 48.8–55.1 mm SL), same locality as MZUSP 53044, 2 Jul 1998, R. L. Moura & R. B. Francini-Filho; MZUSP 46327 (1, 76.2 mm SL), Fernando de Noronha Archipelago (03°56'S, 35°24'W), Pernambuco State, 20 Jun 1985, A. Carvalho-Filho; USNM 357499 (1, 77.5 mm SL), Arembepe (12°47'S, 37°30'W), Bahia State, 10 Jun 1985, A. Carvalho-Filho; MZUSP 60536 (1, 78.8 mm SL), Abrolhos Archipelago (17°57'S, 38°41'W), Bahia State, 14 Mar 1999, R. L. Moura, C. H. Flesch & R. B. Francini-Filho; MZUSP 52256 (1, 49.4 mm SL), same locality as MZUSP 60536, 1 Jan 1997, I. Sazima & R. L. Moura; MZUSP 44936 (1, 69.0 mm SL), Três Ilhas (20°42'S, 40°24'W), Guarapari, Espírito Santo State, Jan 1992, J. L. Gasparini; LIRP 1126 (1, 69.6 mm SL), Farol dos Moleques (23°49'44"S, 45°25'24"W), Canal de São Sebastião, São Paulo State, 14 Mar 1996, B. S. Daher, H. G. Santos & F. B. Santos, 0.5–7 m depth; LIRP 1127 (1, 51.4 mm SL), same locality as LIRP 1126, 14 May 1996, H. F. Santos & F. Z. Gibran, 0–10 m depth; USNM 357498 (1, 65.6 mm SL) Laje de Santos (24°19'S, 46°11'W), São Paulo State, 17 Jun 1990; MZUSP 44594 (1, 68.9 mm SL), same locality and collector as USNM 357498, 9 Jun 1990; MZUSP 45630 (1, 68.6 mm SL), Queimada Grande

Table 1.—Summary of fin-ray counts for the six Atlantic species of *Canthigaster*.

	Dorsal			Anal		Pectoral		
	9	10	11	8	9	14	15	16
<i>C. capistrata</i>	4	8			11	2	6	2
<i>C. sanctaehelenae</i>	2	7		1	8		4	4
<i>C. rostrata</i>		44	1		45	1	16	28
<i>C. supramacula</i>	1	1			2		2	
<i>C. figueiredoi</i>	5	12			18		10	8
<i>C. jamestyleri</i>	4				4		1	3

Island (24°29'S, 46°41'W), São Paulo State, 2 May 1993, R. L. Moura; MZUSP 55434 (1, 64.2 mm SL), Arvoredo Island (27°17'S, 48°21'W), Santa Catarina State, 24 Dec 1998, R. L. Moura & R. B. Francini-Filho.

*Additional material examined* (2 specimens, non-types).—ANSP 101831 (2, 70.6–73.2 mm SL), off Colombia (12°37'S, 71°10'W), 25 Sep 1963, R/V *Oregon*, sta. 4394.

*Diagnosis*.—*Canthigaster figueiredoi* is distinguished from its Atlantic congeners, except *C. jamestyleri*, by the long anterior extension of the lower horizontal dark stripe on the flank (composed of irregular horizontal and diagonal bars and originating as a solid stripe on the ventral caudal-fin margin). This stripe reaches the pectoral-fin base in *C. figueiredoi*; by contrast, this

stripe is restricted to the caudal-fin margin in *C. sanctaehelenae*, *C. capistrata* and *C. supramacula*, while the stripe does not surpass the anal-fin base in *C. rostrata*. *Canthigaster figueiredoi* is readily distinguished from *C. jamestyleri*, which also has a lower dark stripe on the flank extending to the pectoral-fin base, by the presence of a dark caudal-fin margin, the absence of vertically oriented bars on the caudal fin, the possession of fewer spots and stripes on the body, particularly on the dorsum, as well as by the absence of a small black irregular spot on the anal-fin base.

*Description*.—See Table 1 for a summary of meristic data and Table 2 for morphometrics. Dorsal-fin rays 9–10 (10); anal-fin rays 9; pectoral-fin rays 15–16 (15).

In alcohol (Fig. 1A), head and body are tan to grayish-brown, darker on dorsum and

Table 2.—Morphometrics of *C. figueiredoi* type specimens. Values for lines two to six expressed as % of standard length, and for lines seven to 14 expressed as % of head length.

	Holotype MZUSP 45608	Range in values	SD	n
1—Standard Length (mm)	72.9	48.8–78.8		15
2—Body Depth	38.4	33.7–43.5	3.20	15
3—Body Width	25.7	21.2–31.0	2.63	15
4—Head Length	37.7	35.9–43.0	1.83	15
5—Tip of Snout to Dorsal-fin Origin	72.2	70.7–78.5	2.26	14
6—Tip of Snout to Anal-fin Origin	74.6	74.1–82.6	2.69	15
7—Snout Length	70.5	58.8–71.6	4.24	15
8—Eye Diameter	27.6	23.3–32.0	2.63	15
9—Interorbital Width	36.0	24.8–36.0	2.65	15
10—Caudal Peduncle Depth	38.5	31.4–41.6	3.02	14
11—Dorsal-fin Base Length	20.4	13.5–24.7	2.88	14
12—Anal-fin Base Length	18.2	13.9–22.5	2.47	15
13—Pectoral-fin Length	39.6	30.2–43.6	4.02	12
14—Post-orbital Length of Head	21.1	15.0–25.5	2.96	15

