Article

A new species of Indo-Pacific fish, *Canthigaster criobe*, with comments on other *Canthigaster* (Tetraodontiformes: Tetraodontidae) at the Gambier Archipelago

JEFFREY T. WILLIAMS[1], ERWAN DELRIEU-TROTTIN[2] & SERGE PLANES[2]

[1] *Division of Fishes, Department of Vertebrate Zoology, National Museum of Natural History, 4210 Silver Hill Road, Suitland, MD 20746, USA, e-mail williamsjt@si.edu*

[2] *Labex "CORAIL", USR 3278 CNRS – EPHE, Centre de Recherche Insulaire et Observatoire de l'Environnement (CRIOBE), Université de Perpignan, 52 Av. Paul Alduy - 66860 Perpignan cedex, France*

Abstract

A new species of the tetraodontid fish genus *Canthigaster* was discovered during a recent expedition to the Gambier Archipelago, French Polynesia. The new species, named *Canthigaster criobe* herein, is the only known species of *Canthigaster* having 12–14 brown stripes along the body (stripes beginning in front of the eye, extending along the body, and abruptly ending at the base of the caudal fin). It also has 17 pectoral rays, the origin of the anal fin inserts posterior to a vertical from the rear base of the dorsal fin and lacks spots on the caudal fin. *Canthigaster criobe* is currently known from a single specimen collected at the Gambier Archipelago. It appears to be most similar to the white-spotted *C. janthinoptera*, a wide-ranging, Indo-Pacific species, which also inhabits the Gambier Archipelago, and to the Hawaiian endemic *C. jactator* forming a species complex that exhibits incomplete lineage sorting. Specimens of *C. axiologus*, or an undescribed but very similar sibling species, were also collected at the Gambier Archipelago. Molecular analysis of these samples reveals an affiliation with *C. axiologus* specimens collected from disjunct localities in the western Central Pacific. *Canthigaster axiologus* was not previously known to occur east of the Tonga Islands. Geographic range expansions are also reported for *C. rapaensis* and *C. amboinensis*.

Key words: taxonomy, Tetraodontidae, *Canthigaster*, new species, French Polynesia, Gambier Archipelago

Introduction

The pufferfish family Tetraodontidae is divisible into two subfamilies, the Tetraodontinae and the Canthigasterinae. The latter subfamily, popularly known as tobies or sharpnose puffers, consists of the marine genus *Canthigaster* Swainson and the freshwater genus *Carinotetraodon* Benl. These fishes are differentiated from the Tetraodontinae by a laterally compressed body, elongate pointed snout (only for *Canthigaster*), erectile ridge of skin middorsally and midventrally, small gill opening, inconspicuous lateral line, 17 vertebrae, and small size. Britz and Kottelat (1999) discuss a synapomorphy for these two genera wherein abdominal vertebrae 1–3 bear independent, unfused, paired parapophyses. In *Canthigaster*, the hemal spines have posterior lobes that are absent in *Carinotetraodon* (Britz & Kottelatt, 1999). The bold color patterns of *Canthigaster* probably serve to advertise their repelling skin toxin (Eger & Starkus 1973).

Randall *et al.* (2008) summarized previous work on the genus and discussed the historical problems faced by taxonomists in distinguishing the species of *Canthigaster*. In addition to the uniformity of morphological characters among *Canthigaster* species, Randall *et al.* (2008) found a high degree of genetic uniformity within the genus. As noted by Randall *et al.* (2008), color pattern reigns as the primary character used to distinguish the known species of *Canthigaster*. Randall *et al.* (2008) described a new species and resurrected a species from synonymy, resulting in the recognition of 35 valid species.

In September and October 2010, the authors collected fish specimens during an expedition to the Gambier Archipelago, French Polynesia, using a variety of collecting techniques and took tissue samples and photographs of

voucher specimens of each fish species collected. Among the specimens collected was a distinctively colored new species of *Canthigaster*. The new species described herein increases the number of recognized *Canthigaster* species to 36.

Geographic range expansions are also reported for *Canthigaster axiologus, C. rapaensis*, and *C. amboinensis*. These three species are recorded for the first time from the Gambier Archipelago.

