The Indo-Pacific tetraodontid fish *Canthigaster coronata*, a complex of three species

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Abstract. The tetraodontid fish *Canthigaster coronata* (Vaillant & Sauvage), formerly with a distribution of Hawaii and Tonga to the east coast of Africa and the Red Sea, is divided into three species: *C. coronata*, endemic to the Hawaiian Islands, *C. axiologa* Whitley from the rest of the Pacific west of the Hawaiian Islands, and *C. cyanospilota*, sp. nov. from the Indian Ocean and Red Sea (type locality, Gulf of Aqaba). In addition to being distinguishable at the control region of their mitochondrial DNA, the three species differ in the following characters: *C. coronata* is distinct in having numerous small yellow spots, but no blue markings (except around the eye), modally 17 pectoral rays (16 in *C. axiologa* from the North Pacific), the origin of the anal fin below or anterior to the rear base of the dorsal fin (below or posterior for the other two species), and a broader gill opening, 3.7-4.75 in head length, compared to 4.8-5.55 for *C. axiologa* and 5.4-6.5 for *C. cyanospilota*. *Canthigaster axiologa* ranges from Japan to New South Wales, east to the Marshall Islands and Tonga. It has bright blue spots associated with yellow spots or lines along the edges of the saddle-like brown bars, as well as elsewhere on the body and head, modally 16 pectoral rays in the North Pacific, and modally 17 in the South Pacific, and a broad interorbital space (3.75-4.4 in head length). *Canthigaster cyanospilota* has numerous small bright blue spots and lines, but no bright yellow spots, the dark saddle-like bars do not reach below the level of the upper end of the gill opening (extend below in *C. axiologa* and *C. coronata*), and a narrow interorbital space (4.25-4.85 in head length). Divergence of the northern Red Sea population of *C. cyanospilota* from that of the Indian Ocean is discussed.

Keywords: taxonomy, Tetraodontidae, *Canthigaster*, new species, Indian Ocean

INTRODUCTION

The 33 species of the fish genus *Canthigaster* Swainston, popularly known as tobies or sharpnose puffers, have been classified by some authors, such as Tyler (1967), as a separate family, the Canthigasteridae, but by most authors as a subfamily of the Tetraodontidae. The study of the order Tetraodontiformes by Tyler (1980) and Alfaro et al. (2007) clearly shows that the genus should not be regarded as a distinct family.

The genus *Canthigaster* is differentiated from the remaining genera of the Tetraodontidae by a laterally compressed body, elongate pointed snout, erectile ridge of skin middorsally and midventrally, small gill opening, inconspicuous lateral line, 17 vertebrae, and small size. The bright colour patterns of the species probably serve to advertise their repelling skin toxin. The first author tried to feed a small one to a snapper (*Lutjanus kasmira*) at the MidPacific Research Laboratory at Enewetak Atoll in the Marshall Islands. It was seized by the snapper and quickly ejected.

Tyler (1967) wrote that the species of *Canthigaster* are the most uniform of the tetraodontiform fishes. He added, "Proportional measurements of the species tend to be the same" and "with few exceptions, the species are distinguished mostly on the basis of colour pattern." He noted that previous authors failed to distinguish *C. coronata* (Vaillant & Sauvage) from *C. valentini* (Bleeker), both with saddle-like black bars on the body. He provided a detailed account to separate the two.

Allen & Randall (1977) reviewed the genus for the Indo-Pacific region, recognizing 22 species. Since their review, *C. flavoreticulata* Matsuura (1986) was described from the Tonga Submarine Ridge in 98–111 m, *C. cyanetron* Randall & Cea Egaña (1989) from Easter Island, *C. punctata* Matsuura (1992) from the Mascarene Submarine Ridge in 92 m, and *C. papua* (Bleeker) was

removed from the synonymy of *C. solandri* (Richardson) (Anderson et al., 1998).

Allen & Randall gave the distribution of *Canthigaster coronata* as the Hawaiian Islands (type locality) to the east coast of Africa and the Red Sea; in the western Pacific from Japan to New South Wales. We have noticed that the species is different in colour in the Hawaiian Islands from elsewhere in the Pacific, and even more different in the Indian Ocean, including the Red Sea. In the present paper we restrict the name *C. coronata* to the population in the Hawaiian Islands and Johnston Island, *C. axiologa* Whitley, type locality Great Barrier Reef, for the species in the North Pacific west of Hawaii and in the South Pacific from Tonga to the west, and we describe the Red Sea and Indian Ocean species as new.

At first, we experienced difficulty finding morphological differences to distinguish the species of these three areas of the Indo-Pacific, so we obtained tissue samples and tried to differentiate them by DNA. The mitochondrial DNA differences were not very large, but support significant phylogenetic breaks among species. On renewing our efforts to find something morphologically diagnostic to correlate with colour and DNA, we were able to distinguish the Hawaiian species by modal differences in pectoral and anal ray counts (Table 1) and in a few measurements (Table 2).