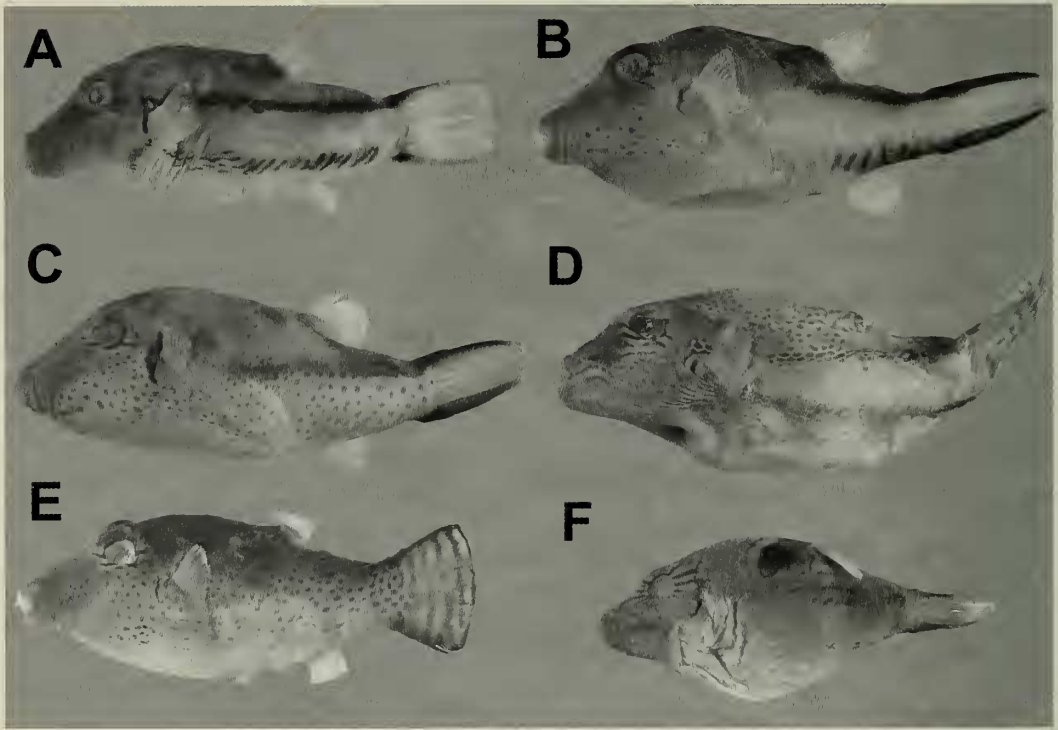


Fig. 1. Atlantic Ocean species of *Canthigaster*: A, holotype of *C. figueiredoi*, n. sp., MZUSP 45608, 72.9 mm SL, Alcatrazes Archipelago (24°06', 45°42'W), São Paulo State, Brazil; B, *C. rostrata*, USNM 318937, 48.7 mm SL, Tobago, Saint Giles Islands (11°21'22"N, 60°32'00"W) Tobago, southern Caribbean; C, neotype of *C. capistrata*, ANSP 103122, 76.4 mm SL, Madeira Islands (17°5'N, 33°00'W), eastern Atlantic; D, holotype of *C. jamestyeri*, n. sp., USNM 325810, 82.6 mm SL, South Carolina (33°48'N, 76°34'W), USA; E, *C. sanctaehelenae*, USNM 267871, 77 mm SL, St. Helena Island (15°58'S, 05°43'W); F, holotype of *C. supramaculata*, n. sp., ANSP 102312, 40.1 mm SL, Abidjan (~05°N, 04°W), Ivory Coast.

paler ventrally, especially ventral to a horizontal through pectoral-fin base. Few inconspicuous small spots sparsely distributed on dorsum. Two conspicuous dark longitudinal stripes on flank; uppermost stripe extending from upper caudal-fin margin to pectoral-fin origin, and lower stripe extending from lower caudal-fin margin to pectoral-fin base. Upper stripe solid; lower stripe composed of smaller and irregularly oriented bars and stripes. Snout tan, with numerous (3–10) thin bars extending dorsally to level of nostrils. Dorsal, anal and pectoral fins hyaline. Caudal fin hyaline, with conspicuous dark stripes that extend along proximal third of dorsal and ventral margins to along entire margins. Some specimens with three to six poorly devel-

oped dark lines radiating from eyes, generally from lower half of eye, most lines horizontally oriented.

In life, body color highly contrasted dorso-ventrally, with yellowish-brown to tan coloration above upper dark longitudinal stripe and almost white below this level. Sparse spots on body and vertical bars on snout bluish. Iris bright yellow. Upper dark longitudinal stripe black with thick bright blue margins. Lower stripe black with thick golden-yellow margins. Pectoral fins and unpaired fins hyaline, except for dark margin of caudal fin.

*Etymology*.—The specific name honors José Lima de Figueiredo for his contributions to the advancement of the taxonomy of Brazilian marine fishes, as well as for his

long-term encouragement and support to the authors. The common name Southern Atlantic Sharpnose-puffer is proposed.

*Distribution and Remarks.*—*Canthigaster figueiredoi* ranges from the southern Caribbean (~9°N) south to the State of Santa Catarina, Brazil (~33°S), including the oceanic islands of Atol das Rocas and Fernando de Noronha. Throughout most of its geographical range south of the mouth of the Amazon River (Moura et al. 1999), it is the only species of *Canthigaster* recorded to date. *Canthigaster figueiredoi* occurs syntopically with *C. rostrata* (Bloch, 1786) in the southern Caribbean, the only area in the Atlantic where two species of *Canthigaster* are recorded syntopically. *Canthigaster rostrata* and *C. jamestyleri* are both recorded in South Carolina and in the Gulf of Mexico, but their depth ranges do not overlap. See remarks under *C. capistrata* for comparison with Indo-Pacific species.

The Southern Atlantic Sharpnose-puffer occurs in a broad range of habitats, including coral-rich areas in the southern Caribbean, coral-poor reefs along the northeastern Brazilian coast, and rocky bottoms along the southeastern and southern Brazilian coast (see Maida & Ferreira 1997). It is almost invariably observed in pairs, hovering over the reefs during the day, in depths ranging from 1 to at least 35 m. Despite being a rather common species, it is not abundant in any of the localities where we collected specimens, which may explain its absence in early accounts of Brazilian marine fishes (e.g., Ribeiro 1915, 1918). The Southern Atlantic Sharpnose-puffer is a popular fish in the Brazilian aquarium trade.

*Canthigaster rostrata* (Bloch, 1786)

Fig. 1B, Tables 1, 3

*Tetrodon rostratus* Bloch, 1786:8, pl. 146 (type locality East Indies).

*Tetrodon ornatus* Poey, 1867:244 (original description, type locality Cuba).—Poey,

1875:433 (listed).—Günther, 1870:303 (listed from St. Croix).