Using the tissue samples obtained during the expedition, we attempted to genetically differentiate the new species from its congeners using mitochondrial DNA sequences.

Materials and Methods

All specimens examined are deposited in the National Museum of Natural History, Washington, D.C. (USNM).

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 (the inflatable abdomen makes the maximum body depth highly variable in species of *Canthigaster*); body width is measured at the base of the pectoral fins; head length (HL) 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 for the new species are presented in the descriptions as proportional measurements of the SL or HL, rounded to the nearest 0.5. Counts of pectoral rays include the short uppermost ray.

To conduct our genetic analysis, whole genomic DNA was extracted from fin clips preserved in 96% EtOH. DNA extraction was performed using QIAxtractor (QIAGEN, Crawley) according to manufacturer's protocols. A fragment of the mitochondrial DNA control region of *Canthigaster* was amplified with the primers CANT-CR-F and CANT-CR-R (Randall *et al.* 2008). PCR amplifications were performed on a Mastercycler® pro (Eppendorf) thermocycler, in a final 25 µl reaction containing: 2.5 µl of the buffer provided by the manufacturer (5 PRIME), 1.25 µl of MgCl2 (25 mM), 3 µl of dNTP (2 mM), 0.4 µl of each primer (l0 mM), 5 U Taq DNA polymerase (5 PRIME), 2.0 mM, and 1–3 µl of total genomic DNA. The thermocycle procedure (35 cycles) was a modified hot-start touchdown PCR, with an initial soak at 94 °C for 3 min, followed by 35 cycles at 94°C for 25s, 52°C for 25s and 72°C for 1 min. The final phase of the procedure was a 3-min elongation period at 72 °C.

The result was visualized on ethidium-bromide stained agarose gels. Sequencing was performed using an ABI3730 Automated Sequencer using the same primers. All samples were sequenced in forward and reverse directions to ensure accuracy of nucleotide designations. Sequences were analyzed using Geneious v5.4 (Drummond *et al.* 2009) and aligned by eye with no ambiguities. All sequences are deposited in Genbank (Accession numbers: JQ241772-JQ241781).

A 678 base-pair fragment of the mitochondrial control region was sequenced for comparative purposes among the three species (*C. axiologus*, *C. cyanospilota*, *C. coronata*) of the *C. coronata* complex (Randall *et al.* 2008), four other species found during the campaign and five specimens obtained from Genbank (Table 1) with a representative of the Tetraodontinae used as the outgroup.

Two different tree-building methods were used to construct branching diagrams. Neighbor-joining (NJ) analysis was conducted using the software package MEGA 5 (Tamura *et al.* 2011). For the maximum-likelihood (ML) approach, the appropriate model of nucleotide substitution was determined using jModeltest version 3.07 (Posada 2008). The ML analysis was run on Phylogeny.fr server (Dereeper *et al.*, 2008) with parameters fixed according to jModeltest specifications. Confidence in topologies was evaluated based on 1000 bootstrap replicates or posterior probability. The two analyses resulted in identical tree topologies. The NJ tree is presented herein.

TABLE 1. Specimens included in the molecular analysis for this study. Asterisk (*) denotes specimens collected and sequenced by us.

Species	Reference for the sequences	GeneBank Accession Number	Sampling location
Canthigaster axiologus		AP006743	Japan
Canthigaster axiologus	Randall et al., 2008		Australia
Canthigaster coronata	Randall et al., 2008		Hawaii
Canthigaster coronata	Randall et al., 2008		Hawaii
Canthigasther cyanospilota	Randall et al., 2008		La Réunion
Canthigasther cyanospilota	Randall et al., 2008		La Réunion
*Canthigaster axiologus**		JQ241775	Gambier Archipelago
*Canthigaster axiologus**		JQ241776	Gambier Archipelago
*Canthigaster axiologus**		JQ241777	Gambier Archipelago
*Canthigaster axiologus**		JQ241778	Gambier Archipelago
*Canthigaster solandri**		JQ241779	Gambier Archipelago
Canthigaster jactator		AP011911	Hawaii
*Canthigaster janthinoptera**		JQ241773	Gambier Archipelago
*Canthigaster janthinoptera**		JQ241774	Gambier Archipelago
*Canthigaster criobe**		JQ241772	Gambier Archipelago
*Canthigaster amboinensis**		JQ241780	Gambier Archipelago
*Canthigaster rapaensis**		JQ241781	Gambier Archipelago
Canthigaster rivulata		AP006744	Japan
Canthigaster valentini		AP011912	Tonga
Arothron meleagris		AP011931	NA

