The Moray Eels of the *Anarchias cantonensis* Group (Anguilliformes: Muraenidae), with Description of Two New Species

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The broadly distributed Indo-Pacific moray eel *Anarchias cantonensis* (Schultz, 1943), heretofore treated as a single species, consists of three species: *A. cantonensis*, *A. exulatus*, a new species, and *A. schultzi*, a new species, based on geographic distribution, coloration, external morphometrics, and vertebral counts. We examined 112 specimens and determined that the true *A. cantonensis* is distributed throughout the eastern Indian Ocean, western Pacific, and tropical central Pacific, and has a mean vertebral formula of 91/93/104. *Anarchias exulatus* is distributed anti-tropically in the central and southeastern Pacific and is characterized by a unique mottling pattern and a mean vertebral formula of 100/103/114. A third species, named here as *A. schultzi*, is characterized by a mean vertebral formula of 96/99/109, a plain brown coloration in adult form, and is restricted geographically to Tonga, New Caledonia, the Solomon Islands, and the Caroline Islands. At the Tonga Islands, which reside on the edge of Australian and Pacific tectonic plates, all three species are present, but maintain their morphological distinctiveness and segregate ecologically.

MORAY eels (Muraenidae) are among the most speciose lineages of Anguilliform fishes, with approximately 200 species (Böhlke et al., 1989). The family Muraenidae is characterized by having the lowest level of endemism among all reef fishes (Hourigan and Reese, 1987). Characteristic of most reef fishes, the center of diversity for Muraenidae is the Indo-Pacific (Briggs, 1999); there are approximately 150 Indo-Pacific species and 50 Atlantic species (Böhlke et al., 1989; Böhlke and Smith, 2002). Within Muraenidae, there are two subfamilies, Muraeninae and Uropterygiinae. The Uropterygiinae are cosmopolitan and characterized by having the dorsal and anal fins restricted to the posterior tip of the body. Moray eels as a group and particularly members of the subfamily Uropterygiinae are broadly distributed, have conflicting or highly variable color patterns, and are frequently misidentified by collectors. Uropterygiinae is subdivided into four genera: *Channomuraena*, *Uropterygius*, *Scuticaria*, and *Anarchias*. Members of the genus *Anarchias* are distinguished from other Uropterygiinae by having an extra head pore medial and adjacent to the posterior nostril, a character unique among all of Muraenidae. Despite a paucity of morphological characters distinguishing recognized species, most species of *Anarchias* can be differentiated from one another by their vertebral formula, which includes the number of predorsal, preanal, and total vertebrae. Within *Anarchias*, there are two Atlantic species (*A. longicauda* and *A. similis*), one eastern Pacific species (*A. galapagensis*), and six Indo-Pacific species. The Indo-Pacific species are *A. maldiviensis* (status uncertain, possibly a synonym of *A. allardicei*), *A. supremus*, and three species complexes: *A. leucurus-seychellensis*, *A. allardicei*, and *A. cantonensis*. *Anarchias supremus* and the *A. leucurus-seychellensis* complex can be differentiated from other *Anarchias* by having the dorsal head pore located slightly posterior and medial to and within the same unpigmented depression as the posterior nostril (Fig. 1, right). The *A. allardicei* complex has the dorsal head pore directly medial to the posterior nostril (Fig. 1, middle). The *A. cantonensis* complex discussed here is unique in having the dorsal head pore located anterior to and medial to the posterior nostril (Fig. 1, left).

We investigated the widely distributed species complex, *A. cantonensis*, throughout most of its range from the central Indian Ocean to the central Pacific; this species is not known to cross the Eastern Pacific Barrier (Ekman, 1953; Briggs, 1961; Grigg and Hey, 1992; Robertson et al., 2004). We surveyed diagnostic morphometric and meristic features and identified three distinct species with supporting evidence drawn from color patterns, geographic distributions, and the geological age of inhabited reefs.

MATERIALS AND METHODS

We examined 112 specimens originally identified as *A. cantonensis* from museum collections (see Material Examined). Specimens were universally collected using the ichthyocide rotenone. We assume that there was no bias across rotenone stations and collecting sites in specimen size or reproductive or maturation stage. The geographic localities sampled span much of the Indo-Pacific and are depicted in Figure 2.

Counts and measurements are as given in Böhlke et al. (1989). We conducted measurements of total length (mm), distance from snout to anus, head length, depth at anus, snout length, eye diameter, and distance from snout to rictus of mouth. Measurements of tooth number and orientation revealed little or no variation among specimens. All measurements were taken by caliper or meter stick by the same researcher (EH), except for the specimens from Tonga, which were taken by a separate author (DGS). Vertebral counts and formulas were calculated by manually counting vertebrae from both film and digital x-rays and recording the number of vertebrae anterior to the origin of the dorsal fin, the number of vertebrae anterior to the origin of the anal fin, and the total number of vertebrae. All external morphological measurements (Table 1) were $\log_{10}$ transformed and regressed against total length. Residuals of each of the six morphometric variables listed above were

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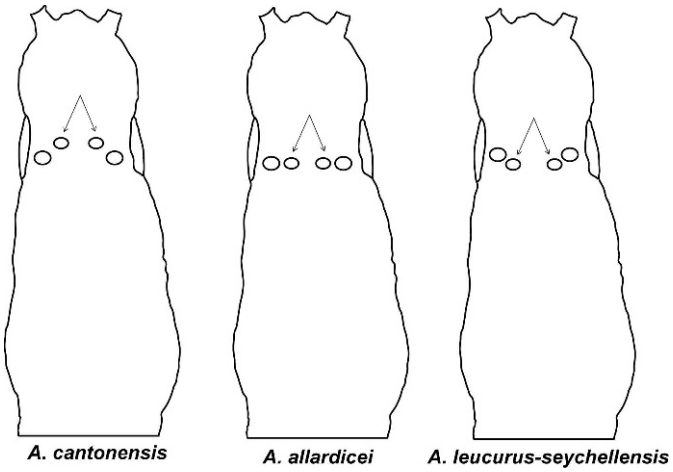

Fig. 1. Schematic of the dorsal view of a moray head distinguishing among three similar species complexes of the genus *Anarchias*. They are differentiated by the location of the dorsal head pore (indicated with arrows) relative to the eye and the posterior nostril.

included with $\log_{10}$ transformed total length in a Principal Component Analysis (PCA) in the program XLSTAT 2009 (Addinsoft, Inc., New York, NY; http://www.xlstat.com). Meristic vertebral measures were included in a separate PCA without transformation. The first principal component (PC) from the morphometric PCA was then combined with the first principal component of the meristic PCA. Three non-overlapping groups identified by the combined PCA were subject to a single-factor pairwise ANOVA of PC scores to demonstrate that the only significant variation present was between and not within groups. The number of vertebrae in moray eels does not change throughout the life of the organism, and is highly diagnostic of species (Böhlke et al., 1989; Böhlke and Smith, 2002). Additional characters include the geographic distributions, geological age of reef systems drawn from the literature, and color patterns which fall into three distinct categories. Specimens were identified as being uniformly brown with no mottling, heavily mottled with sharp and well-defined blotches of white on a brown background, or diffuse and blotched mottling oriented vertically (Fig. 3).