*Canthigaster rostrata*: Goode, 1876:75 (listed for Bermuda).—Jordan & Edwards, 1886:246 (diagnosis).—Bean, 1906:80 (listed for Bermuda).—Jordan et al., 1930:320 (listed).—Beebe & Teevan, 1933:246 (diagnosis, key).—Fraser-Bruner, 1943:15 (listed).—LeDanois, 1961:317 (listed).—Starck & Davis, 1966:345 (listed for Florida, night habits).—Starck, 1968:36 (listed for Florida).—Böhlke & Chaplin, 1968:691 (diagnosis, key, illustration).—Randall, 1968:281 in part (diagnosis, photograph).—Mago-Leccia, 1970:122 in part (listed from Venezuela).—Collette & Talbot, 1972:124 (activity patterns).—Smith & Tyler, 1972:162 (notes on day and night behavior, illustrations).—Walls, 1975:408 (diagnosis, illustration, color photograph).—Hoese & Moore, 1977:268 (diagnosis).—Tyler et al., 1980:274 (osteology).—Robins et al., 1980:66 (listed, common name).—Robins & Ray, 1986:305 in part (diagnosis, illustration).—Knopf, 1988:301 in part (description, color photograph, distribution, biological information).—Randall, 1996:344 in part (diagnosis, color photograph).—Böhlke & Chaplin, 1993:691 (diagnosis, key, illustration).—Humann, 1994:326 in part (diagnosis, color photograph).—Burgess et al., 1994:222 (listed for Cayman Islands).—Lieske & Myers, 1996:315 in part (listed, illustration).—Eschmeyer, 1998:1473 (listed, type specimens).—Smith-Vaniz et al., 1999:355 (listed for Bermuda).

*Types.*—No type specimens are known to exist at the Museum für Naturkunde in Berlin (Eschmeyer 1998). Since the original description fits any Atlantic *Canthigaster* species, identification of *C. rostrata* is based on plate 146 of Bloch's (1786) monograph (see "Remarks and distribution"). For this reason, specimen USNM 276209 (74.5 mm SL) from Twin Cays, Belize, a

Table 3.—Morphometrics of examined specimens and neotype of *C. rostrata*. Values for lines two to six expressed as % of standard length, and for lines seven to 14 as % of head length.

	Neotype USNM 276209	Range in values	SD	n
1—Standard Length (mm)	75.5	29.3–80.1		21
2—Body Depth	33.9	32.2–38.5	1.69	21
3—Body Width	31.1	22.7–32.1	2.73	21
4—Head Length	40.9	36.8–50.3	2.92	21
5—Top of Snout to Dorsal-fin Origin	72.1	70.5–75.5	1.65	21
6—Tip of Snout to Anal-fin Origin	77.2	73.9–81.5	2.39	21
7—Snout Length	76.1	57.4–82.7	7.80	20
8—Eye Diameter	16.5	16.5–34.6	4.87	21
9—Interorbital Width	28.8	18.2–38.5	4.09	21
10—Caudal Peduncle Depth	34.3	27.0–42.7	3.71	20
11—Dorsal-fin Base Length	20.7	15.9–23.0	1.91	21
12—Anal-fin Based Length	13.9	11.5–20.9	2.41	21
13—Pectoral-fin Length	28.8	28.8–49.2	4.98	20
14—Post-orbital Length of Head	22.7	12.2–26.6	4.10	21

site within the original broad type locality (“east Indies”), is herein designated as the neotype of *Tetrodon rostratus* Bloch, 1786.

*Material examined* (20 specimens).—USNM 151979 (1, 70.2 mm SL), Long Bay (33°37'N, 76°54'W), South Carolina, USA, R/V *Albatross*, 10 Feb 1950; USNM 178605 (1, 80.1 mm SL), Bermuda (32°18'N, 64°46'W), W. Beebe, 1934; USNM 178696 (1, 61.1 mm SL), same locality and collector as USNM 178605, 1–14 Oct 1931; USNM 337750 (2, 64.1–75.0 mm SL), same locality as USNM 178605, 10 m depth, B. B. Collette, 26 Jul 1995; USNM 318937 (6, 29.4–48.7 mm SL), Tobago, Saint Giles Islands (11°21'22"N, 60°32'00"W), Tobago, J. T. Williams, G. D. Johnson, J. Howe, S. Blum & M. Nizinski, 12 Sep 1990; USNM 318941 (3, 29.3–60.3 mm SL), Pirates Bay (11°19'32"N, 60°32'58"W), Charlotteville, Tobago, J. T. Williams, J. Howe, M. Nizinski, S. Blum, T. Munroe, 5 Sep 1990; USNM 318934 (5, 31.4–60.4 mm SL), Charlotteville (19°08'N, 60°33'W), Tobago, J. T. Williams, 8 Sep 1990; USNM 194010 (1, 63.3 mm SL), Los Roques, Venezuela, P. Bottom, 5 Jul 1958.

*Diagnosis*.—*Canthigaster rostrata* (Bloch, 1786) is distinguished from all other Atlantic species by a short upper dark longitudinal

stripe, presence of few spots on flank and dorsum, and absence of a conspicuous (larger than eye) spot on the dorsum. The upper dark longitudinal stripe of *C. rostrata* extends from caudal-fin dorsal margin to the vertical through dorsal-fin base. Although a horizontal line of dark spots extends anterior to the anterior portion of the horizontal dark stripe in some specimens, and sometimes even surpasses the dorsal-fin base, this line of spots never forms a continuous stripe as it does in *C. figueiredoi*, *C. jamestyleri* and *C. capistrata*. From the two species that have shorter upper dark longitudinal stripe, *C. sanctaehelenae* and *C. jamestyleri*, *C. rostrata* is also readily distinguished by the absence of vertically oriented bars on the caudal fin and by the presence of bars on the snout (horizontal lines in *C. jamestyleri* and absent in *C. sanctaehelenae*). Finally, *C. rostrata* can be distinguished from *C. supramaculata* by the absence of a conspicuous spot on the dorsum and by the lower longitudinal dark stripe, which extends anteriorly onto the caudal peduncle and posterior portion of trunk (restricted to caudal-fin margin in *C. supramaculata*).

*Description*.—See Table 1 for a summary of meristic data and Table 3 for morphometrics. Dorsal-fin rays 10–11 (1 spec-

imen with 11) (10); anal-fin rays 9; pectoral-fin rays 14–16 (16).