MATERIALS AND METHODS

Specimens of the new species are deposited in the Academy of Natural Sciences of Philadelphia (ANSP); the Natural History Museum, London (BMNH); Bernice P. Bishop Museum, Honolulu (BPBM); Hebrew University, Jerusalem (HUJ); National Museum of Nature and Science, Tokyo (NSMT); South African Institute for Aquatic Biodiversity, Grahamstown (SAIAB); and the National Museum of Natural History, Washington, D.C. (USNM). Other specimens for this study have been sent on loan from the Australian Museum, Sydney (AMS); Academy of Natural Sciences of Philadelphia (ANSP); California Academy of Sciences, San Francisco (CAS, SU); the University of Guam, Mangilao (UG); and the Royal Ontario Museum, Toronto (ROM).

The length of specimens is given as standard length (SL), measured from the median anterior end of the upper dental plate to the base of the caudal fin (posterior end of the hypural plate); body depth is the slightly oblique measurement from the origin of the dorsal fin to the origin of the anal fin (maximum body depth is too variable in species of *Canthigaster*); body width is measured at the base of the pectoral fins; head length is taken from the front of the upper dental plate to the dorsal end of the gill opening; orbit diameter is the greatest diameter of the unpigmented skin over the eye, and interorbital width the least bony width; snout length is measured from the upper dental plate to the nearest unpigmented cutaneous edge of the eye; length of the gill opening is taken by inserting divider tips and spreading for the maximum firm edges; caudal-peduncle depth is the least depth, and caudal-peduncle length the horizontal distance between verticals at the rear base of the anal fin and the caudal-fin base; lengths of fins are the length of the longest rays.

Morphometric data were taken for specimens 47 mm or more in standard length. The measurements for the new species are presented in Table 3 as percentages of the standard length; in the descriptions as proportional measurements of the standard length or head length, rounded to the nearest 0.5. Some specimens are too misshapen for measurements but were used for counts.

The counts of pectoral rays include the short uppermost ray.

Meristic and morphometric data in parentheses refer to paratypes.

Genomic DNA was extracted from fin clips. In order to address differentiation at the species level, two new primers (CANT-CR-F: 5′ CCA AAG CCA GCA TTC TCA AT 3′; and CANT-CR-R: 5′ CTC GGG GGT TTC CTG TTT C 3′) were used to amplify the mitochondrial DNA (mtDNA) control region of *Canthigaster*. These primers were constructed based on the alignment of the entire mitochondrial DNA sequences of *C. coronata* and *C. rivulata* (Genbank accession numbers AP006743 and AP006744 respectively). PCR conditions and sequencing protocols are described in detail by Rocha (2004).

Canthigaster coronata (Vaillant & Sauvage)

(Plate 1A, B; Tables 1, 2)

Tetraodon (Anosmius) coronatus Vaillant & Sauvage, 1875: 286 (type locality, Hawaiian Islands).
Canthigaster cinctus (non Solander) Jordan & Evermann, 1905: 433, fig. 189 (type locality, Hawaiian Islands).

DIAGNOSIS. Dorsal rays 9–11 (usually 10, rarely 9); anal rays 9 or 10 (usually 10); pectoral rays 15–18 (usually 17); gill rakers 7–9; body depth between origins of dorsal and anal fins 2.8–3.25 in SL; head length 2.3–2.55 in SL; interorbital width 3.9–4.45 in head length; gill opening 3.7–4.75 in head length; origin of anal fin below or anterior to rear base of dorsal fin, the preanal length 1.35–1.4 in SL; longest dorsal ray 2.2–2.5 in head length; colour in alcohol pale grey to pale tan with three triangular dark brown saddle-like bars dorsally on body, progressively more oblique posteriorly, the first extending narrowly to ventral edge of gill opening, the second to level of lower edge of pectoral-fin base and enclosing base of dorsal fin posteriorly, and the last ending at upper base of caudal fin; a dark brown band across posterior interorbital and anterior occiput; a dark brown spot below base of pectoral fin; many small pale spots (most about half pupil diameter) on head and body, faint or absent on paler parts of body but very

evident on edges, within dark bars, and on head where ground colour darker; narrow pale bands and spots around eye; lips pale, encircled with a narrow dusky band; a thin dark brown line midventrally on abdomen and chest present or absent (may be broken to long segments); fins pale, the upper and lower margins of caudal fin with a broad brown band, darker at base; colour when fresh as in Plate 1A; colour in life shown in Plate 1B (noteworthy are the many small yellow spots, and the lack of blue spots—blue only between yellow markings around eye). Largest specimen examined, 111 mm SL.

Remarks. Vaillant & Sauvage (1875) described *Canthigaster coronata* from the Hawaiian Islands in a brief but diagnostic description. They did not list their material, but Tyler (1967: 63) examined the holotype, MNHN 9006, 103.2 mm SL.