Canthigaster criobe new species
Common Name: Striped toby
(Figure 1, 2)

Holotype: USNM 400521, 38.7 mm SL when fresh (37.6 mm SL after preservation), Gambier Archipelago, Kouaku Island, on SE side of archipelago, small surge channel in outer reef; 23.22°S, 154.88°W; 15–20 m depth; field number GAM-2010-01; tissue sample number GAM-001; collected by S. Planes, J.T. Williams, E. Delrieu-Trottin, M. Kulbicki, P. Sasal. 29 September 2010.

Diagnosis: Dorsal rays 9; anal rays 9; pectoral rays 17; body depth between origins of dorsal and anal fins 2.6 in SL; head length 2.3 in SL; fleshy pigmented skin interorbital width 3.1 in HL; gill opening 8.2 in HL; origin of anal fin posterior to rear base of dorsal fin 3.1 in SL, the preanal length 1.2 in SL; longest dorsal ray 2.3 in HL; color in life: body pale tan with orangish brown stripes; head with uniformly orangish brown snout anteriorly, at middle of snout about 4 narrow, orangish brown stripes radiate posteriorly below eye, three stripes extend posteriorly from rear margin of eye, one stripe runs along ridge of erectile tissue on top of head, at deepest part of body there are about 14 narrow orangish brown stripes, middle five of those stripes continue to base of caudal fin where they abruptly end.

Description: Dorsal rays 9; anal rays 9; dorsal and anal rays branched, except the first; principal caudal rays 9, all branched but lowermost; a single small segmented upper and lower procurrent caudal ray; pectoral rays 17 (on right side; 16 on left, but left side appears to have been damaged earlier in life and healed, possibly losing a ray in the middle); vertebrae 17; mouth small, oval, and terminal, exposing about terminal half of upper dental plate; lips fleshy and papillose.

Body depth between origins of dorsal and anal fins 2.6 in SL; body moderately compressed, the width 1.6 in depth; head length 2.3 in SL; snout length 1.7 in HL; dorsal profile of snout slightly concave; eye diameter (unpigmented skin over eye) 3.9 in HL; bony orbit diameter 3.0 in HL; interorbital space slightly concave, the least bony interorbital width 3.7 in HL; gill-opening length 8.2 in HL; caudal-peduncle depth 2.3 in HL; caudal-

peduncle length 2.7 in HL; predorsal length 1.3 in SL; dorsal-fin base 4.9 in HL; third dorsal ray usually longest, but adjacent rays nearly as long, 2.3 in HL; origin of anal fin below rear base of dorsal fin, the preanal length 1.2 in SL; anal-fin base 6.2 in HL; fourth anal ray longest, but adjacent rays nearly as long, 2.7 in HL; caudal fin truncate, 3.4 in SL; upper and lower portions of pectoral fins rounded, fin deeply incised in the middle; third pectoral ray longest, 2.5 in HL.