RESULTS

The first axis of the morphometric PCA explained 37.8% of the variation, and the first axis of the meristic PCA explained 97.1% of the variation. The first morphometric axis loaded heavily (squared cosine of variable >0.5) with snout–anus length, distance from snout to rictus of mouth, and snout length. The meristic PC axis included all three vertebral measures with squared cosines of the variables greater than 0.95. The results of the combined PCA identified three groups of individuals primarily along the meristic PC axis (Fig. 4). Pairwise single-factor ANOVA identified all significant variation as being among and not within groups (all pairwise comparisons had *P*-values less than 0.05). The three groups identified by the PCA and substantiated by ANOVA corresponded without exception to three distinct color morphs. The first group, with crisp mottling, has a vertebral count range that encompasses the holotype specimen of *A. cantonensis* and thus retains that name. This group is represented by 73 specimens sampled in

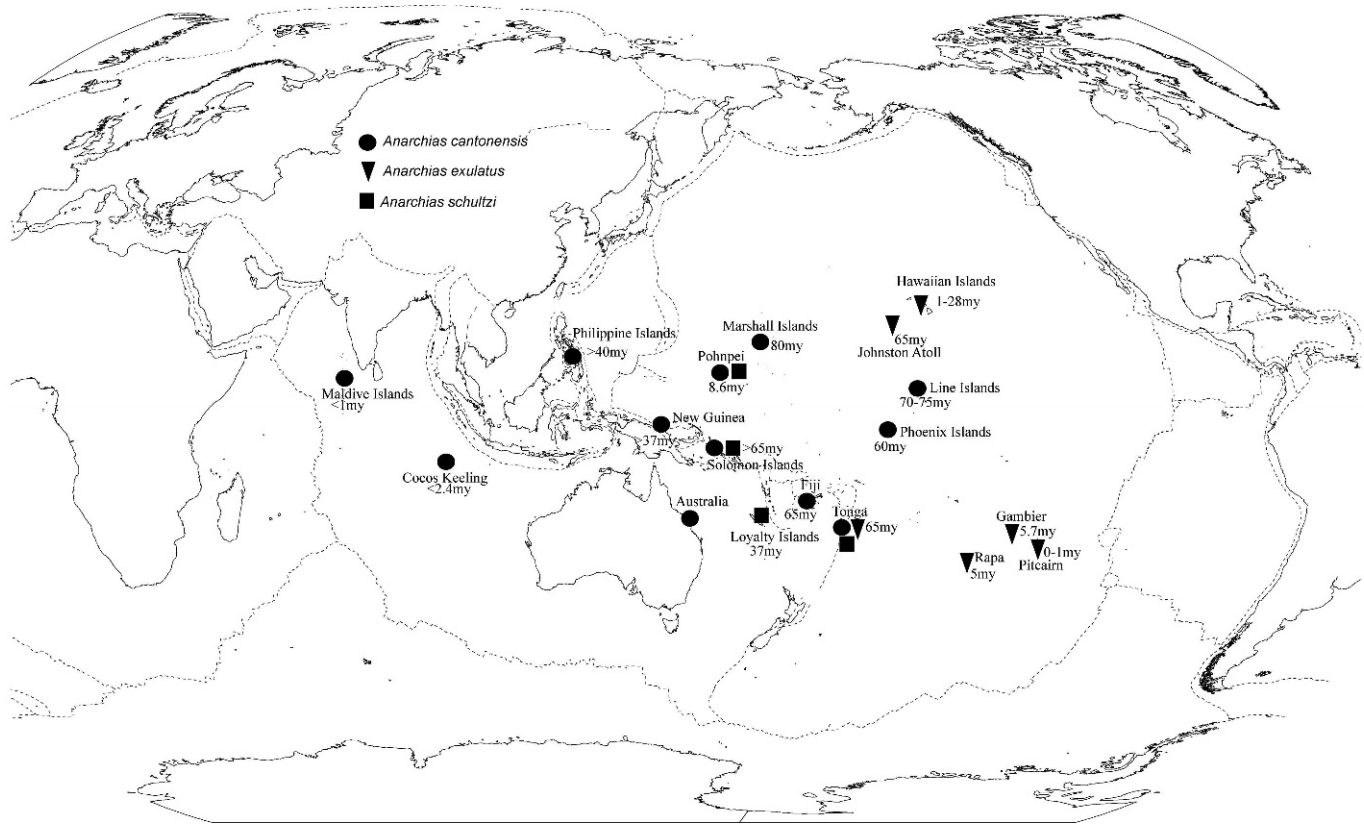

Fig. 2. Map of the Indo-Pacific with sampled localities for the three species of the *Anarchias cantonensis* species complex. Geological ages of reefs surrounding islands are listed with citations in text. Also presented are tectonic plate boundaries, with notable placement of Tonga Island along the edge of the Pacific plate to the east and Australian–Indian plate to the west, where all three species were sampled.

Table 1. Number of Specimens Examined, the Range, and Arithmetic Mean for Each of Ten Morphological Characters for Each of Three Species of the Genus *Anarchias*.

	A. cantonensis			*A. exulatus*			*A. schultzi*		
	n	Range	Mean	*n*	Range	Mean	*n*	Range	Mean
Total length (TL) (mm)	73	49–217	NA	28	58–293	NA	11	39–159	NA
Snout–anus (%TL)	68	45.1–50.6	47.0	28	40.3–45.1	43.1	11	41.5–45.4	43.8
Head length (HL) (%TL)	68	11.3–15.0	13.1	28	11.9–15.0	13.1	10	11.6–14.6	12.9
Depth at anus (%TL)	67	2.9–6.1	4.3	28	3.2–5.5	4.0	10	3.4–5.4	4.0
Eye (%TL)	69	7.2–12.9	9.6	28	8.1–11.0	9.9	10	8.1–11.0	9.4
Snout–eye (%HL)	69	10.9–20.9	15.6	28	13.2–16.9	15.3	10	13.8–17.3	15.4
Snout–rictus (%HL)	69	28.3–40.7	35.1	28	26.0–35.0	31.5	10	31.8–36.2	34.0
Predorsal vertebrae	64	86–94	91.0	28	96–105	100.3	10	93–100	96.2
Preanal vertebrae	62	89–97	93.4	27	97–107	102.7	9	96–103	98.6
Total vertebrae	68	98–108	103.6	27	110–117	113.9	10	105–113	108.8

the Indian Ocean and the western and central Pacific Ocean. The second group, described here as *A. exulatus*, consists of 28 specimens in an anti-tropical distribution that contains the central Pacific islands of Hawaii, Johnston Atoll, the Pitcairn group, Gambier, and Rapa, and Tonga to the west. The third group of 11 specimens is described as *A. schultzi* and is characterized by a uniformly brown coloration, atypical of *A. cantonensis* adults, an intermediate but distinct vertebral count, and localities that largely lie along the boundaries of the Pacific and the Australian–Indian tectonic plates.