In alcohol (Fig. 1B), head and body tan to light brown, darker on dorsum and paler ventrally, especially below horizontal through pectoral-fin base. A few small, inconspicuous darker spots sparsely distributed on dorsum. Some specimens with diffuse darker area slightly anterior and ventral of dorsal-fin base. Venter conspicuously spotted. Two conspicuous dark longitudinal stripes on dorsal and ventral margins of caudal fin; uppermost stripe extending anteriorly to level of dorsal-fin base and lower extending to level of anal-fin base. Upper dark longitudinal stripe mostly solid, but terminating anteriorly as horizontal series of small spots. Lower stripe solid only on caudal-fin ventral margin, comprising short irregular bars on caudal peduncle and posterior portion of trunk. Snout tan, with numerous (3–10) dark bars extending dorsally to level of nostrils. Dorsal, anal, and pectoral fins hyaline; caudal fin hyaline and pigmented only on dorsal and ventral margins. Some specimens with three to six poorly developed lines radiating from eyes, generally from ventral half of eyes, lines roughly horizontally oriented.

In life, body color highly contrasted dorso-ventrally, yellowish-brown to tan above upper dark longitudinal stripe and whitish-brown below that stripe. In addition to grayish blue horizontal stripes on the snout, some specimens also bearing two to four horizontally oriented bars, radiating from the mouth onto the snout. These bars disappear immediately after preservation. Scattered spots on body and bars on snout bluish; iris bright yellow. Spots on sides of body not as visible as in preserved specimens. Longitudinal stripes black with thick bright-blue margins. Pectoral fin hyaline; unpaired fins hyaline, except for blackish dorsal and ventral caudal-fin margins. The highly mottled night-time resting pigment pattern of *C. rostrata* is significantly different than the day-time and preserved pigment pattern described above (see Smith &

Tyler 1972 for illustration of both). However, this mottled pattern (and other patterns that can be induced by fright or chemical injections) is unlike that of any of the day-time patterns of other species of *Canthigaster*, and changes to the normal *C. rostrata* day-time pattern when preserved (Smith & Tyler 1972). Night-time resting pigmentation pattern is not known from any of the other Atlantic species.

*Remarks and distribution.*—Despite the fact that there are no remaining type specimens, and an inexact type locality (“east Indies”) was given in the original description of *C. rostrata*, plate 146 in Bloch (1786) allows the unequivocal establishment of its identity. The illustrated specimen has short longitudinal dark stripes on the caudal fin and side of the body, these stripes not extending anteriorly beyond the level of dorsal fin, an exclusive combination of features of the north-western Atlantic *Canthigaster* species known as the sharpnose puffer (Robins et al. 1980). *Canthigaster rostrata* occurs in shallow reefs to at least 40 m depth, including marginal habitats such as seagrass beds. It ranges from South Carolina, USA, and Bermuda, south to Tobago and the Lesser Antilles (Randall 1996, Böhlke & Chaplin 1996). See remarks under *C. capistrata* for comparison with Indo-Pacific species.

Despite bearing a well-established common name (Robins et al. 1980), we propose the amendment *Caribbean* sharpnose-puffer to avoid confusion with other Atlantic sharpnose puffers recognized herein.

*Canthigaster capistrata* (Lowe, 1839)

Fig. 1C, Tables 1, 4

*Tetrodon capistratus* Lowe, 1839:90 (original description, type locality Madeira Island).

*Canthigaster rostrata* (not of Bloch, 1786). LeDanois, 1961:317 in part (listed, synonymy).—Tortonese, 1973:647 in part (listed from the eastern Atlantic and Macaronesia).—Tortonese, 1984:1341 in



Table 4.—Morphometrics of examined specimens of *C. capistrata*. Values for lines two to six expressed as % of standard length, and for lines seven to 14 as % of head length.

	Range in values	SD	n
1—Standard Length (mm)	40.0–88.7		14
2—Body Depth	29.7–39.0	2.16	12
3—Body Width	26.0–30.6	1.89	4
4—Head length	35.2–38.6	1.41	4
5—Tip of Snout to Dorsal-fin Origin	69.8–76.7	1.82	14
6—Tip of Snout to Anal-fin Origin	72.5–87.5	3.87	14
7—Snout Length	62.2–69.9	3.35	4
8—Eye Diameter	26.8–32.4	2.44	4
9—Interorbital Width	26.1–27.9	0.75	4
10—Caudal Peduncle Depth	39.0–41.8	1.30	4
11—Dorsal-fin Base Length	22.1–26.9	2.53	4
12—Anal-fin Base Length	18.2–24.0	2.43	4
13—Pectoral-fin Length	36.4–38.9	1.26	3
14—Post-orbital Length of Head	15.0–15.8	0.32	4

part (key, listed from the eastern Atlantic and Macaronesia).—Dooley et al., 1985: 43 (specimens from Canary Islands, distribution).—Azevedo & Heemstra, 1995: 7 (specimens from Azores).—Santos et al., 1997:144 (listed from Azores).—Debelius, 1997:294 in part (recorded from Azores, Madeira, Canary and Cape Verde).—Garcia, 1999:unpaginated (record for the Mediterranean, color photograph).

*Syntypes*.—Eschmeyer (1998) cited the “possibly two” syntypes as “whereabouts unknown”. We recently (2000) searched the BMNH fish collections and failed to find any specimens labelled as types.

*Material examined* (13 specimens).—ANSP 103122 (4, 57.5–76.4 mm SL), Madeira Islands (17° 5'N, 33°00'W), 22 Jun 1965; BMNH 1868.5.13:6 (1, 64.0 mm SL), Funchal, Madeira Islands, R. J. Lowe; BMNH 1895.7.16:9 (1, 57.1 mm SL), Madeira Islands, J. Y. Johnson; BMNH 1927.11.2:2 (1, 56.4 mm SL), Madeira Islands; BMNH 1953.11.1.582-592 (3 of 10, 55.0–74.5 mm SL), Madeira Islands, D. W. Tucker. Sep 1953; BMNH 1982.4.27 (1, 72.7 mm SL), Brava Island, Cape Verde (~15°00'N, 25°00'W), R. Lubbock, A. Edwards and D. Lindsay, 1982; BMNH 1983.10.11.265 (1, 80.2 mm SL), BMNH

1983.10.11.266 (1, 88.7 mm SL), Canary Islands (28–29°N, 14–18°W), Capt. Tottom.