Jordan & Evermann (1905: 433) believed that *Tetrodon cinctus* Solander in Richardson (1845: 125) is an older available name for the species and used it in their volume on Hawaiian fishes. However, the name *cinctus* was merely mentioned in Richardson's description of *Canthigaster solandri* (then in *Tetrodon*) as seen on a drawing by Sydney Parkinson of a species from Tahiti obtained during Captain Cook's first circumnavigation. Since the species was not described by Richardson, Jordan & Evermann became the authors of the name *cinctus* for a Hawaiian species. Tyler (1967: 61) explained that Günther (1910: 466) saw the drawing by Parkinson and realized it was the young of the puffer *Arothron stellatus*. Jordan & Seale (1906: 373) used the name *Canthigaster cinctus* in their volume, *The Fishes of Samoa*, and placed *Tropidichthys valentini* Bleeker and *Tetraodon coronatus* Vaillant & Sauvage in the synonymy of *C. cinctus*. Tyler showed that *C. valentini* is a valid species similar to *C. coronata* and that *C. cinctus* Jordan & Evermann is a synonym of *C. coronata*. He listed no specimens of *C. coronata* from the South Pacific but examined specimens of *C. valentini* east to the Society Islands and Tuamotu Archipelago.

We first suspected that *Canthigaster coronata* was endemic to the Hawaiian Islands when we noticed that it lacks blue spots on the body, including those along the edge of the dark saddles, as seen on fish identified as *C. coronata* elsewhere; also there is no solid, curved orange-yellow stripe on the lower side of the head. We then found a strong modal count of 17 pectoral rays, compared to 16 in specimens from the North Pacific to the west of Hawai'i, and a higher percentage of specimens with 10 anal rays (see Table 1). The modal count of 17 pectoral rays in our few specimens from the southwest Pacific is an independent divergence (see account of *C. axiologa* below). We made 12 morphometric measurements of our specimens as percentages of the SL (Table 2). The gill opening is longer in *C. coronata* (9.2–10.7% SL compared to 6.4–8.6% SL), the dorsal fin is higher (17.0–18.8% SL, compared to 14.0–17.6%), and the preanal length is shorter on the average, 70.6–74.8% SL, compared to 72.5–78.8% SL). This was evident when we noticed that the origin of the anal fin is directly below or anterior to the rear base of the dorsal fin (below or posterior on the other two species).

No specimens of *C. coronata* have been collected at Johnston Island, an outlier of the Hawaiian Archipelago, but the species was reported as a sight record for the island by Kosaki et al. (1991: 196), and it was illustrated by Lobel (2003: 120, middle fig.) from an underwater photograph.

Canthigaster coronata generally occurs at depths of 12 m or more; however, it has been collected in as little as 6 m. When shallow, it is usually found in lagoons or bays. The usual habitat is sand or sand and rubble bottom or algal flats, often in the vicinity of coral reefs. Gilbert (1905: 626) listed specimens from trawl stations in 79–165 m off Moloka'i, Maui, and Kaua'i. Struhsaker (1973: 141) obtained 7–48 individuals per station in three trawl hauls on the Penguin Bank in the

Table 1. Fin-ray counts of species of the *Canthigaster coronata* complex.

JER *Canthigaster* Table 1

	Dorsal rays			Anal rays			Pectoral rays[1]		
	9	10	11	8	9	10	15	16	17
C. coronata (Hawaiian Islands)	1	33	3		23	14		9	61
C. axoliogia (NW Pacific)[2]	4	23		2	25		11	32	11
C. axoliogia (SW Pacific)[3]		11	1		10	2		6	14
C. cyanospilota (Indian Ocean)[4]		17	1		17	1		13	15
C. cyanospilota (Red Sea)[5]	6	2		1	7		4	12	

Table 2. Range in proportional measurements of the species of the *Canthigaster coronata* complex as percentages of the standard length.

Kaiwi Channel (between O'ahu and Moloka'i). The first author speared nine in a single tank dive for food-habit study off Waimea Bay, O'ahu at a depth 12–15 m. Five individuals of the endemic *Canthigaster jactator* were sighted during the same dive. Allen & Randall (1977: 487) listed the stomach and gut contents of 12 specimens of *C. coronata* from O'ahu as 13% algae and detritus, 11.9% gastropods, 10.0% crabs, 9.7% pelecypods, 8.9% polychaetes, 7.7% sponge, 7.0% sipunculids, 6.7% ophiuroids, 5.9% bryozoans, 4.7% tunicates (mostly didemnids), 3.3% echinoids, 2.4% foraminifera, 1.7% amphipods, 0.7% shrimps, 0.1% isopods, and 6.6% unidentified.

Material examined. **Hawaiian Islands**: O'ahu, BPBM 8497, 73 mm; BPBM 9045, 92 mm; BPBM 11484, 9: 50-85 mm; SAIAB 2374, 3: 81-86 mm. Moloka'i, BPBM 24019, 9: 66-102 mm. Midway, BPBM 35367, 83 mm. Middle Bank (22°44'N, 161°4'W), BPBM 24903, 50 mm; BPBM 24908, 2: 74-85 mm; BPBM 24918, 8: 67–91 mm; BPBM 24928, 69 mm.

Canthigaster axiologa Whitley

(Fig. 1; Plate 1 C–1 H, Plate 2 A, B; Tables 1, 2)

Canthigaster axiologus Whitley, 1931: 333 (type locality, near Capricorn Group, Great Barrier Reef).