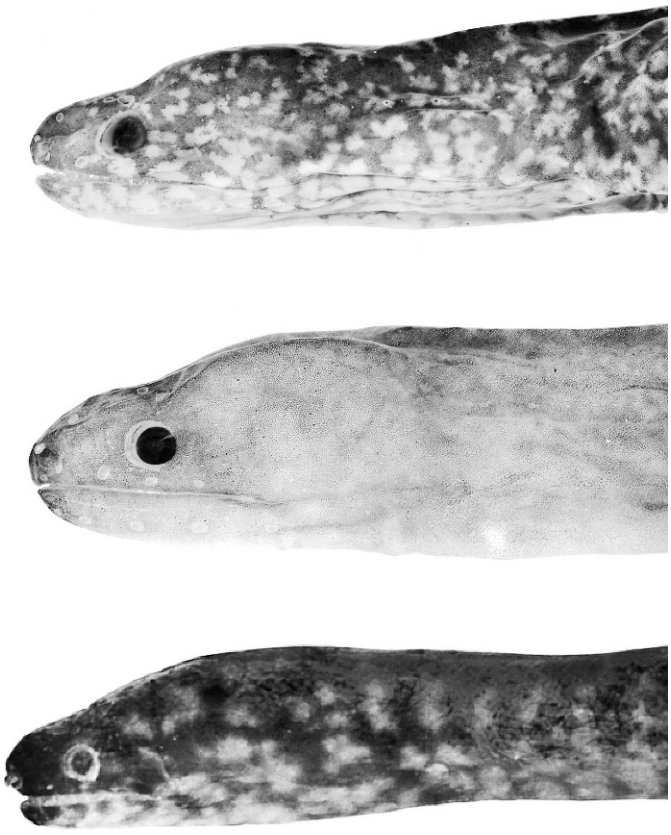

Fig. 3. Photographs depicting different color morphs corresponding to the crisp mottling of *Anarchias cantonensis* (top), the lack of mottling and uniform brown color in *A. schultzi* (middle), and the diffuse and blurred blotches, becoming vertically oriented posteriorly in *A. exulatus* (bottom).

Anarchias cantonensis (Schultz, 1943)

Figures 3 (top), 5, 7; Table 1

Uropterygius cantonensis Schultz, 1943:27 [Type locality: Phoenix Islands, Canton Island].
Anarchias cantonensis.—Schultz, 1953:146.

Diagnosis.—*Anarchias cantonensis* is distinguished from all other species except *A. exulatus* and *A. schultzi* by the position of the fourth supraorbital pore, anteromedial to the posterior nostril and separated from it by an interval of normal, pigmented skin. It has fewer vertebrae (98–108) than *A. exulatus* and *A. schultzi* (110–117 and 105–113, respectively) and a longer snout–anus distance (45.1–50.6% TL vs. 40.3–45.1% and 41.5–45.4%). It also differs in color pattern from *A. exulatus* and *A. schultzi* by having discrete, sharply defined pale spots, as opposed to larger, more diffuse pale areas oriented vertically in *A. exulatus* and the uniform brown of *A. schultzi*.

Description.—Meristic and morphometric characters in Table 1. Body moderately elongate, anus at or slightly before midlength. Gill opening low on side of body. Head and snout relatively blunt, tip of snout broadly rounded; eye moderate in size, about midway between tip of snout and rictus. Anterior nostril tubular, near tip of snout, projecting anterolaterally; posterior nostril with low rim, on top of head above middle of eye. Lateral line reduced to two pores at anterior end of canal above and before gill opening. Supraorbital canal with four pores: one at tip of snout below and slightly ahead of anterior nostril (the ethmoidal pore), one directly medial to anterior nostril, one on top of snout slightly behind level of anterior nostril, and one adjacent to and slightly anteromedial to posterior nostril, separated from nostril by narrow section of pigmented skin. Infraorbital canal with four pores along upper jaw: one below and slightly behind anterior nostril, one between anterior nostril and eye, one below middle of eye, and one slightly behind posterior margin of eye; no pores behind eye. Preoperculomandibular canal with six pores, first at tip of lower jaw, last directly below rictus; no pores in preopercular section of canal.

Maxillary teeth biserial, those of outer series small, fixed, conical, recurved, and closely spaced, continuous around front of jaw with outer row of intermaxillary teeth, similar in size and shape; inner row maxillary teeth fewer, larger, and more widely spaced, conical, straight, depressible,