*Diagnosis*.—*Canthigaster capistrata* (Lowe, 1839) is readily distinguished from its Atlantic congeners by the following combination of characters: absence of a dark stripe extending anteriorly from the ventral caudal-fin margin onto the caudal peduncle and/or flank, presence of a horizontal dark stripe extending from the dorsal caudal-fin margin anteriorly to the pectoral-fin base, and absence of a conspicuous (larger than eye) spot slightly ahead and below the dorsal-fin base. From *C. jamestyleri* and *C. sanctaehelenae* it is further distinguished by the absence of bars on the caudal fin.

*Description*.—See Table 1 for a summary of meristic data and Table 4 for morphometrics. Dorsal rays 9–10 (9); anal rays 9; pectoral rays 14–16 (15).

In alcohol (Fig. 1C), head and body tan, darker on dorsum and paler ventrally, especially below horizontal through ventral margin of orbit. Head and sides of body spotted except for area above pectoral fins, interorbital space and dorsal third of snout. One prominent dark longitudinal stripe extending from superior margin of caudal peduncle anteriorly to pectoral-fin base. This

stripe sometimes embedded with numerous black spots. Few specimens with spots on ventral half of caudal peduncle coalescing to form series of about five irregular stripes. Caudal fin mostly hyaline with dark dorsal and ventral margins and a few faded spots scattered on medial area. Snout tan with three to five vertically oriented bars extending dorsally to nostril level. Dorsal, anal, and pectoral fins hyaline. Three to six lines radiating from eye, generally from its lower half, lines oriented approximately horizontally.

In life, body coloration sharply contrasted dorso-ventrally, yellowish-brown to tan above upper dark longitudinal stripe, paler ventrally. Body heavily spotted ventral to upper longitudinal stripe, spots varying from bluish gray to bright blue. Snout with bluish gray to bright blue vertically oriented bars. Pectoral fin and unpaired fins hyaline, except for dorsal and ventral margins of caudal fin. Spots on caudal fin bluish gray, sometimes barely visible. Iris bright yellow.

*Remarks and distribution.*—Despite the fact that the original description of *C. capistrata* fits any Atlantic sharpnose puffer species, *C. capistrata* can be readily identified because all *Canthigaster* specimens so far recorded from the Madeira Islands belong to *C. capistrata*. This species is known from the Macaronesian Region (sensu Stock 1995, Beyhl et al. 1995) and sometimes strays into the Mediterranean Sea. Examined specimens were captured from localities around the Cape Verde and Madeira Islands, but *C. capistrata* has a much broader distribution within Macaronesia. Debelius (1997:294) provided an underwater color photograph of this species and recorded it from the Azores and Canary islands (as *C. rostrata*). Specimens from the Canary Islands were also reported by Doolley et al. (1985), as *C. rostrata*. A fine underwater photograph taken in Tarifa, Spain, published in a popular diving magazine (Garcia 1999), also depicts a specimen of *C. capistrata*. As mentioned by Garcia (1999), the Tarifa record represents a stray

individual, because this species is not regularly sighted in the Mediterranean. A common name, Macaronesian Sharpnose-puffer is proposed for the species.

The pigment patterns of the Atlantic species *C. figueiredoi*, *C. capistrata* and *C. rostrata* resemble those of the Indo-Pacific species *C. marquesensis* Allen & Randall, 1977, *C. inframacula* Allen & Randall, 1977, *C. smithae* Allen & Randall, 1977, and *C. rivulata* (Temminck & Schlegel, 1850) (see Fig. 1 of the present paper and figs. 4, 5 and 7 of Allen & Randall 1977), with which they share the presence of one or two prominent, solid, longitudinal dark stripes on the body. From *C. marquesensis* and *C. inframacula*, *C. figueiredoi* and *C. rostrata* differ by having two, instead of one, dark longitudinal stripes on the flank, and *C. capistrata* differs by having dark dorsal and ventral caudal-fin margins. From *C. smithae* these three Atlantic species differ by the shorter lower dark longitudinal stripe, which does not surpass a vertical through the pectoral-fin base. Finally, from *C. rivulata*, they differ in lacking a dark area in front of the gill openings.

*Canthigaster jamestyeri*, new species  
Fig. 1D, Tables 1, 5

*Holotype.*—USNM 325810 (1, 82.6 mm SL), South Carolina (33°48'N, 76°34'W), USA, 100 m, South Carolina Marine Resources Research Institute, 14 May 1981.

*Paratypes* (3 specimens).—GMBL 74-147 (1, 73.0 mm SL), off South Carolina (32°06'N, 79°13'W), USA, R/V *Dolphin*, 15 Aug 1974; GMBL 78-129 (2, 60.4-85.2 mm SL) off South Carolina (32°45.2'N, 78°29.2'W), USA, R/V *Dolphin*, 4 Oct 1979.

*Diagnosis.*—*Canthigaster jamestyeri* is readily distinguished from all Atlantic congeners by the absence of dark dorsal and ventral margins on the caudal fin and the presence of a small irregular dark spot on the dorsal-fin-base. It can be further distinguished from all Atlantic congeners, except

Table 5.—Morphometrics of type specimens of *C. jamestyleri*. Values for lines two to six expressed as % of standard length, and for lines seven to 14 expressed as % of head length.

	Holotype USNM 325810	Range in values	SD	n
1—Standard Length (mm)	83.3	60.4–85.2		4
2—Body Depth	35.3	27.9–35.3	3.83	4
3—Body Width	21.8	21.5–24.0	1.09	4
4—Head Length	39.4	35.8–39.4	1.48	4
5—Tip of snout to Dorsal-fin Origin	74.5	70.7–80.8	4.17	4
6—Tip of Snout to Anal-fin Origin	77.2	76.6–78.6	0.84	4
7—Snout Length	55.5	55.5–63.4	3.29	4
8—Eye Diameter	27.7	20.8–27.7	3.29	4
9—Interorbital Width	27.1	23.9–27.1	1.59	4
10—Caudal Peduncle Depth	32.3	30.1–36.0	2.49	4
11—Dorsal-fin Base Length	13.1	12.7–17.6	2.66	4
12—Anal-fin Base Length	16.2	10.9–16.2	2.38	4
13—Pectoral-fin Length	36.9	32.9–39.9	3.51	3
14—Post-orbital Length of Head	17.4	17.4–24.6	3.26	4

*C. sanctaehelenae*, by the presence of bars on the caudal fin. From the latter, *C. jamestyleri* can be further distinguished by the presence of diagonally oriented lines on the snout, and the presence of two darker longitudinal stripes on the side of its body.