DIAGNOSIS. Dorsal rays 9–11 (usually 10, rarely 11); anal rays 9 or 10 (usually 9); pectoral rays 15–18 (modally 16 in the North Pacific and 17 in the South Pacific); gill rakers 7–9; body depth between origins of dorsal and anal fins 3.0–3.3 in SL; head length 2.3–2.5 in SL; interorbital width 3.75–4.4 in head length; gill opening 4.8–5.55 in head length; origin of anal fin below or posterior to rear base of dorsal fin, the preanal length 1.25–1.35 in SL; longest dorsal ray 2.4–2.9 in head length. Colour in alcohol pale grey to pale tan with three saddle-like, dark brown bars on body as described above for *C. coronata*, the edges of bars with close-set, small, pale-edged dark spots or short lines, irregularly alternating with unpigmented pale spots or lines; ventral part of body with or without small pale spots or pale-edged dark spots; a broad dark brown band across posterior interorbital and anterior occiput; a dark brown spot below base of pectoral fin; a narrow curved pale band edged in small dark spots from chin to below gill opening; a pale area around eye with radiating dark brown lines (except adjacent interorbital band); a midventral dark brown line on head and abdomen varying from faint to conspicuous; lips pale, usually rimmed by a dusky band; fins pale grey, the upper and lower edges of caudal fin with or without a broad dark marginal band. Colour when fresh shown in Plate 1 C from Japan and Plate 1 E of a juvenile from Palau with yellow spots within the dark brown bars; colour in life in Plate 1 D and F–H from the Ogasawara Islands, Taiwan, Indonesia, and the Great Barrier Reef. Largest specimen examined, 101 mm SL, from Japan.

REMARKS. McCulloch (1922: 245, Plate 14, fig. 1) identified a specimen of *Canthigaster* 131 mm long from near the Capricorn Group of the southern Great Barrier Reef as *C. cinctus* (Richardson) Jordan & Evermann. Whitley (1931: 333) realized that *C. cinctus* is not a valid name, so he proposed the new name *C. axiologus* for McCulloch's fish (changed to *axiologa* because *Canthigaster* is feminine). The holotype, QM I.3549, is in the Queensland Museum, Brisbane. It now measures 127.5 mm total length and 100 mm SL (Jeffrey W. Johnson, pers. comm.). We reproduce McCulloch's figure here as Fig. 1.

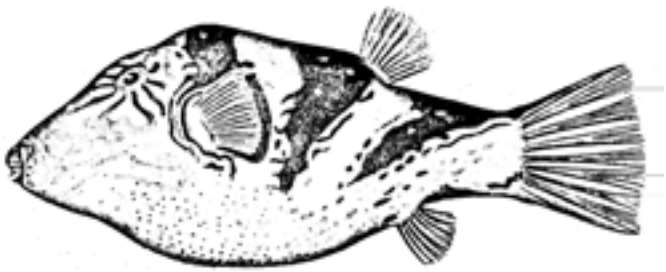

Fig. 1. Holotype of *Canthigaster axiologa* Whitley, QM I.3549, 100 mm (after McCulloch, 1922).

We are applying the name *C. axiologa* to specimens we have examined from the Marshall Islands, Caroline Islands, Mariana Islands, Palau, mainland Japan, Ogasawara Islands, Ryukyu Islands, Taiwan, Macclesfield Bank (South China Sea), Philippines, Vietnam, Great Barrier Reef, New South Wales and Tonga. Allen & Swainson (1988: 156, Fig. 1043) recorded the species for Western Australia from Exmouth Gulf northwards; Kuiter (1992: 276, Fig. C) from Flores, Indonesia, and Laboute & Grandperrin (2000: 470, upper fig.) from New Caledonia, all as *C. coronata*.

Canthigaster axiologa is distinct from *C. coronata* in having a narrower gill opening (7.4–8.5% SL, compared

to 9.2–10.5% for *C. coronota*), a shorter dorsal fin (14.2–17.6 % SL vs. 17.0–18.8%), a longer preanal length (73.8–78.8% SL vs. 71.6–74.7% SL), and in colour, principally in having blue spots or short lines associated with yellow spots or lines along the margins of the dark saddles on the body, scattered small blue spots mixed with yellow spots on the ventral part of the body, especially posteriorly (these spots may be pale), and a distinct curved orange-yellow band bordered by small blue spots on the lower side of the head. In addition, specimens from the North Pacific west of Hawai'i have modally 16 pectoral rays, compared to 17 for *C. coronata*, and 8 or 9 (rarely 8) instead of 9 or 10 anal rays (Table 2).

Individuals of *C. axiologa* from Japan and Taiwan tend to have more small blue spots scattered with the yellow on the ventral half of the head and body, often broadly rimmed by yellow as shown by our Plate 1 G from Taiwan, and more extremely in Shen & Lim (1974: 18, Fig. 2), Masuda et al. (1984: Plate 332, Fig. I), and Masuda & Kobayashi (1994: 426, Fig. 3).

Specimens in the South Pacific have modally 17 pectoral rays, compared to 16 for those from the North Pacific. We could find no morphometric or colour differences to link with the pectoral-ray count. We should add, however, that we have examined only 11 specimens from the South Pacific, all but two less than 53 mm SL. It should also be noted that the colour photograph identified as *Canthigaster coronata* in the book on the fishes of the Great Barrier Reef and Coral Sea (Randall et al., 1990: 476, upper fig.) was taken in Bali (Roger C. Steene, pers. comm.).