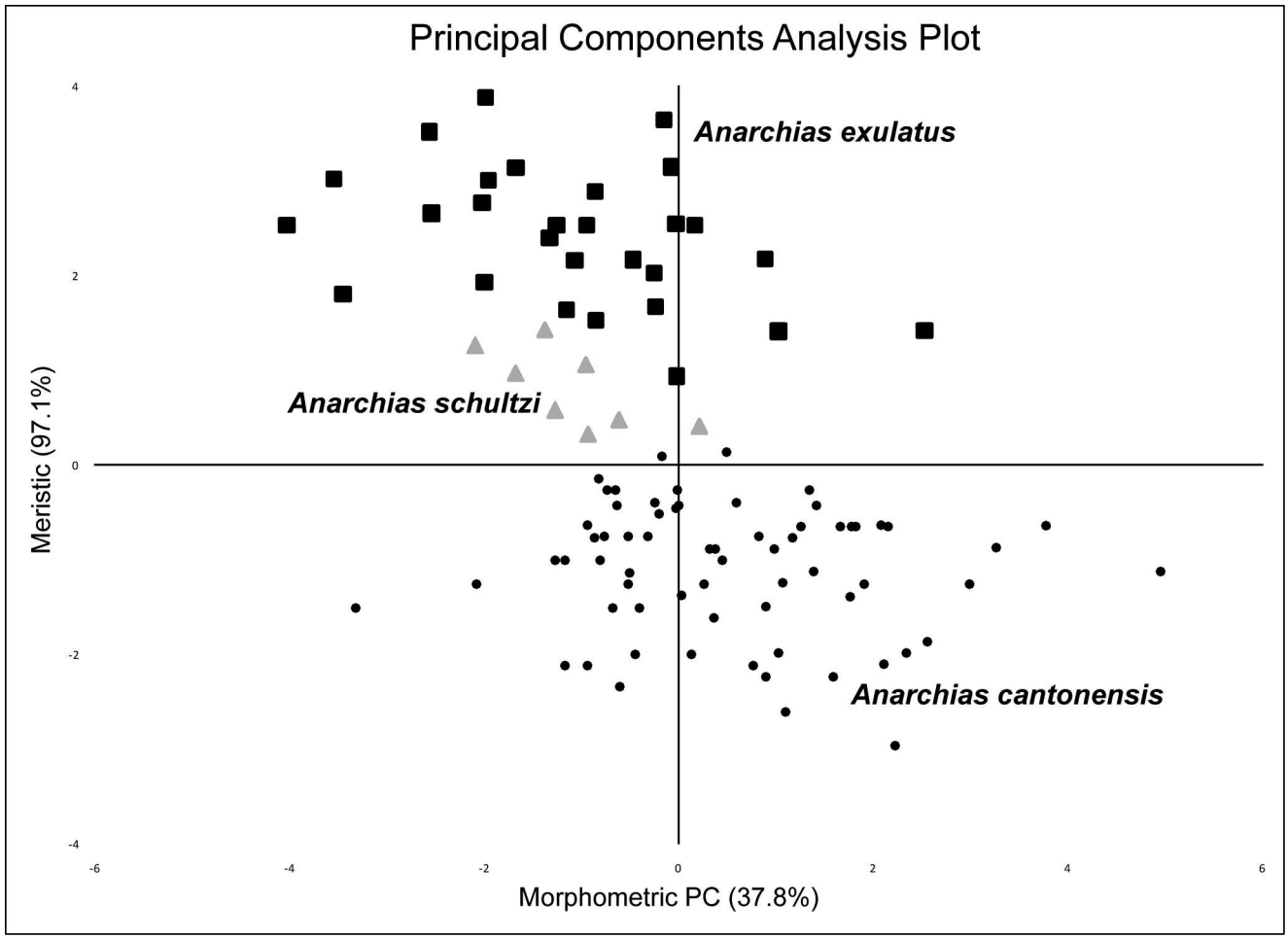

Fig. 4. Results of the Principal Component Analysis identifying three non-overlapping groups of individuals corresponding to the three uniquely colored and geographically distributed species of *Anarchias cantonensis* (circles), *A. schultzi* (triangles), and *A. exulatus* (squares).

extending posteriorly to approximate end of outer series, and continuous anteriorly with intermediate row of intermaxillary teeth, similar in size and shape. Two to three median conical, straight, depressible intermaxillary teeth, increasing in size posteriorly. Vomerine teeth small, conical, uniserial, in line with but well separated from median intermaxillary teeth. Mandibular teeth biserial, outer teeth small, fixed, recurved, continuous around front of jaw; inner teeth larger, straight, depressible, more widely spaced, continuous around front of jaw (Fig. 6).

Adults with pale, irregular stellate spots on brown background, spots usually well defined, about same size, not forming indistinct bars. Juveniles with small, round pale spots on brown background, becoming more irregular with growth (Fig. 7). A small species, the largest specimen examined 219 mm TL.

Habitat.—Most specimens have been collected in relatively shallow water on coral reefs and rocky areas along the shore. We have no records deeper than 10 meters. They are cryptic in habit and are rarely if ever seen except when collected using ichthyocides.

Distribution.—Tropical Indo-West Pacific from the central Indian Ocean in the west to the Phoenix and Line Islands in the east. The southernmost records are from about 21°S in Tonga, the northernmost from about 19°N in the Philippines. It occurs in the eastern Indian Ocean but has not been

Fig. 5. *Anarchias cantonensis*, USNM 115904, holotype, 156 mm TL.

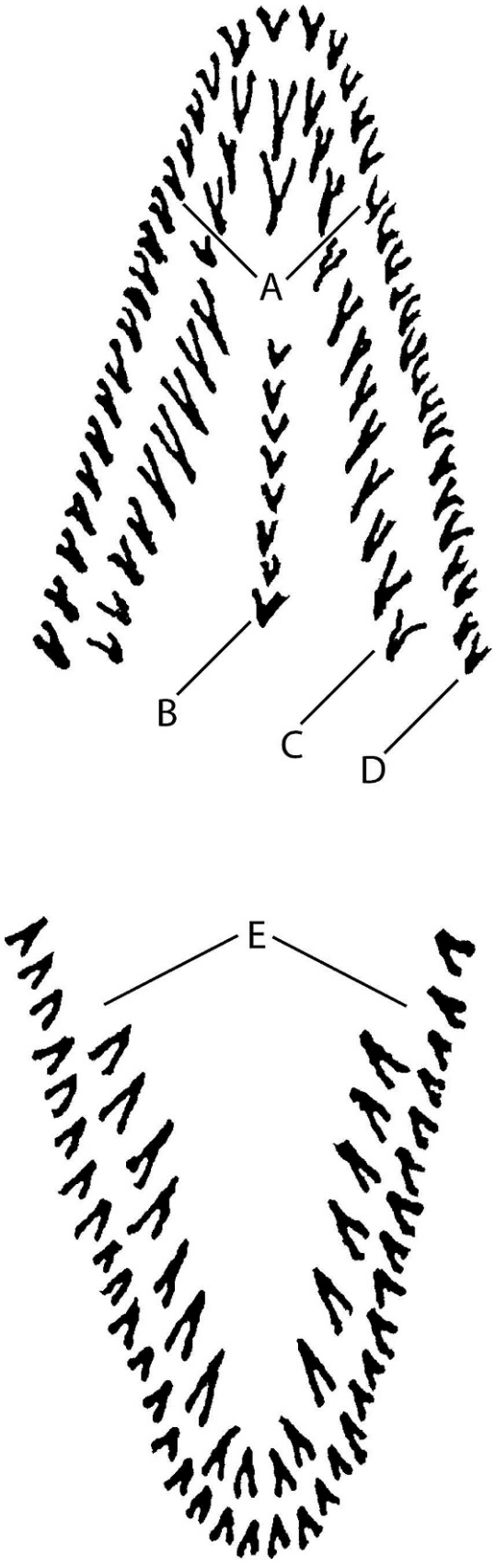

Fig. 6. Generalized tooth pattern for *Anarchias cantonensis*, *A. exulatus*, and *A. schultzi*, after Schultz (1943:fig. 3a). A = 5 rows of intermaxillary teeth above black lines (outer and intermediate intermaxillary rows are continuous with outer and inner maxillary rows, respectively), B = single row of vomerine teeth, C = inner row maxillary teeth, D = outer row of maxillary teeth, E = inner and outer rows of mandibular teeth.

recorded anywhere west of the Maldives. Although it reaches as far as Palmyra Island in the east, it does not occur in the Hawaiian Islands or anywhere in French Polynesia.

Anarchias exulatus, new species

Figures 3 (bottom), 8; Table 1

Anarchias cantonensis.—Gosline and Brock, 1960:105, 109.–Tinker, 1982:116.
Anarchias allardicei?—Gosline and Brock, 1960:105, 110.–Tinker, 1982:116.
Anarchias spp. (part).—Randall et al., 2003:6.
Anarchias sp.—Mundy, 2005:113.

Holotype.—USNM 328944, 180 mm, Tonga Islands, Tonga, Eua, fringing reef at base of cliff on NW shore, spur and groove right in the surf zone, very high energy area, 3 November 1993, J. Williams.