*Description.*—See Table 1 for a summary of meristic data and Table 5 for morphometrics. Dorsal-fin rays 9; anal-fin rays 9; pectoral-fin rays 15–16 (16).

In alcohol (Fig. 1D), head and body tan, darker on dorsum and flank, paler ventrally, especially below horizontal through pectoral-fin base. Body highly striped and spotted, with roundish spots on the dorsum, flank and ventral region and irregular diagonal lines ventral to pectoral-fin base. Horizontally elongate lines on side of head and snout. Area between orbits and upper portion of snout devoid of spots and stripes. Two prominent dark longitudinal stripes on body, uppermost extending from dorsal caudal peduncle margin to dorsal end of pectoral-fin base, lower stripe extending from ventral caudal peduncle margin to pectoral-fin base. Longitudinal stripes not solid, with numerous embedded irregular dark spots. Snout tan with three to five conspicuous horizontally and irregularly oriented lines extending posteriorly to vertical through the nostril. All specimens exam-

ined with obvious dark brown lines radiating from lower portion of eye, sometimes plus one or two similar stripes below eye. Dorsal fin transparent with irregular black spot on the anterior portion of its base, this spot not extending onto trunk. Anal and pectoral fins transparent. Caudal fin hyaline, without pigment on its margins, but with numerous vertically oriented irregular brownish stripes. No information available on life colors.

*Remarks and distribution.*—*Canthigaster jamestyleri* seems to be restricted to deep (>90 m), most probably hard bottom, formations off the southeastern coast of North America. We examined material from South Carolina (see material examined), and Luis A. Rocha (pers. comm.) informs us of a recent collection of this species from off the Gulf coast of USA, also in waters deeper than 100 m. Specimens observed during submersible dives off North Carolina by Parker & Ross (1986) probably represent additional records of this species. Additional collections from deep reefs may show that this species has a broader distribution than presently known.

The pigment pattern of *Canthigaster jamestyleri* resembles that of the Indo Pacific species *C. rivulata*, with which it shares the presence of two longitudinal dark stripes on

the flank and numerous lines on the head plus a highly striped body (see Fig. 1D of the present paper and fig. 5A of Allen & Randall 1977). However, *C. jamestyleri* is distinguished from *C. rivulata* in having a spotted instead of reticulated dorsum, as well as in having well-developed transverse dark stripes on the snout, overlying a background devoid of spots.

*Etymology*.—This species is named for James C. Tyler for his help and advice to the authors, as well as for his many contributions to the study of the systematics of plectognath fishes.

*Canthigaster sanctaehelena* (Günther, 1870)

Fig. 1E, Tables 1, 6

*Tetrodon sancta helenae* Günther, 1870:304 (type locality St. Helena Island).—Mellis, 1875:112 (listed from St. Helena Island).—Fowler, 1936:1114 (listed from St. Helena Island).—Cadenat & Marchal, 1963:1304 (listed from St. Helena Island).

*Canthigaster sanctaehelena*.—Fraser-Burner, 1943:15 (listed).—Tortonese, 1973:647 (listed from Ascension and St. Helena Islands).—Lubbock 1980:298 (listed from Ascension Island).—Tortonese, 1984:1341 (diagnosis, key, distribution).—Edwards & Glass, 1987:669 (diagnosis, description).—Debelius, 1997:293 (brief description, color photograph).

*Canthigaster rostrata* (not of Bloch, 1786).—Le Danois, 1961:316 (synonymized *C. sanctaehelena* with *C. rostrata* Bloch).

*Syntypes* (2 specimens).—BMNH 1868.6.15.22–24 (95.2–88.8 mm SL) St. Helena Island (15°58'S, 05°43'W).

*Additional material examined* (7 specimens, 66.2–88.3 mm SL, all from St. Helena Island).—USNM 267871 (1, 77 mm SL), 15–20 m, A. Edwards & C. Glass, 18 Jun 1983; BMNH 1984.7.16.281 (1, 78.2 mm SL), A. Edwards, 18 Jul 1983; BMNH 1979.1.5.242 (1, 66.2 mm SL); BMNH

1979.1.5.243 (1, 38.2 mm SL); BMNH 1965.12.1.161 (1, 82.7 mm SL), BMNH 1965.12.1.162 (1, 88.3 mm SL), BMNH 1965.12.1.163 (1, 83.8 mm SL), A. Lovridge, 22 Jan 1965.

*Diagnosis*.—*Canthigaster sanctaehelena* (Günther, 1870) is distinguished from all Atlantic congeners, with the exception of *C. supramacula*, by the absence of longitudinal dark stripes on the side of the body and/or the caudal peduncle. *Canthigaster sanctaehelena* can be readily distinguished from *C. supramacula* by the absence of a conspicuous dark spot on the dorsum.

*Description*.—See Table 1 for a summary of meristic data and Table 6 for morphometrics. Dorsal-fin rays 9–10 (9); anal-fin rays 9 (9); pectoral-fin rays 15–16 (15).

In alcohol (Fig. 1E), head and body predominantly tan, darker onto dorsum, becoming paler ventrally, especially below horizontal through ventral margin of orbit. Body with numerous small dark spots. Caudal fin translucent with dark ventral and dorsal margins and bearing numerous dark bars, sometimes even on its posterior margin. Snout tan, without bars. Dorsal, pectoral and anal fins transparent. Series of short and approximately horizontal dark stripes radiating from eye.

In life, upper portion of body light brown, becoming paler ventrally. Body spots grayish blue to bright blue. Iris bright yellow. Pectoral, dorsal, and anal fins hyaline. Caudal fin dark brown with numerous conspicuous bright blue spots.