FIGURE 1. Holotype of *Canthigaster criobe*, USNM 400521, 38.7 mm SL, Gambier Archipelago (J.T. Williams).
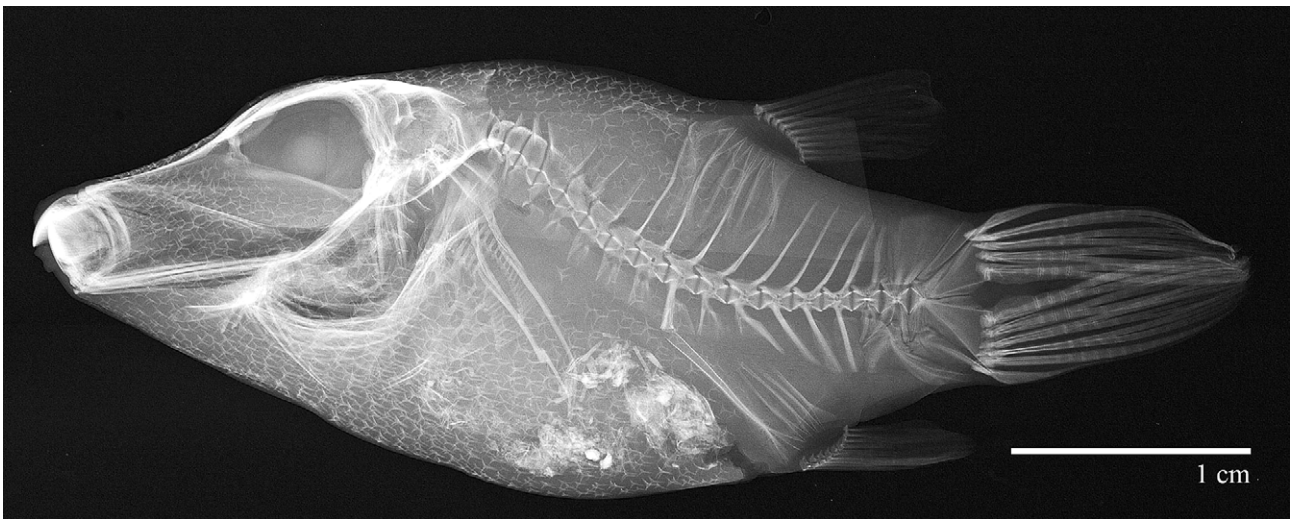
FIGURE 2. Radiograph of holotype of *Canthigaster criobe*, USNM 400521, 38.7 mm SL, Gambier Archipelago, showing skin spinule pattern (J.T. Williams).

Skin with numerous small spinules directed posteriorly, each fitting into a longitudinal groove; skin smooth when stroked posteriorly, but spinules apparent when stroked anteriorly; spinules densely cover head, nape and belly, but are absent from the body immediately behind the pectoral-fin base and from body posterior to an imaginary line between origin of dorsal fin and origin of anal fin.

Color of holotype when fresh shown in Fig 1. Body pale tan with orangish brown stripes; head with uniformly orangish brown snout anteriorly, at middle of snout about 4 narrow, orangish brown stripes radiate posteriorly below eye, three stripes extend posteriorly from rear margin of eye, one stripe runs along ridge of erectile tissue on top of head, at deepest part of body there are about 14 narrow orangish brown stripes, middle five of those stripes

continue to and end abruptly at base of caudal fin; lips brown; orangish brown coloration on snout becomes paler, but continues posteriorly across chest and abdomen as a diffuse orangish tint that reaches anus; fins unpigmented and translucent; base of dorsal fin with a poorly developed dark blotch.

Color of holotype in alcohol similar to life colors except stripes are dark brown on tan background.

Etymology: We name this species *criobe* after the Centre de Recherche Insulaire et Observatoire de l'Environnement (CRIOBE), Moorea, French Polynesia, in recognition of the laboratory's continuing support of marine research in French Polynesia. The species name is treated as a noun in apposition.

Remarks: Although it is known from only a single specimen, the longitudinally striped color pattern of *Canthigaster criobe* is unique within the genus and easily distinguishes *C. criobe* from all other described *Canthigaster* species. Although *C. janthinoptera* has its body covered with blue centered white spots, the orangish brown reticulations are similar in color to the stripes of *C. criobe*. In both of these species the base of the caudal fin has narrow brown lines extending onto the bases of the fin rays (Figs. 1, 3). Some specimens of *C. janthinoptera* have a few lines on the upper part of the body (Fig. 3), but never a striped pattern like that of *C. criobe*. *Canthigaster criobe* and *C. janthinoptera*, along with the Hawaiian endemic *C. jactator* form a species complex within *Canthigaster*.

FIGURE 3. *Canthigaster janthinoptera*, USNM 400502, 50.6 mm SL, Gambier Archipelago (J.T. Williams).

Comments on other *Canthigaster* at the Gambier Archipelago

During the 2010 expedition to the Gambier Archipelago, we collected six additional species of *Canthigaster,* including: *C. janthinoptera* (Bleeker, 1855)*, C. amboinensis* (Bleeker, 1864)*, C. axiologus* Whitley, 1931*, C. solandri* (Richardson, 1844)*,* and *C. rapaensis* Allen and Randall, 1977. The sixth species, *C. bennetti* (Bleeker, 1854), was observed during the expedition and a single specimen was collected on the last day, but was not tissue sampled or retained as a voucher.