Paratypes.—Gambier: BPBM 13582, 1, 122, Gambier Isl., Mangareva, SW side of Tenoko Islet, outside reef in 12 m, 11 December 1970, J. Randall et al. Hawaiian Islands: BPBM 10071, 3, 58–140, Hawaii, Honaunau, Kona Coast of Hawaii, 0.8 km N of City of Refuge, rocky shore in 0.3–6 m, 20 August 1970, J. Randall et al.; BPBM 03622, 1, 183, Hawaii, French Frigate Shoal, 1923 Tanager Expedition; BPBM 11975, 1, 211, Hawaii, Oahu, Kahe Point Beach Park, reef in 11 m, 30 March 1968, J. Randall, G. Allen, et al.; BPBM 12705, 1, 189, Hawaii, Oahu, Hanauma Bay, 6 October 1951, W. Gosline and class; BPBM 03603, 1, 165, Hawaii, French Frigate Shoal, 1923 Tanager Expedition; USNM 108849, 1, 86.5, Hawaii, shallow water on reef off Mokuleia, Waialua, Oahu, 1937, O. Degener. Johnston Atoll: BPBM 11037, 1, 89.5, Johnston Atoll, outside reef about 183 m NE of small boat channel (N of W end of Johnson Is.), 6–9 m, rock and coral rubble bottom with little live coral, 26 July 1968, J. Randall et al.; BPBM 07188, 1, 125.5, lagoon reef just inside barrier reef N of W end of Johnston Is., 1–6 m, 30 July 1968, J. Randall et al.; BPBM 12676, 3, 143–163, inner reef, 23 February 1951, W. Gosline et al. Pitcairn Islands: BPBM 17069, 1, 237, Henderson Is., 0.8 km S of NW corner, rocky shore, 0–1 m, 17 January 1971, J. Randall et al. Rapa: USNM 378334, 2, 203–293, Rapa, cave at Pt. Kopaga iki, S tip of Rapa at channel between Rapa and Isle Karapoo iti, inside a steep-sided cave with surge, 9 November 2002, J. Williams et al.; BPBM 13003, 1, 242.5, Rapa, S side of Mei Point, rocky shore, 0–3 m, 14 February 1971, J. Randall and D. Cannoy. Tonga: USNM 338851, 4,103–151, Tonga, Vava'U Group, Vava'U Island, Port of Refuge on W side of Vava'U Island, on reef top and spur and groove formations at shore, 0–6 m, 18 November 1993, J. Williams et al.; USNM 397048, 5, 114–176, same data as holotype.

Diagnosis.—*Anarchias exulatus* is distinguished from all other species of the genus except *A. schultzi* and *A. cantonensis* by the position of the fourth supraorbital pore, anteromedial to the posterior nostril and separated from it by an interval of normal, pigmented skin. It has more vertebrae (110–117) than either *A. cantonensis* or *A. schultzi* (98–108 and 105–113, respectively) and can be distinguished from *A. cantonensis* by having a shorter snout–anus distance (40.3–45.1% TL vs. 45.1–50.6%). It also differs in color pattern from *A. cantonensis* and *A. schultzi*, with blurred, diffuse, and poorly defined pale spots oriented vertically, as opposed to

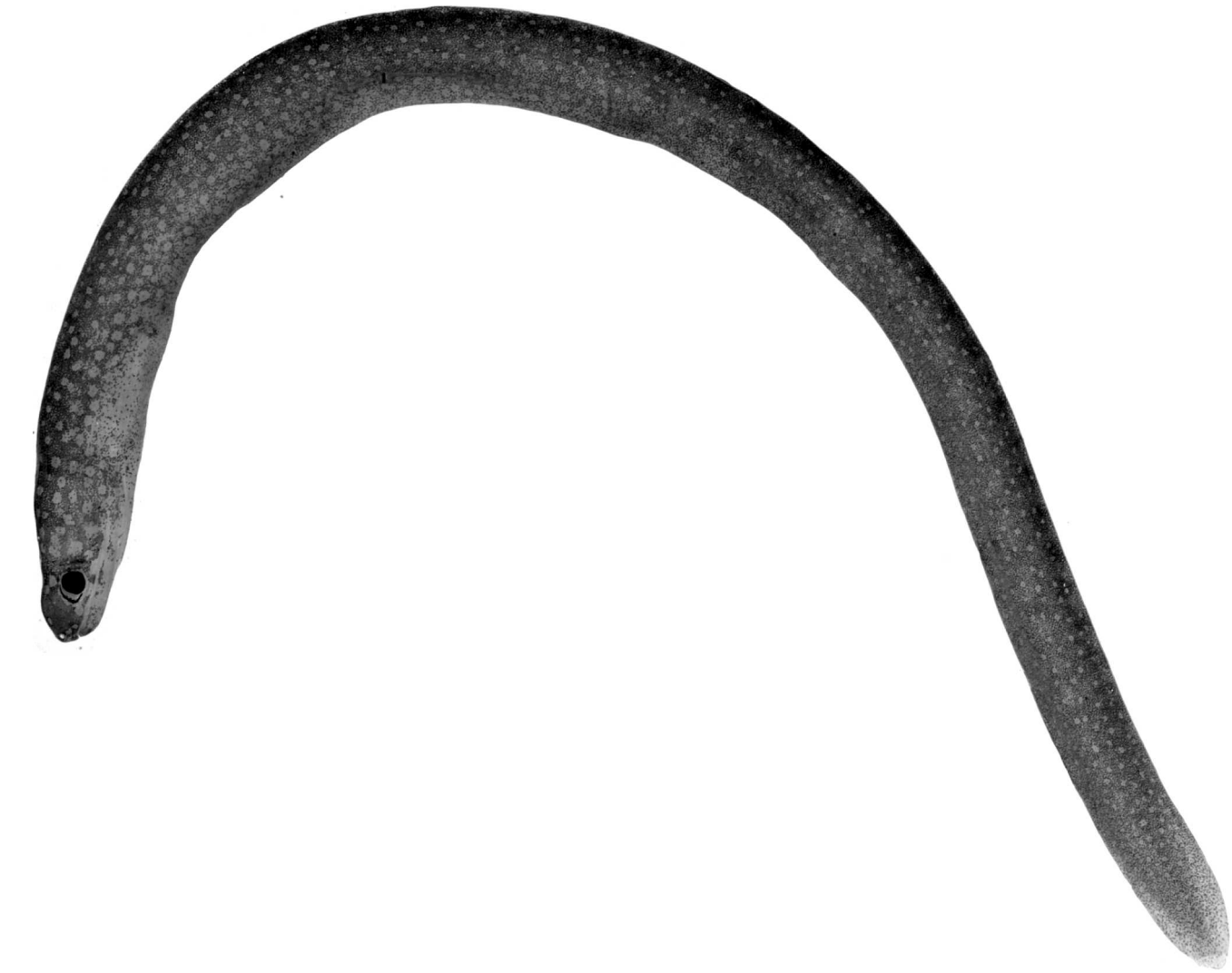

Fig. 7. Juvenile spotting in *A. cantonensis* (USNM 257324).