Canthigaster axiologa inhabits the same sheltered habitat as *C. coronata*, often on open sand and rubble bottom near reefs. It appears to be far less common than *C. coronata*.

Material examined. **Marshall Islands**: Kwajalein Atoll, BPBM 18436, 50 mm. **Caroline Islands**: Ifalik (Ifaluk) Atoll, CAS 15424, 54 mm. **Mariana Islands**: Guam, UG 6557, 55 mm. **Palau**: Ngeruktabel Island, ROM 79420, 33 mm. **Japan:** Ogasawara Islands, Chichi-jima, NSMT-P 31917, 84 mm. Haha-jima, NSMT-P 32799, 3: 22–101 mm. Izu Islands, Miyake-jima, NSMT-P 22211, 2: 36–48 mm; NSMT-P 22287, 32 mm; NSMT-P 30678, 59 mm. Honshu, Wakayama Prefecture, BPBM 7287, 52 mm. Shizuoka Prefecture, NSMT-P 19081, 2: 41–43 mm. Chiba Prefecture, NSMT-P 60320, 50 mm. Ryukyu Islands, Okinawa, BPBM 19159, 24 mm (bad condition). **Taiwan**: BPBM 23280, 65 mm. **Philippines:** Negros, SU 68574, 2: 76–77 mm. Siquijor, USNM 227245, 2: 67–68 mm. **South China Sea**: Macclesfield Bank, USNM 387502, 107 mm; USNM 387503, 69 mm; USNM 387505, 76 mm; USNM 387508, 84 mm. Vietnam, BPBM 40492, 68 mm. **Australia:** Great Barrier Reef, AMS I.15681-061, 27 mm; AMS I.18268-001, 52 mm; BPBM 40489, 2: 58–67 mm; ROM 38231, 86 mm. New South Wales, AMS I.15573, 37 mm; AMS I.16952-00l, 29 mm; AMS I.19500-001, 47 mm; AMS I.41268-022, 24 mm; AMS I.41273-040, 23 mm; AMS I.41846, 27 mm. **Tonga**: BPBM 37938, 65 mm; USNM 334535, 78 mm.

Canthigaster cyanospilota sp. nov.

(Plate 2 C–H; Tables 1–3)

Canthigaster coronata (non Vaillant & Sauvage) Tyler, 1967: 62, Figs. 1–5 (Seychelles, Gulf of Aqaba, and Somalia).

Holotype: BPBM 13898, 85.0 mm, Red Sea, Gulf of Aqaba, Israel, off the Interuniversity Institute of Eilat, 12 m, spear, J. E. Randall, 7 June 1972.

Paratypes: BMNH 1951.1.16.700, 63.9 mm, Red Sea, Gulf of Aqaba, Jordan, 18 m, fish trap, "Manihine" Expedition, N.B. Marshall, 1949/1950; HUJ 16669, 48.5 mm, Gulf of Aqaba, Israel, Eilat, North Beach, near Jordanian border, coral reef and adjacent sand, 1-4 m, rotenone, E. Clark, 5 September 1960; USNM 191710, 54.5 mm, same data as preceding; USNM 387501, 85.1 mm, northern Gulf of Aqaba, Israel, G. Kissil, 1970; NSMT-P 77636, 41.3 mm, and SAIAB 79818, 82.8 mm, same data as holotype; HUJ 9393, 104.0 mm, Gulf of Aqaba, Israel, Sinai Peninsula, Nuweiba, A. Baranes, 16 October 1976.

Diagnosis. Dorsal rays 9–11 (modally 9 in the Red Sea); anal rays 8–10 (modally 9); pectoral rays 15–17 (rarely 15); gill rakers 9–10; body depth between origins of dorsal and anal fins 3.15–3.6 in SL; head length 2.2–2.5 in SL; interorbital width 4.25–4.85 in head length: gill-opening length 5.4–6.5 in head length; origin of anal fin below of posterior to rear base of dorsal fin, the preanal length 1.25–1.35 in SL; longest dorsal ray 2.6–2.95 in head length; colour in alcohol pale grey to pale tan with three oblique, saddle-like, brown bars on body, not extending below level of upper end of gill opening; a broad dark brown band across posterior interorbital and anterior occiput; dark brown dots and short lines on head and body, including ones radiating from eye and margins of brown saddles (also within saddles on Red Sea specimens); dark lines on snout behind mouth vertical; a dark brown spot below base of pectoral fin; a midventral brown line on head and abdomen; fins pale yellowish. In life the dark dots and lines are bright blue; the caudal fin is conspicuously marked with longitudinal blue lines or rows of small blue spots and short lines; the snout is often green dorsally.

Description. Dorsal rays 9 (six paratypes with 9, and two with 10); anal rays 9 (one of 7 paratypes with 8, the rest with 9); dorsal and anal rays branched, except the first; caudal rays 11, uppermost and lower two unbranched; gill rakers 9 (8–9); vertebrae 17.