*Remarks and distribution*.—Le Danois (1961), in recognizing only four *Canthigaster* species worldwide, was the only author to consider *C. sanctaehelena* as a junior synonym of *C. rostrata*, in a clear misinterpretation of the variation and distribution of pigment characters. *Canthigaster sanctaehelena*, commonly known as the St. Helena Puffer (Debelius 1992) or bottlefish (Edwards & Glass 1987), is known only from St. Helena and Ascension islands (Lubbock 1981, Edwards & Glass 1987), on the Mid-Atlantic Ridge. Recorded

Table 6.—Morphometrics of *C. sanctaehelenae* specimens (including the syntypes). Values for lines two to six expressed as % of standard length, and for lines seven to 14 as % of head length.

	Range	SD	n
1—Standard Length (mm)	38.2–95.2		9
2—Body Depth	35.3–38.5	1.00	9
3—Body Width	58.0	—	1
4—Head Length	41.3	—	1
5—Tip of Snout to Dorsal-fin Origin	72.8–77.9	1.66	9
6—Tip of Snout to Anal-fin Origin	78.5–84.9	2.27	9
7—Snout Length	51.6	—	1
8—Eye Diameter	21.7	—	1
9—Interorbital Width	24.5	—	1
10—Caudal Peduncle Depth	39.9	—	1
11—Dorsal-fin Base Length	19.5	—	1
12—Anal-fin Base Length	17.3	—	1
13—Pectoral-fin Length	30.8	—	1
14—Post-orbital Length of Head	24.8	—	1

depths range from tidepools to 45 m (Edwards & Glass, 1987). Debelius (1997: 293) provided a fine underwater color photograph of this species.

The general pigment pattern of *C. sanctaehelenae* resembles those of the Indo Pacific species *C. rapaensis* Allen & Randall, 1977 and *C. callisterna* (Ogilby, 1889), with which it shares the presence of a darkish spotted body over a pale background (compare Fig. 1E of the present paper with Figs. 4C and 5B of Allen & Randall 1977). However, *C. sanctaehelenae* is easily distinguished from these two Indo-Pacific species in lacking a diffuse blackish patch, or imperfect ocellus, at the base of the dorsal fin.

*Canthigaster supramacula*, new species  
Fig. 1F, Table 1

*Canthigaster rostrata* (not of Bloch, 1786).—Tortonese, 1973: 647 in part (listed from eastern Atlantic).—Tortonese, 1984:1341 in part (key, listed from eastern Atlantic).—Debelius 1997: 294 in part (recorded from west Africa).

*Holotype*.—ANSP 102312 (1, 40.1 mm SL), off Abidjan (~05°N, 04°W), Ivory Coast, 15 Jun 1963.

*Additional material examined* (1 specimen, poorly preserved).—BMNH 1977.3.21.194

(1, 39.0 mm SL), off Jema (~06°N, 01°W), Ghana, 25 m, R. Lubbock, 21 Mar 1977.

*Diagnosis*.—*Canthigaster supramacula* is readily distinguished from all Atlantic congeners by the presence of a conspicuous dark spot resembling an ocellus on the dorsal portion of the trunk anteroventral to origin of dorsal fin, the dorsal portion of this spot extending to the dorsal-fin origin. The spot is about 1.5 times larger than eye in the holotype and about the same size as the eye in the other specimen examined. In addition, *C. supramacula* lacks conspicuous dark stripes along the sides of the body, bearing only two to four irregular lines that extend from the caudal peduncle to about a vertical through the dorsal-fin base.

*Description*.—Dorsal rays 10; anal rays 9; pectoral rays 16 (Table 1). Body depth 37.7% SL, body width 23.4% SL, head length 39.2% SL, tip of snout to dorsal-fin origin 71.6% SL, tip of snout to anal-fin origin 75.8% SL, snout length 56.1% HL, eye diameter 26.8% HL, least interorbital width 28.0% HL, least depth of caudal peduncle 31.2% HL, length of dorsal-fin base 19.1% HL, length of anal-fin base 17.2% HL, pectoral-fin length 42.0% HL, postorbital length of head 21.0% HL.

In alcohol (Fig. 1F), head and body tan, darker on dorsum, becoming paler ventral-

ly, especially below horizontal through pectoral-fin base. Body with few and sparse spots, two to four thick and irregular lines extending from caudal peduncle to vertical through dorsal-fin base. A conspicuous spot situated slightly anterior to and below dorsal-fin base, lower portion reaching horizontal through the dorsal margin of pupil, posterior portion reaching vertical through dorsal-fin origin. Spot surrounded by one to two roundish dark lines. Dorsal, pectoral, and anal fins hyaline. Caudal fin hyaline with dark margins not extending onto body. Prominent dark stripes radiating from eye, extending posteriorly to about the vertical through pectoral-fin base and anteriorly onto snout, the longest meeting the vertical lines at anterior end of snout. No information available on life colors.

*Remarks and distribution.*—*Canthigaster supramacula* is known only from off the Ivory Coast and Ghana, West Africa, along a coastal range of less than 600 km. It is the only *Canthigaster* species recorded from coastal West African reefs. Additional sampling along tropical West African coasts will likely reveal a broader distribution for this species. Pigment pattern of *C. supramacula* does not resemble that of any Indo-Pacific species.

*Etymology.*—The specific name, *supramacula*, refers to the conspicuous ocellus-like spot on the side of the body, slightly ventral and anterior to the dorsal-fin base. The common name of West African sharpnose-puffer is proposed.

#### Comparative Material Examined

*Canthigaster amboinensis*, USNM 33739 8 (1, 46.8 mm SL, Vanuatu); *C. bennetti*, USNM (1, 69.3 mm, Vanuatu); *C. compressa*, USNM 345614 (1 of 19, 46.1 mm SL, Philippines); *C. cyanetron*, USNM 287594 (1, paratype, Easter Island, 54 mm SL); *C. epilampra*, USNM 259463 (1, 57.1 mm SL, Fiji); *C. inframacula*, USNM 208483 (1, holotype, 75.5 mm SL, Hawaii); *C. jactator*, USNM 167350 (1, 55.4 mm SL, Gil-

berts Islands); *C. janthinoptera*, USNM 347476 (1, 45.3 mm SL, Vanuatu); *C. leoparda*, USNM 287042 (1, 37.8 mm SL, Fiji); *C. margaritatus*, USNM 191686 (3, 51.8–53.7 mm SL, Red Sea); *C. marquesensis*, USNM 208267 (1, 68.5 mm SL, Marquesas); *C. natalensis*, USNM 345780 (1, 39.2 mm SL, Mauritius); *C. ocellicineta*, USNM 348477 (2, 22.6–40.7 mm SL, Vanuatu); *C. punctatissima* USNM 321847 (4, 45.6–49.2 mm SL, Pacific Panama).