The discovery and collection of several specimens of *Canthigaster axiologus* (USNM 400503, 400522, 400533, 400534) at the Gambier Archipelago was surprising as the geographically closest known population of *C. axiologus* is at the Tonga Islands over 4,000 km to the west. There is a slight difference in coloration in that the Gambier specimens have 0–1 yellow spots (versus numerous yellow and blue spots) on the caudal peduncle and no spots (versus numerous spots at least basally) on the caudal fin (Fig. 4). The Gambier specimens of *C. axiologus* are currently under study to determine if this isolated population has evolutionarily diverged from the western Pacific form and warrants recognition as a distinct species (see below).

FIGURE 4. *Canthigaster axiologus*, USNM 400503 , 73.9 mm SL, Gambier Archipelago (J.T. Williams).

The collection of a specimen (Fig. 5) of *Canthigaster rapaensis* (USNM 400531) at the Gambier Archipelago represents a geographic range extension from Rapa, Austral Islands. This is the first record of *C. rapaensis* occurring at a locality other than Rapa.

FIGURE 5. *Canthigaster rapaensis*, USNM 400531, 71.4 mm SL, Gambier Archipelago (J.T. Williams).

The single specimen (Fig. 6) of *Canthigaster amboinensis* (USNM 399907), taken on the eastern side of the Gambier Archipelago on the outer reef slope at a depth of 10–25 m, represents the first report of the species from the Gambier Archipelago. There is one record of this species from the Galapagos (presumably a waif), but previously in French Polynesia the easternmost reports of this species were from the Society Islands and the Marquesas.
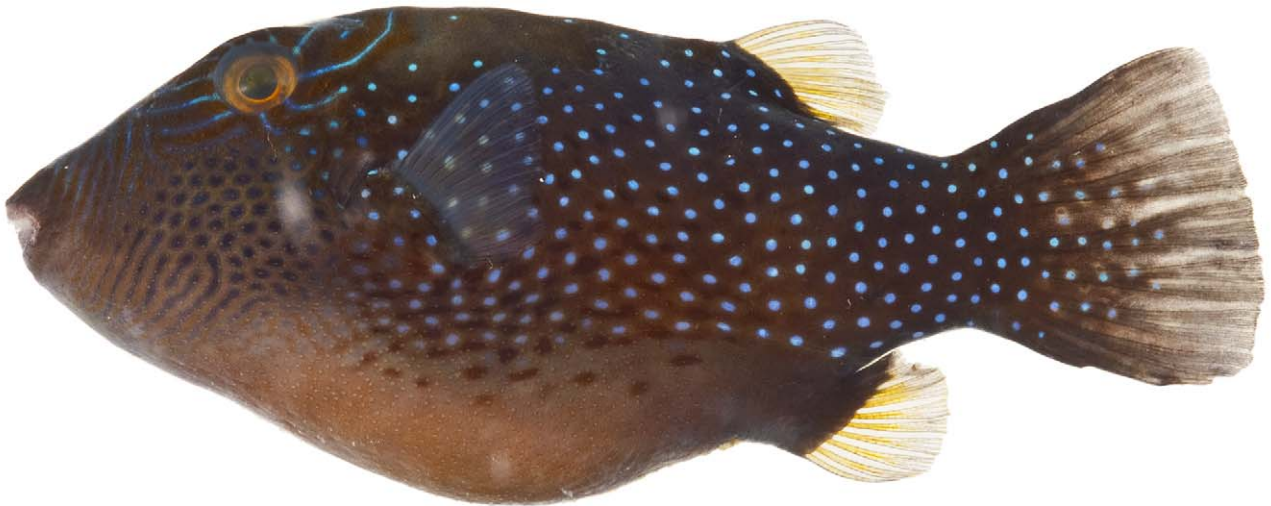
**FIGURE 6.** *Canthigaster amboinensis*, USNM 399907, 81.6 mm SL, Gambier Archipelago (J.T. Williams).