Body depth between origins of dorsal and anal fins 3.4 (3.15–3.6) in SL; body moderately compressed, the width 1.4 (1.25–1.45) in depth; head length 2.45 (2.2–2.5) in SL; snout long, 1.45 (1.4–1.7) in head length; dorsal

profile of snout straight to slightly concave; eye small, the diameter 4.55 (3.8–5.75) in head length; interorbital space slightly concave, the least width 4.35 (4.25–4.85) in head length; mouth small, oval, and terminal, exposing about terminal half of upper dental plate; lips fleshy and papillose; gill-opening length 5.4 (5.4–6.5) in head length; caudal-peduncle depth 2.5 (2.5–2.95) in head length; caudal-peduncle length 2.05 (2.0–2.45) in head length.

Predorsal length 1.4 (1.35–1.4) in SL; dorsal-fin base 4.95 (4.65–6.0) in head length; third dorsal ray usually longest, but adjacent rays nearly as long, 2.6 (2.7–2.95) in head length; origin of anal fin below or posterior to rear base of dorsal fin, the preanal length 1.3 (1.25–1.35) in SL; anal-fin base 5.75 (5.95–6.75) in head length; second or third anal rays usually longest, but adjacent rays nearly as long, 3.0 (3.1–3.4) in head length; caudal fin slightly rounded, 3.3 (3.05–3.55) in SL; upper half of pectoral fins slightly rounded, the lower half slightly emarginate; third or fourth pectoral rays usually longest, 2.9 (2.85–3.2) in head length.

Skin with numerous small spinules that are directed posteriorly, each fitting into a longitudinal groove; skin smooth when stroked posteriorly, but spinules apparent when stroked anteriorly; very few spinules on flat ventral part of body between anal and caudal fins (only three found on holotype).

Colour of holotype in alcohol pale tan with three triangular, saddle-like, brown bars on upper two-fifths of body that are progressively more oblique posteriorly, the first bar ending above base of pectoral fin, the second extending slightly more ventral and enclosing base of dorsal fin at its posterior end, and the third bar covering most of space between dorsal and caudal fins, its lower edge nearly horizontal; a transverse brown band across posterior interorbital and anterior occipital; pale space between saddle-like brown spots and transverse brown band varying in width from pupil to eye diameter; a horizontally elongate brown spot below base of pectoral fin; a midventral brown line (on a low ridge in some paratypes) extending forward from origin of anal fin, and dividing to two lines on anterior half of snout that join at base of lower lip (some paratypes with dark line extending to chin, others with line interrupted by vertical brown lines); three dark brown lines extending posteriorly from rear edge of eye, the uppermost linked by a dark brown line over upper edge of eye to a dark brown line extending anteriorly from eye; two dark brown lines directed obliquely anterior from ventral edge of eye; a dark brown line encircling lips except

Table 3. Proportional measurements of the type specimens of *Canthigaster cyanospilota* as percentages of the standard length.

	Holotype	**Paratypes**						
	BPBM 13898	NSMT-P.77636	HUJ 16669	USNM 191710	BMNH 1951.1.16	SAIAB 79818	USNM 387501	HUJ 9393
Standard length (mm)	85.0	41.3	48.5	54.5	63.9	82.8	85.1	104.0
Body depth	29.5	30.5	28.8	30.2	28.9	28.0	31.1	31.7
Body width	21.1	21.7	23.3	23.6	20.9	21.5	22.8	22.1
Head length	40.6	45.1	45.0	45.0	42.2	43.1	40.9	40.3
Snout length	28.4	27.4	26.5	30.3	26.6	29.2	27.3	28.4
Orbit diameter	8.9	11.8	10.3	9.2	9.8	8.6	8.1	7.0
Interorbital width	9.3	9.4	9.5	9.6	9.4	9.5	8.4	9.5
Gill-opening length	7.5	7.3	7.3	6.9	7.8	7.8	7.1	6.8
Caudal-peduncle depth	16.2	15.2	16.2	16.7	15.2	16.3	16.5	15.4
Caudal-peduncle length	19.8	20.6	19.3	21.0	17.7	17.6	20.3	19.4
Predorsal length	71.8	72.4	71.8	73.4	73.7	73.2	72.2	72.5
Preanal length	76.0	78.5	74.0	75.2	75.0	77.2	74.3	75.2
Dorsal-fin base	8.2	8.9	8.1	7.6	8.0	7.2	8.8	7.0
Dorsal-fin length	15.5	16.8	15.3	16.0	14.9	14.5	15.2	14.1
Anal-fin base	7.1	7.2	7.1	7.3	7.2	6.7	6.8	6.0
Anal-fin length	13.5	14.5	13.5	14.1	13.1	13.4	13.1	11.8
Caudal-fin length	30.4	32.6	30.7	31.8	29.1	32.0	31.8	28.1
Pectoral-fin length	14.0	14.6	14.3	14.4	14.0	13.9	14.3	12.6

dorsally, with parallel shorter lines behind; many small dark brown spots and short lines on head and body, including within and along edges of dark saddles; fins pale yellowish; a hemispherical brown spot centred ventrally on caudal-fin base; upper caudal-fin base with posterior end of third saddle-like brown bar.

Colour of holotype when fresh shown in plate 2 C. Plates 2 D and 2 E are underwater photographs of individuals from the Gulf of Aqaba, the type locality. The small dark brown spots and short lines of preserved specimens are bright blue in life, and there are no yellow spots. The spaces between the blue lines radiating from the eye on some individuals are yellow, and the brown saddle-like bars may be yellowish along the edges.