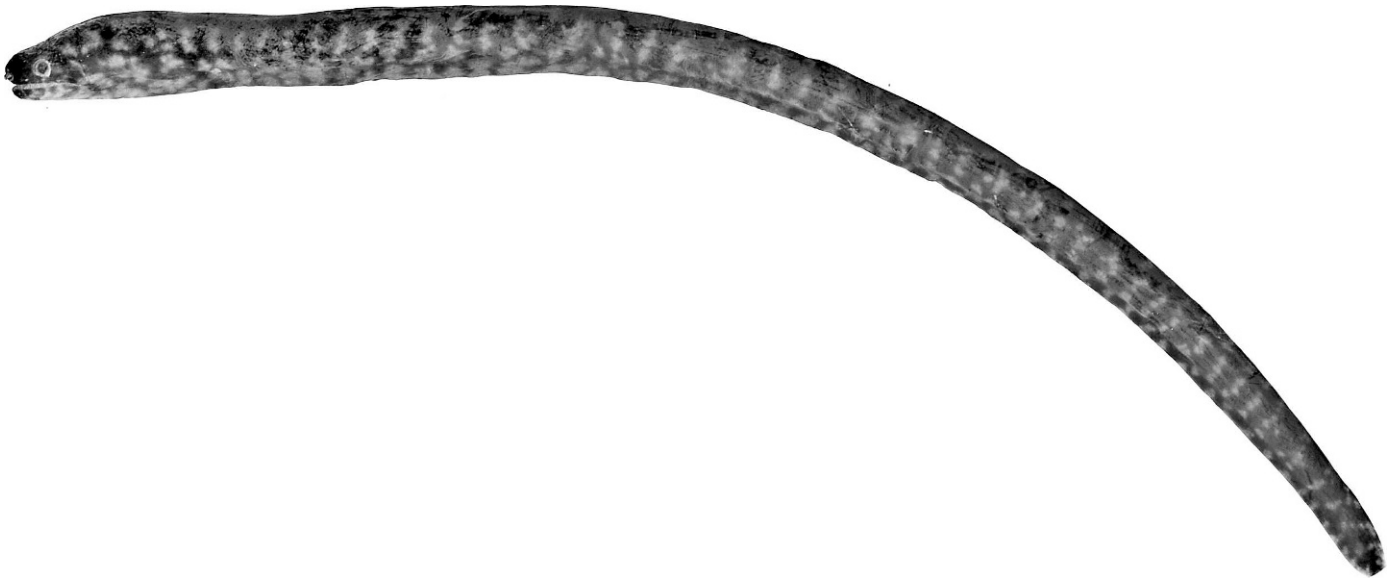

Fig. 8. *Anarchias exulatus*, USNM 328944, holotype, 180 mm SL.

Fig. 9. *Anarchias schultzi*, USNM 334773, holotype, 148 mm SL.

the clearly defined and non-vertically oriented spots of *A. cantonensis* and the uniform brown of *A. schultzi*.

Description.—Meristic and morphometric characters of the holotype as follows. TL 180 mm, snout–anus 78 mm (43.3% TL), head 23.7 mm (13.2% TL), depth at anus 7.8 mm (5.1% TL), snout 3.5 mm (16% HL), eye 1.4 mm (10% HL), snout–rictus 7.9 mm (33.3% HL), predorsal vertebrae 101, preanal vertebrae 103, total vertebrae 114. Range and mean of characters for other specimens in Table 1.

Body form moderately elongate, anus at or slightly before midlength. Gill opening low on side of body. Head and snout relatively blunt, tip of snout broadly rounded; eye moderate in size, located about midway between tip of snout and rictus. Anterior nostril tubular, near tip of snout, projecting anterolaterally; posterior nostril with low rim, on top of head above middle of eye. Lateral line reduced to two pores at anterior end of canal above and before gill opening. Supraorbital canal with four pores: one at tip of snout below and slightly ahead of anterior nostril (the ethmoidal pore), one directly medial to anterior nostril, one on top of snout slightly behind level of anterior nostril, one adjacent to and slightly anteromedial to posterior nostril, separated from nostril by narrow section of pigmented skin. Infraorbital canal with four pores along upper jaw: one below and slightly behind anterior nostril, one between anterior nostril and eye, one below middle of eye, one slightly behind posterior margin of eye; no pores behind eye. Preoperculomandibular canal with six pores, the first at tip of lower jaw, last directly below rictus; no pores in preopercular section of canal.

Maxillary teeth biserial, those of outer series small, fixed, conical, recurved, closely spaced, continuous around front of jaw with outer row of intermaxillary teeth, similar in size and shape; inner row maxillary teeth fewer, larger, more widely spaced, conical, straight, depressible, extending posteriorly to approximate end of outer series, continuous anteriorly with intermediate row of intermaxillary teeth, similar in size and shape. Two to three median conical, straight and depressible intermaxillary teeth, increasing in size posteriorly. Vomerine teeth small, conical, uniserial, in line with but well separated from median intermaxillary teeth. Mandibular teeth biserial, outer teeth small, fixed, recurved, continuous around front of jaw; inner teeth larger, straight, depressible, more widely spaced, continuous around front of jaw (Fig. 6).

Adults and juveniles with pale, irregular, diffuse and blurred pale spots on brown background, oriented vertically and forming irregular bars posteriorly. A small species, the largest specimen examined 293 mm TL.

Habitat.—Most specimens have been collected in relatively shallow water on coral reefs and rocky areas along the shore. One individual was found at a depth of 12 meters. They are cryptic in habit and are rarely if ever seen except when collected using ichthyocides.

Distribution.—Anti-tropical distribution in the central Pacific, sampled in the Hawaiian Islands, Johnston Atoll, Rapa, Gambier, and Pitcairn islands. The westernmost record is in the Tonga Islands, where all three members of this group occur.

Remarks.—The existence of this species has been known for some time and was alluded to by Böhlke and Randall (2000) and Mundy (2005). There is some confusion over what Gosline and Brock (1960) were referring to when they recorded *A. allardicei* from Hawaii. In their key they distinguished it along with *A. cantonensis* from *A. leucurus* by the position of the pore, anteromedial to the posterior nostril. The true *A. allardicei* has the pore directly medial to the nostril rather than anteromedial, so by that criterion their specimens could not be *A. allardicei*, which is not known to occur in Hawaii. They distinguished *A. ''allardicei''* from *A. cantonensis* by the lack of ''distinct dark markings'' on the head. Many of the Hawaiian specimens of *A. exulatus* that we examined from the BPBM were quite faded, and the markings were difficult to see. Based on their description of the pore–nostril configuration, we assume that their *A. allardicei* specimens were simply faded specimens of *A. exulatus*. Tinker (1982) may have just been following Gosline and Brock when he also recorded *A. allardicei* from Hawaii. There is no evidence that *A. schultzi* (see below), which does have a plain brown coloration, occurs anywhere near Hawaii.

Etymology.—The Latin word *exulatus*, meaning banished or exiled, and alluding to the geographic distribution of the species, having an anti-tropical distribution restricted to the outer fringes of the Indo-West Pacific faunal region.