Molecular analysis

The topology of our NJ tree (Fig. 7) is similar to that of Alfaro *et al.* (2007) based on 12S and 16S sequences and that of Randall *et al.* (2008) based on the control region. In our Fig. 7, the two *C. cyanospilota* do not group together. The Randall *et al.* (2008) tree was supported by a low bootstrap probability (53) in the Randall *et al.* (2008) study and our study includes additional species.

Canthigaster criobe appears to belong to a group of closely related species including *C. janthinoptera* and *C. jactator* (Jenkins, 1901). Alfaro *et al.* (2007) reported that the Hawaiian endemic *C. jactator* and the Indo-Pacific *C. janthinoptera* were genetically very similar. Incomplete lineage sorting or mitochondrial introgression might explain this finding as these processes have been reported to produce similar phylogenetic patterns (Avise & Ball 1990; Morando *et al.* 2004). Mitochondrial introgression, as discussed by Allendorf *et al.* (2001) and McGuire *et al.* (2007), describes two divergent haplotypes of geographically separated taxa becoming very similar in intermediate areas where the taxa overlap in distribution. The mitochondrial haplotypes of the *C. janthinoptera* sampled at the Gambier Archipelago are similar to those of *C. criobe*, currently known only from the Gambier Archipelago, but that of *C. jactator* also is similar, even though it is a Hawaiian endemic found over 5,500 km to the northwest. This similarity with a geographically separated taxon suggests incomplete lineage sorting instead of mitochondrial introgression. The speciation events may have occurred so recently that the neutral genes have not had time to accumulate independent mutations (McCartney *et al.* 2003, Shultz *et al.* 2007, McGuire *et al.* 2007, Rocha *et al.* 2007). The absence of lineage partitioning coinciding with distinctive species-specific color pattern characters has been reported in other genera of Osteichthyes in addition to that reported for *Canthigaster* (Randall *et al.* 2008), such as: *Centropyge* (Pomacanthidae, Bowen *et al.* 2006), *Halichoeres* (Labridae, Rocha 2004) and *Scaphirhynchus* (Acipenseridae, Campton *et al.* 2000). *Canthigaster criobe* appears to be another example of incomplete lineage sorting in the subfamily Canthigasterinae. Our analysis provides additional support to the Randall *et al.* (2008) hypothesis that "this group undergoes fast colour/morphological differentiation combined with slow mtDNA evolution."