#### Key to the Atlantic Ocean species of *Canthigaster*

1. A prominent dark spot on dorsum slightly anterior and ventral to dorsal-fin origin, this spot larger than eye and surrounded by irregular curved lines, resembling an ocellus . . . . . *C. supramacula*, n. sp. (tropical West Africa, off Ghana and Ivory Coast)
- No prominent spot on dorsum, although a darker diffuse area slightly anterior and ventral to dorsal-fin origin may be present, but this darker area inconspicuous, smaller than eye, and never surrounded by lines . . . . . ×2
2. Caudal fin with conspicuous superior and inferior dark margins, at least along proximal one-third, with or without vertically or nearly vertically oriented dark bars; no black spot on dorsal-fin base . . . . . ×3
- Caudal fin without distinctive superior and inferior dark margins, bearing vertically or nearly vertically oriented dark bars; a small irregular black spot on dorsal-fin base . . . . . *C. jamestyleri*, n. sp. (deep reefs off South Carolina, USA, and the Gulf of Mexico)
3. No vertically oriented bars on caudal fin; snout with vertically oriented bars; side of body or caudal peduncle, or both, with horizontal dark stripes . . . . . ×4
- Vertical bars present on caudal fin; no vertically oriented bars on snout; no horizontal dark stripes on side of body and caudal peduncle . . . . . *C. sanctaehelenae* (Ascension and St. Helena Islands)
4. One or two conspicuous horizontal dark stripes on flank, caudal peduncle, or

- both; lower one, when present, extending from caudal-fin margin to anal-fin base . . . . . ×5
- Two conspicuous horizontal dark stripes on flank, lower one composed of irregular bars and stripes and extending from inferior margin of caudal peduncle to pectoral-fin base . . . . . *C. figueiredoi*, n. sp. (east coast of South America, including the southern Caribbean)
- 5. Upper horizontal stripe extending from superior margin of caudal fin to pectoral-fin base; dorsum with numerous spots . . . . . *C. capistrata* (Macaronesia and Mediterranean)
- Upper horizontal stripe extending maximally from superior margin of caudal fin to vertical through origin of dorsal fin, generally restricted to caudal peduncle; dorsum without spots . . . . . *C. rostrata* (shallow reefs off southern USA, Gulf of Mexico, Bermuda and the Caribbean)

Discussion

In the western Atlantic there are at least three sharpnose puffer species: *C. rostrata*, occurring from South Carolina and Bermuda throughout the Caribbean, *C. figueiredoi*, occurring from Tobago and Venezuela south to southern Brazil, and *C. james-tyleri*, a deep-dwelling species known from deep reefs off South Carolina and the coast of the Gulf of Mexico. Throughout their ranges, only *C. rostrata* and *C. figueiredoi* occur syntopically, in the southern Caribbean, a peripheral area in the geographic ranges of both species.

In the eastern Atlantic, at least two sharpnose puffers species occur: *C. capistrata*, distributed in the Macaronesian Region (sensu Stock 1995, Beyhl et al. 1995) and sometimes straying into the Mediterranean (Garcia 1999), and *C. supramacula*, apparently restricted to coastal regions off tropical West Africa. The sixth Atlantic species, *C. sanctaehelenae*, is restricted to the mid-Atlantic islands of Ascension and St. Helena, contributing to the high endemism levels recorded for these areas (e.g., Lubbock 1980, Edwards & Glass 1987). No

sharpnose puffers are known from St Paul’s Rocks (Lubbock and Edwards 1981), the most probable “stepping stone” for East to West dispersion of Pan-Atlantic reef fishes (see Heiser et al. 2000).

With the exception of *C. sanctaehelenae*, all Atlantic sharpnose pufferfish species recognized herein have been misidentified as the northwestern Atlantic species *C. rostrata*. The widespread assumption of a single widely distributed species of *Canthigaster* occurring in the Atlantic (e.g., Nelson 1994) probably precluded previous critical examination of its status. However, recent recognition of a number of shallow-water reef fishes endemic to the southwestern Atlantic (e.g., Moura 1995, Sazima et al. 1997, 1998, Rocha & Rosa 1999, Moura et al. 1999, 2001, Heiser et al. 2001) led us to investigate the status of the putative *C. rostrata* from the southwestern Atlantic. Our recognition of a distinct and undescribed species from that area led us to the study of comparative material from throughout the entire geographic range of “*C. rostrata*”, leading to the recognition of six *Canthigaster* species in the Atlantic Ocean.

Considering the obvious morphological and/or pigment pattern differences occurring among Atlantic sharpnose puffers, as well as among other complexes of species that until recently were considered to contain single widespread species (e.g., Heiser et al. 2000, Moura et al. 2001), it would not be surprising if critical taxonomic appraisal would lead to the recognition of a number of additional species in what are now considered to be widely distributed Atlantic reef species (e.g., the multi-patterned pomacentrid *Chromis multilineata*, the labrisomid *Labrisomus nuchipinnis*). Such wide-ranging reef and shore fish “species” must be more critically examined, using not only traditional taxonomic features, but also additional characters derived from underwater observations such as live coloration, life history and behavior, as well as data from molecular studies (see Gill 1997, Gill

& Kemp 2001, Bowen et al. 2001, Muss et al. 2001).

The phylogenetic interrelationships of *Canthigaster* species are unknown, precluding the proposal of a hypothesis regarding the historical biogeography of the group. The assumption that the Caribbean and Brazil are sister areas (Floeter & Gasparini 1999) must be confirmed with congruent cladograms for various unrelated reef fish lineages before it can become a meaningful and falsifiable scientific hypothesis (Humphries & Parenti 1986).

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