***Anarchias schultzi*, new species**

Figures 3 (middle), 9; Table 1

Anarchias spp. (part).—Randall et al. (2003).

Holotype.—USNM 334773, 148, Tonga Islands, Tongatapu Group, reef just N of Atata Island, a pit in top of reef on N side of reef, 8–14 m, 28 October 1993, J. Williams et al.

Paratypes.—Caroline Islands: USNM 224067, 1, 76, Pohnpei, just east of entrance to Jokaj passage, 8 September 1980, V. Springer et al.; USNM 224439, 1, 61, Pohnpei, Nanmatol, 3 September 1980, V. Springer et al. Loyalty Islands: USNM 323563, 1, 135, Ouvea Atoll, Recif Draule, 5 m, 16 November 1991, J. Williams et al. Solomon Islands: USNM 380808, 2, 115–123, Santa Cruz Islands, Tomotu Island, coral surge channel on northwest coast just south of Neo Village, 29 September 1998, J. Williams et al. Tonga Islands: USNM 397049, 5, 108–159, same data as holotype.

Diagnosis.—*Anarchias schultzi* is distinguished from all other species of the genus except *A. cantonensis* and *A. exulatus* by the position of the fourth supraorbital pore, anteromedial to the posterior nostril and separated from it by an interval of normal, pigmented skin. It has an intermediate number of total vertebrae (105–113), with some overlap relative to *A. cantonensis* (98–108) and *A. exulatus* (110–117), but is readily

distinguished by the lack of mottling or white spots and a uniform brown color in the juvenile and adult forms.

Description.—Meristic and morphometric characters of holotype as follows. TL 148 mm, snout–anus 66 mm (44.6% TL), head 19.5 mm (13.2% TL), depth at anus 6.6 mm (4.1% TL), snout 3.1 mm (15.7% HL), eye 1.2 mm (8.1% HL), snout–rictus 6.2 mm (31.8% HL), predorsal vertebrae 94, preanal vertebrae 96, total vertebrae 108. Range and mean for other specimens in Table 1.

Body moderately elongate, anus at or slightly before midlength. Gill opening low on side of body. Head and snout relatively blunt, tip of snout broadly rounded; eye moderate in size, located about midway between tip of snout and rictus. Anterior nostril tubular, near tip of snout, projecting anterolaterally; posterior nostril with low rim, on top of head above middle of eye. Lateral line reduced to two pores at anterior end of canal above and before gill opening. Supraorbital canal with four pores: one at tip of snout below and slightly ahead of anterior nostril (the ethmoidal pore), one directly medial to anterior nostril, one on top of snout slightly behind level of anterior nostril, one adjacent to and slightly anteromedial to posterior nostril, separated from nostril by narrow section of pigmented skin. Infraorbital canal with four pores along upper jaw: one below and slightly behind anterior nostril, one between anterior nostril and eye, one below middle of eye, one slightly behind posterior margin of eye; no pores behind eye. Preoperculomandibular canal with six pores, the first at tip of lower jaw, last directly below rictus; no pores in preopercular section of canal.

Maxillary teeth biserial, those of outer series small, fixed, conical, recurved, closely spaced, continuous around front of jaw with outer row of intermaxillary teeth, similar in size and shape; inner row maxillary teeth fewer, larger, more widely spaced, conical, straight, depressible, extending posteriorly to approximate end of outer series, continuous anteriorly with intermediate row of intermaxillary teeth, similar in size and shape. Two to three median conical, straight and depressible intermaxillary teeth, increasing in size posteriorly. Vomerine teeth small, conical, uniserial, in line with but well separated from median intermaxillary teeth. Mandibular teeth biserial, outer teeth small, fixed, recurved, continuous around front of jaw; inner teeth larger, straight, depressible, more widely spaced, continuous around front of jaw (Fig. 6).

Adults and juveniles uniform light brown, without pale spots or mottling present in other two species. Holotype with small, inconspicuous dark spots scattered over body, a feature not found in other specimens. A small species, the largest specimen examined 159 mm TL.

Habitat.—Most specimens have been collected in shallow water on coral reefs and rocky areas along the shore. One individual was found at a depth of 14 meters. They are cryptic in habit and are rarely if ever seen except when collected using ichthyocides.

Distribution.—Tropical distribution in the western Pacific, sampled in the Solomon Islands, Pohnpei, and the Loyalty Islands. The easternmost record is in the Tonga Islands, where all three members of this group occur.

Etymology.—Named after Leonard P. Schultz, who described the first species of this group (*A. cantonensis*) and collected extensively in the west-central Pacific.

DISCUSSION

Moray eels are a highly understudied group. The taxonomy of Indo-Pacific morays was last thoroughly reviewed in Böhlke and Smith (2002). Current species are delimited largely on the characters of color pattern, dentition, and vertebral counts. Cryptic variation in widely distributed taxa often obscures species-level differences among taxa. In this case, we differentiate among three species based on a suite of morphological features including skeletal and external morphology. There is no reason *a priori* to expect that vertebral formulas vary in any particular direction; however, we are assuming that this feature varies stochastically according to drift and that diagnostic differences in this feature are representative of accumulated differences between divergent groups that have maintained independent evolutionary trajectories.

Anarchias cantonensis, as previously understood, is actually three species, *A. cantonensis*, *A. exulatus*, and *A. schultzi*. These groups are identified independently by a principal component analysis of external morphology and vertebral counts, and subsequent ANOVA of PC scores. Figure 4 clearly demonstrates the independent groupings represented by transformed morphological and skeletal measurements for the three species, with little to no overlap among clusters. These three groupings also correspond to three distinct color morphs: the crisply mottled *A. cantonensis*, the blotched *A. exulatus*, and the uniformly brown *A. schultzi*. A third line of evidence comes from the geographic distributions of the three species and the geological age of the inhabited reefs. *Anarchias cantonensis* is distributed throughout the central Indian Ocean (Maldives: <1 my [Kench et al., 2005; Gischler et al., 2008]; Cocos-Keeling: <2.4 my [Castillo et al., 1988]) and into the tropical central Pacific. The geological ages of islands inhabited on the Pacific Plate are all greater than 37 my old (Fig. 2)—Fiji: 65 my (Karig, 1970); Line Islands: 70–75 my (Haggerty et al., 1982; Sager and Keating, 1984; Schlanger et al., 1984); Marshall Islands: 60–140 my (Schwab, 1989); New Guinea: >37 my (Petterson et al., 1997); Phoenix Islands: 60 my (Maragos et al., 2008); Philippines: >40 my (Geary et al., 1988; David et al., 1997); Pohnpei: 38.6 my (Keating et al., 1984); Solomon Islands: >65 my (Petterson et al., 1997); Tonga: 65 my (Karig, 1970), with the exception of Pohnpei. In contrast, *A. exulatus* has an anti-tropical distribution and inhabits islands in the Pacific of much younger geological age (Pitcairn: <1 my [Blake, 1995]; Gambier: 5.7 my [Guillou et al., 1994]; Rapa: 5 my [Turner and Jarrard, 1982]; Hawaii: <1 my [Fleischer et al., 1998]). The only exception to this pattern is Johnston Atoll, which is 85 my in age (Keating, 1985, 1992). Populations of reef fish around Johnston Atoll are known to maintain gene flow with Hawaiian populations (Schultz et al., 2006), and several ''endemic'' Hawaiian reef fishes are also found there (DeMartini and Friedlander, 2004); thus, it is not surprising that it is characterized by the ''young'' island species. Tonga, the only locality where all three species coincide, is located on the boundary of the Pacific and Australian–Indian tectonic plates. The third species, *A. schultzi*, is exclusively found along the tectonic plate boundaries in Tonga and the Loyalty Islands (37 my [Neall and Trewick, 2008]) except for two specimens sampled in Pohnpei. These distributions indicate a possible correlation between the environmental and ecological factors that are determined by the geological age of a reef, the role of tectonic plate boundaries in delimiting species boundaries (Springer, 1982), and tropically vs. anti-tropically distributed sister-taxa.