Molecular analysis groups the four Gambier specimens of *C. axiologus* with the western Pacific *C. axiologus* lineage (Fig. 7). Yet, a well-supported differentiation can be observed for two of the specimens. Considering the slight difference in the coloration and the geographic isolation of the Gambier population, we consider this population to be in an early stage of evolutionary differentiation. Other populations of this species may occur between Tonga and Gambier, but the species has not been reported from the intervening geographic regions.
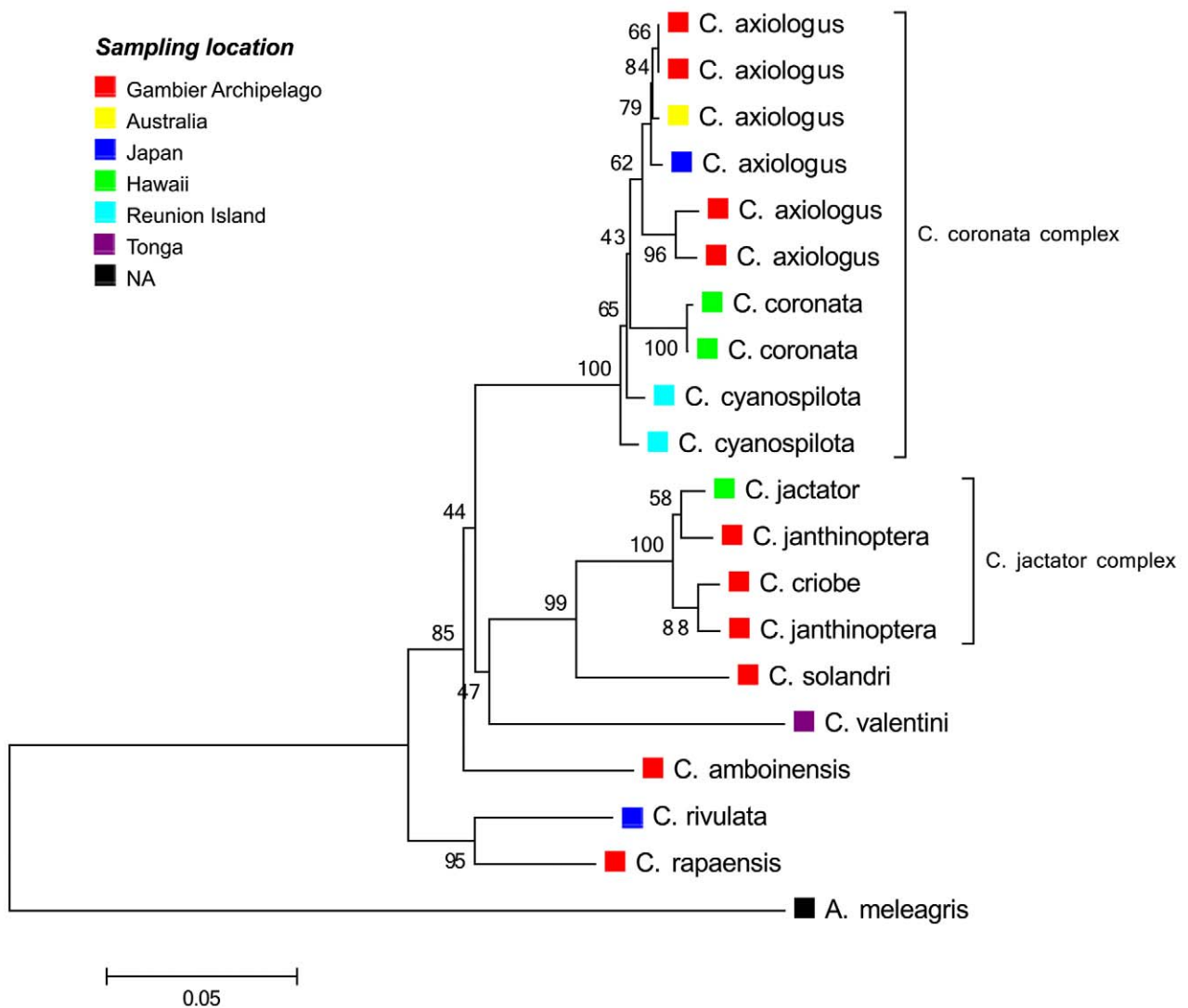
FIGURE 7. Neighbor-Joining tree based on K2P model of sequence evolution (with 1,000 bootstrap replicates) for selected members of the subfamily Canthigasterinae, with *Arothron meleagris* as the outgroup.

Acknowledgements

References

Alfaro, M.E., Santini, F. & Brock, C.D. (2007) Do reefs drive diversification in marine teleosts? Evidence from the pufferfishes and their allies (order Tetraodontiformes). *Evolution,* 61, 2104–2126.

Allen, G.R. & Randall, J.E. (1977) Review of the sharpnose puffers (subfamily Canthigasterinae) of the Indo-Pacific. *Records of the Australian Museum*, 30, 475–517.

Allendorf, F.W., Leary, R.F., Spruell, P. & Wenburg, J.K. (2001) The problems with hybrids: setting conservation guidelines. *Trends in Ecology and Evolution,* 16, 613–622.

Avise, J.C. & Ball, R.M. (1990) Principles of genealogical concordance in species concepts and biological taxonomy. *Oxford Surveys in Evolutionary Biology*, 7, 45– 67.

Bleeker, P. (1854) Vijkfe bijdrage tot de kennis der ichthyologische fauna van Amboina. *Natuurkundig Tijdschrift voor Nederlandisch Indië,* 6, 455–508.

Bleeker, P. (1855) Zesde bijdrage tot de kennis der ichthyologische fauna van Amboina. *Natuurkundig Tijdschrift voor Nederlandisch Indië,* 8, 391–434.

Bleeker, P. (1864) Description de quelques espèces inédites de poissons de l'Archipel des Moluques. *Nederlandsch Tijdschrift voor de Dierkunde*, 2, 177–181.