Etymology. We name this species *cyanospilota* from the Greek meaning blue-spotted, in reference to the numerous small bright blue markings.

Remarks. We have long known that *Canthigaster coronata* in the Indian Ocean is different in colour from the form in the Pacific—most obviously the many blue markings and lack of yellow spots. In a book on the fishes of the Maldives, Kuiter (1998: 243) wrote, "Indian Ocean and Pacific populations slightly different and both forms occur in Bali, Indonesia." Preserved specimens can be distinguished by the blue markings that persist as dark brown dots and lines. Also, the dark saddle-like bars do not extend as far ventrally on Indian Ocean and Red Sea specimens. As mentioned, initial efforts to find some morphological or DNA difference to correlate with the colour were not successful. We finally determined that the bony interorbital space is narrower in the Indian Ocean species than in *C. axiologa* of the western Pacific, 8.5–9.6% SL, compared to 9.6–11.2% for *C. axiologa*. This is the measurement that can be taken with greatest accuracy in the species of *Canthigaster*. We are now confident to describe the Indian Ocean fish as the new species *C. cyanospilota*.

We noticed from our underwater photographs that Red Sea individuals of *Canthigaster cyanospilota* have blue markings within the dark saddle-like bars, whereas those from the east coast of Africa and islands of the Indian Ocean (Plate 2 F–H) do not, at least as adults, and Red Sea fish tend to have more blue lines than small blue spots on the body and caudal fin than in the Indian Ocean. Also, the Red Sea specimens have modally one fewer dorsal rays than the Indian Ocean specimens and fewer average number of pectoral rays (see Table 1). We have only eight specimens from the Red Sea, all from the Gulf of Aqaba. We found no obvious differences in morphometrics, so these specimens are included with those from the Indian Ocean in Table 2. The seven specimens we have from the Somali coast of the Gulf of Aden all have 10 dorsal rays like specimens from the rest of the Indian Ocean, but all have small dark brown spots within their brown saddle-like bars, although fewer than specimens from the Gulf of Aqaba (one had only a single small spot, and another only three). Therefore, the Gulf of Aden specimens appear to be intermediate to the Gulf of Aqaba specimens and those in the rest of the Indian Ocean. Although we regard all as *C. cyanospilota*, we have designated only the Gulf of Aqaba specimens as type material, and list the Indian Ocean specimens below as non-types.

Colour photographs of *C. cyanospilota* have been published (as *C. coronata*) by Randall (1983: 175, upper fig., from the Red Sea); Smith & Heemstra (1986: 899, plate 140, Fig. 268.11, from Mauritius); Allen & Steene (1987: plate 134, Fig. 4, from Mauritius); Randall & Anderson (1993: 44, Plate 8, Fig. H, from the Maldive Islands); Kuiter & Tonozuka (2001: 838, Figs. D and E, from Java); and Lieske & Myers (2004: 221, lower fig., from the Gulf of Aqaba).

Genetic Comparisons. In order to determine if there were any genetic differences among the three species, a 678 base-pair mitochondrial DNA fragment of the control region was sequenced for two individuals from Oahu, one from Australia (Great Barrier Reef) and two from Réunion. In addition, the control region sequences of individuals of *C. axiologa* and of *C. rivulata* from Japan were obtained from Genbank (accession numbers AP006743 and AP006744) for comparative purposes.

Even though the genetic difference in the control region was small, it was well supported in a

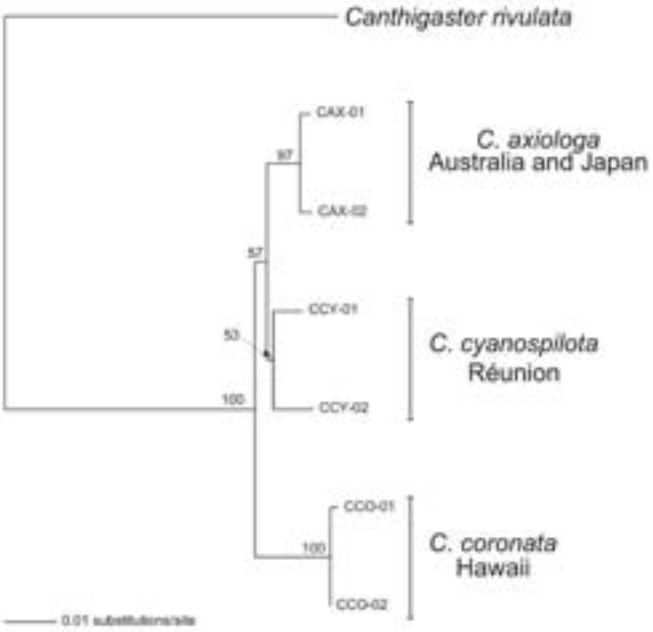

Fig. 2. Phylogenetic tree of relationships among *Canthigaster* species constructed using the minimum evolution (distance) criterion; maximum parsimony and maximum likelihood analyses resulted in identical tree topology. Support for the resulting tree was evaluated using 500 bootstrap replicates with the software PAUP* version 4.0b10 (D. L. Swofford, Sinauer, Sunderland, MA, 2002, unpubl.) and is shown as percentages above branches.