Although all three species occur in Tonga, two or more were never taken at the same station, suggesting that they may be segregating themselves ecologically. Based on the field notes, there are no obvious differences in the collection localities, such as depth, but there could be some ecological factors that the three species differentially favor.

KEY TO THE INDO-PACIFIC SPECIES OF *ANARCHIAS*

1a. Fourth supraorbital pore anteromedial to posterior nostril, separated from it by a narrow space of normal, pigmented skin 2
1b. Fourth supraorbital pore medial or posterior to posterior nostril, both included in an unpigmented depression 4
2a. Color uniform brown, no markings ..... ***Anarchias schultzi*, new species** (western Pacific)
2b. Mottled or spotted 3
3a. Discrete, sharply defined pale markings on a brown background, not oriented vertically as diffuse bars; snout to anus 45–51% TL; total vertebrae 98–108 ..... ***Anarchias cantonensis*** (Indo-West Pacific)
3b. Large, diffuse pale markings, oriented vertically as irregular bars; snout to anus 40–45% TL; total vertebrae 110–117 ..... ***Anarchias exulatus*, new species** (central Pacific)
4a. Fourth supraorbital pore directly medial to posterior nostril ..... ***Anarchias allardicei*** (Indo-West Pacific)
4b. Fourth supraorbital pore posteromedial or posterior to posterior nostril 5
5a. Dorsal and anal fins greatly reduced to a few rays at tip of tail; total vertebrae circa 104 ..... ***Anarchias galapagensis*** (eastern tropical Pacific)
5b. Dorsal and anal fins less reduced, extend a short but significant distance anteriorly from tip of tail; total vertebrae circa 116–135 6
6a. Pale spots along lower half of flanks, posterior half of body with diffuse white bands, tip of tail white; total vertebrae circa 135 ..... ***Anarchias supremus*** (deep water, Kermadec Ridge)
6b. Color not as above, total vertebrae fewer than 135, circa 116–131 ..... ***Anarchias leucurus/seychellensis* complex** (shallow water, Indo-West Pacific)

MATERIAL EXAMINED

Anarchias cantonensis: Holotype: USNM 115904, 156 mm, Phoenix Islands, Canton Is., lagoon, among coral heads, 23–25 May 1939, L. Schultz. Paratypes: USNM 115905, 8, 99–161, same data as holotype; USNM 115906, 1, 88, Canton Is., reef of widest shallow channel, 13 May 1939, L. Schultz; USNM 115907, 1, 151 (erroneously reported as 93 mm by Schultz), Canton Is., lagoon, 23 April–12 May 1939, L. Schultz et al. Non-type material: Australia: USNM 236080, 1, 217, Queensland; One Tree Island tidal pool on reef flat n SE side of island, 27 November 1966, V. Springer et al. Caroline Is.: USNM 223419, 1, 125, Pohnpei, North Coast, 4 September 1980, V. Springer et al.; USNM 224440, 1, 126, same. Cocos Keeling Is.: ANSP 130617, 3, 63.5–88.5, West Island, near S end of airstrip, on ocean side, 30 March 1974, W. Smith-Vaniz et al. Fiji: USNM 257324, 1, 57, Kandavu Id, Levuka (just E of), 13 May 1982, V. Springer et al.; USNM 257328, 4, 72–98.5, same; USNM 257331, 1, 95, same; USNM 312820, 1, 132, same. Line Is.: BPBM 14078, 2, 94–142, Palmyra Is., reef flat on N side of Cooper Is. near outer edge in 0.3 m at low tide, 13 November 1968, J. Randall. Maldive Is.: FMNH 75491, 5, 87–125, Imma Is., Male Atoll, Te Vega Sta. 119, 21 March 1964, L. Woods et al.; SIO 69200, 1, 101, E side of Huele, Male Atoll, 8 November 1964, L. Taylor. Marshall Is.: ANSP 124310, 1, 152, from Bikar, Taka, or Kwajalein Atolls, 15 October 1964, A. Amerson; ANSP 138750, 7, 53.5–162, from Bikar, Taka, or Kwajalein Atolls, 15 October–11 November 1964; USNM 141670, 1, 68, Rongerik Atoll, Bock Island, ocean reef, tidal pool not fully isolated, but high up near shore with scattered coral, 24 April 1946, V. Brock; USNM 141685, 1, 186, Bikini Atoll, Romurikku (Romuk) Island, lagoon side along ledge, with some crevices, near shore, 2 April 1946, L. Schultz; USNM 141686, 1, 133, Rongelap Atoll, Enyubarbar Island, isolated tidal pool at southern end of Enyubarbar Island, 18 June 1946, L. Schultz; USNM 154559, 3, 86–141, Kwajalein, NE tide pool, 24 June 1949, E. Clark. New Guinea: AMS 17102054, 7, 89–147, ANSP 144824, 3, 90.5–146, Ninigo Islands, Meman Island, Mid-East shore, 27 October 1978, V. Springer et al. Philippines: ANSP 141411, 1, 74.5, Siquijor Island; W side ca. 2 km NW of Paliton Village, 10 May 1978, V. Springer et al.; USNM 318043, 5, 76–130, Maybag Island (Babuyan Island group), saltwater coral and tide pool area along SE coast of island, 7 March 1990, C. Ross et al.; USNM 328908, 1, 56, east coast of Luzon, San Bernardino Strait to San Miguel Bay: Port Gubat, 23 June 1909, Albatross; USNM 341477, 1, 73, Maybag Island (Babuyan Island Group), saltwater, coral, and tide pool area along SE coast of island, 7 March 1990, C. Ross. Solomon Is.: USNM 383453, 1, 49, Santa Cruz Islands, Duff Islands, Lakao at NW point in a small cove in surge channels in big boulders, 24 September 1998, J. Williams et al.

Anarchias schultzi: USNM 382401, 1, 39, Santa Cruz Islands, Ndendo Island (Santa Cruz Island), steep reef face northeast side of Nemya Island in dense live coral, 28 September 1998, J. Williams et al. (excluded from type series because of its small size and our inability to obtain a vertebral count).

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