Bowen, B.W., Muss, A. J., Rocha L.A. & Grant, W.S. (2006) Shallow mtDNA coalescence in Atlantic pygmy angelfishes (genus *Centropyge*) indicates a recent invasion from the Indian Ocean. *Journal of Heredity*, 97, 1–12.

Britz, R. & Kottelat, M. (1999) *Carinotetraodon imitator*, a new freshwater pufferfish from India (Teleostei: Tetraodontiformes). *Journal of South Asian Natural History*, 4, 39–47.

Campton, D.E., Bass, A.L., Chapman, F.A. & Bowen, B.W. (2000) Genetic distinction of pallid, shovelnose, and Alabama sturgeon; emerging species and the U.S. endangered species act. *Conservation Genetics,* 1, 17–32.

Dereeper, A., Guignon, V., Blanc, G., Audic, S., Buffet, S., Chevenet, F., Dufayard, J.F., Guindon, S., Lefort, V., Lescot, M., Claverie, J.M. & Gascuel, O. (2008) Phylogeny.fr: robust phylogenetic analysis for the non-specialist. *Nucleic Acids Research*, 1, 36.

Drummond, A., Ashton, B., Cheung, M., Cooper, A., Duran, C., Field, M., Heled, J., Kearse, M., Markowitz, S., Moir, R., Stones-Havas, S., Sturrock, S., Thierer, T. & Wilson, A. (2009) Geneious v4.6, Available from http://www.geneious.com/.

Eger, W.H. & Starkus, J.G. (1973) Morphological aspects of the skin from toxic Caribbean pufferfishes (Tetraodontiformes). *Proceedings of the Association of Island Marine Laboratories of the Caribbean,* 8, 20–21.

Jenkins, O.P. (1901) Descriptions of fifteen new species of fishes from the Hawaiian Islands. Bulletin of the U. S. Fish Commission, 19 (1899), 387–404.

McCartney, M.A., Acevedo, J., Heredia, C., Rico, C., Quenoville, B., Bermingham, E. & McMillan, W.O. (2003) Genetic mosaic in a marine species flock. *Molecular Ecology,* 12, 2963–2973.

McGuire, J.A., Linkem, C.W., Koo, M.S., Hutchison, D.W., Lappin, A.K., Orange, D.I., Lemos-Espinal, J., Riddle, B.R. & Jaeger, J.R. (2007) Mitochondrial introgression and incomplete lineage sorting through space and time: phylogenetics of crotaphytid lizards. *Evolution*, 61, 2879–2897.

Morando, M., Avila, L.J., Baker, J. & Sites Jr, J.W. (2004) Phylogeny and phylogeography of the *Liolaemus darwinii* complex (Squamata: Liolaemidae): evidence for introgression and incomplete lineage sorting. *Evolution,* 58, 842–861.

Posada, D. (2008) jModelTest: Phylogenetic Model Averaging. *Molecular Biology and Evolution,* 25, 1253–1256.

Randall, J.E., Williams, J.T. & Rocha, L.A. (2008) The Indo-Pacific tetraodontid fish *Canthigaster coronata*, a complex of three species. *Smithiana Bulletin*, 9, 3–13.

Richardson, J. (1844) Ichthyology. *In:* Hinds, B.R. (Ed.) *The Zoology of the Voyage of H.M.S.* Sulphur. Smith, Elder & co., London, pp. 51–150.

Rocha, L.A (2004) Mitochondrial DNA and color pattern variation in three western Atlantic *Halichoeres* (Labridae), with the revalidation of two species. *Copeia,* 2004, 770–782.

Rocha, L.A., Craig, M.T. & Bowen, B.W. (2007) Phylogeography and the conservation of coral reef fishes. *Coral Reefs*, 26, 501–512.

Schultz, J.K., Pyle, R.L., DeMartini, E. & Bowen, B.W. (2007) Genetic connectivity among color morphs and Pacific archipelagos for the flame angelfish, *Centropyge loriculus*. *Marine Biology*, 151, 167–175.

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. & Kumar, S. (2011) MEGA5: Molecular Evolutionary Genetics Analysis using Maximum Likelihood, Evolutionary Distance, and Maximum Parsimony Methods. *Molecular Biology and Evolution*, 28, 2731–2739.

Whitley, G.P. (1931) New names for Australian fishes. *Australian Zoologist*, 6, 310–334.