phylogenetic analysis (Fig. 2), reinforcing the validity of the species. As pointed out by Rocha et al. (2007), species start to differentiate in morphology and colour before their neutral genes start to diverge. The pygmy angelfishes of the genus *Centropyge* in the Atlantic are a classic example. The three recognized species there, *C. argi* (Bloch), *C. aurantonotus* Burgess, and *C. resplendens* Lubbock & Sankey, maintain color differences despite no genetic difference on the same DNA region analysed in this study and some range overlap in the southern Caribbean (Bowen et al. 2006). The pattern of slow mtDNA evolution relative to colour evolution is also evident in another pair of closely related species of *Canthigaster*. Alfaro et al. (2007) detected almost no difference between the Hawaiian *C. jactator* (Jenkins) and the Indo-Pacific *C. janthinoptera* (Bleeker). Moreover, a genetic analysis also revealed no difference for three similar Atlantic species, *C. rostrata* (Bloch), *C. figueiredoi* Moura & Castro, and *C. supramacula* Moura & Castro (L. A. Rocha, unpublished data), reinforcing our hypothesis that this group undergoes fast colour/ morphological differentiation combined with slow mtDNA evolution.

Non-type material examined. **Somalia**: Gulf of Aden, USNM 306624, 4: 70–88 mm; USNM 306628, 78 mm; USNM 306634, 67 mm; USNM 306641, 54 mm. Indian Ocean, ANSP 103616, 65 mm. **Kenya**: BPBM 40488, 49 mm. **South Africa**: KwaZulu-Natal, Sodwana Bay, SAIAB 10018, 111 mm; Aliwal Shoal, SAIAB 57318, 41 mm; SAIAB 57355, 39 mm. **Réunion**: BPBM 20022, 64 mm. **Mauritius**: BPBM 18070, 65 mm; BPBM 40515, 3: 96-103 mm. **Seychelles**: Mahé, ANSP 99949, 81 mm; ANSP 99950, 74 mm.

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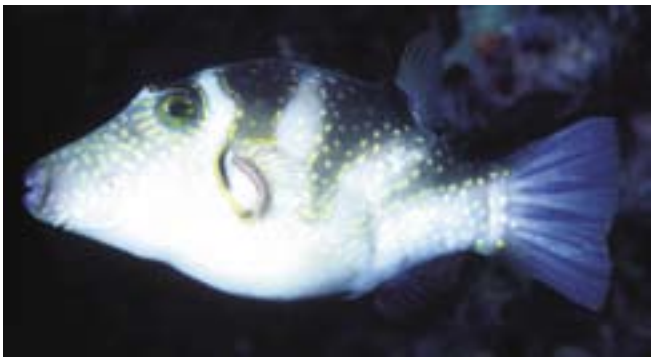
PLATE 1

A. *Canthigaster coronata*, BPBM 8497, 73 mm, O'ahu, Hawaiian Is. (J. E. Randall).

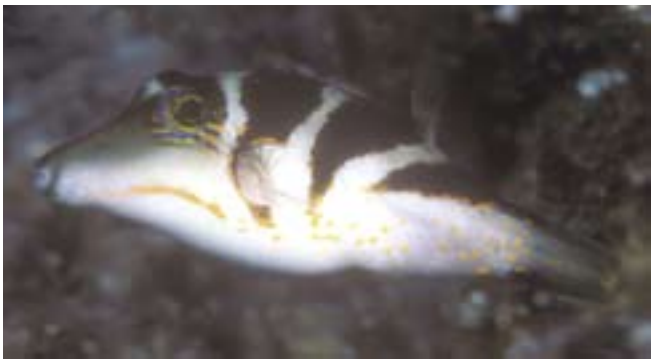


B. *Canthigaster coronata*, O'ahu, Hawaiian Is. (J. E Randall).

C. *Canthigaster axiologa*, BPBM 7267, 54 mm, Shirahama, Japan (J. E. Randall).

D. *Canthigaster axiologa*, Guam, Mariana Is. (R. F. Myers).

E. *Canthigaster axiologa*, Palau, ROM 79420, 33 mm (R. Winterbottom).



F. *Canthigaster axiologa*, Chichi-jima, Ogasawara Islands (J. E. Randall).

G. *Canthigaster axiologa*, Lan Yu, Taiwan (J. E. Randall).

H. *Canthigaster axiologa*, Bali, Indonesia (R. F. Myers).

PLATE 2

A. *Canthigaster axiologa*, Alor, Indonesia (J. E. Randall).

B. *Canthigaster axiologa*, Lady Musgrave I., Great Barrier Reef (J. E. Randall).

C. *Canthigaster cyanospilota*, holotype, BPBM 13898, 85 mm, Gulf of Aqaba (J. E. Randall).

D. *Canthigaster cyanospilota*, Gulf of Aqaba (J. E. Randall).

E. *Canthigaster cyanospilota*, Gulf of Aqaba (J. E. Randall).

F. *Canthigaster cyanospilota*, BPBM 20022, 64 mm, Réunion (J. E. Randall).

G. *Canthigaster cyanospilota*, Mauritius (J. E. Randall).

H. *Canthigaster cyanospilota*, North Malé Atoll, Maldive Islands (J. E. Randall).