



***Pomacentrus flavioculus*, a new species of damselfish from Fiji and Tonga (Teleostei: Pomacentridae)**

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Abstract

Pomacentrus flavioculus n. sp. is described on the basis of 140 specimens, 17.1–86.8 mm SL, from Fiji and Tonga in the South Pacific Ocean. The new species was formerly identified as *Pomacentrus imitator* (Whitley, 1964), which now appears to be restricted to the Coral Sea. The new species clearly differs from *P. imitator* on the basis of several color-pattern features, including a bright yellow ring that encircles the pupil, a more uniform body color (vs. contrasting pale scale centers and dark scale margins), a yellowish caudal fin (vs. whitish), and a small orange marking immediately above the large black spot that covers the pectoral-fin base (absent in *P. imitator*). Although meristic and morphological features are broadly similar, *P. flavioculus* has a strong mode of 14 anal-fin rays vs. 15 in *P. imitator*. Additionally, *P. flavioculus* usually has a greater preanal distance and almost always has a longer pelvic-fin spine. A phylogenetic analysis of concatenated mtDNA sequences shows the new species is 8.4% divergent (average pairwise distance) from its nearest relatives and is part of the broad *Pomacentrus philippinus* species complex.

Key words: coral reef fishes, taxonomy, systematics, ichthyology, Indo-Pacific Ocean, mitochondrial DNA

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Introduction

Pomacentrus philippinus Evermann & Seale, 1907, was described from southeastern Luzon, Philippines, but then subsequently reported from numerous locations in the East Indies and adjacent regions, from the Great Barrier Reef north to the Ryukyu Islands of Japan, and the Maldives east to Micronesia and Samoa (Allen 1975, 1991, Randall *et al.* 1990, Myers 1989, 1999, Allen & Erdmann 2012). However, a study by Allen *et al.* (2017) revealed that this species is actually a complex of several cryptic species, separable on the basis of color pattern differences and occasional modal meristic differences, and breaking up into several divergent mtDNA lineages that correspond to the color morphs. The members of this species complex form a monophyletic set of mtDNA lineages and share similar morphological and meristic features, as well as a characteristic appearance made up of a network pattern on the sides of the body imparted by thick, dark scale margins, and the frequent presence of scales on either or both of the preorbital and suborbital bones. Most species also possess abruptly pale posterior dorsal- and anal-fin rays, which, depending on the species, are translucent, whitish, orange, or yellow with matching caudal-fin coloration. They are also characterized by having several short filaments on the posterior edge of the caudal fin, often concentrated at the apex of the upper and lower lobes. Unlike many other members of the genus, juveniles lack an ocellus on the dorsal fin and are generally bluish or bluish gray.

Four new species belonging to the *P. philippinus* group, including *P. albiaxillaris* (Palau), *P. flavoaxillaris* (Ulithi, Chuuk, and Pohnpei), *P. magniseptus* (Great Barrier Reef), and *P. nigriradiatus* (Vanuatu, New Caledonia, and Samoa) were described by Allen *et al.* (2017). These authors noted that *P. imitator* (Whitley, 1964), originally described from the Coral Sea and supposedly ranging eastward to Fiji and Tonga (Allen 1991, Randall 2005), was also a member of the *P. philippinus* group, despite almost always lacking any preorbital or suborbital scales, as found in other members. More recently, an underwater photograph of *P. imitator* from the Coral Sea (sent to the first author by Dianne Bray of Museums Victoria, Melbourne, Australia), prompted a detailed comparison with the Fiji and Tonga population. We conclude on the basis of color-pattern and morphological and meristic differences that the population from Fiji and Tonga represents a new species.

Materials and Methods

Type specimens are deposited at the Royal Ontario Museum, Toronto, Canada (ROM), National Museum of Natural History, Washington, D.C. (USNM), and Western Australian Museum, Perth (WAM). Although we did not examine specimens at the California Academy of Sciences (CAS), there are 53 lots of non-type specimens of the new species deposited there (D. Greenfield, pers. comm.).

Lengths of specimens are given as standard length (SL) measured from the anterior end of the upper lip to the base of the caudal fin (posterior edge of the hypural plate); head length (HL) is measured from the same anterior point to the posterior edge of the opercle flap; body depth is the maximum depth taken vertically between the belly and base of the dorsal-fin spines; body width is the maximum width just posterior to the gill opening; snout length is measured from the anterior end of the upper lip to the anterior edge of the eye; orbit diameter is the horizontal fleshy diameter, and interorbital width the least fleshy width; upper-jaw length is taken from the front of the upper lip to the posterior end of the maxilla; caudal-peduncle depth is the least depth, and caudal-peduncle length is the horizontal distance between verticals at the rear base of the anal fin and the caudal-fin base; lengths of fin spines and rays are measured to their extreme bases (i.e. not from the point where the ray or spine emerges from the basal scaly sheath); caudal-fin length is the horizontal length from the posterior edge of the hypural plate to a vertical at the tip of the longest ray; caudal concavity is the horizontal distance between verticals at the tips of the shortest and longest rays; pectoral-fin length is the length of the longest ray; pelvic-fin length is measured from the base of the pelvic-fin spine to the filamentous tip of the longest soft ray; pectoral-fin ray counts include the small splint-like uppermost rudimentary ray; only the tube-bearing anterior lateral-line scales are counted; a separate count is given for the deeply pitted scales occurring in a continuous series midlaterally on the caudal peduncle; the decimal figure “.5” appearing in the scale row count refers to a small truncated scale at the base of the fin; gill-raker counts include all rudiments and are presented as separate counts for the upper and lower limbs as well as a combined count; the last fin-ray element of the dorsal and anal fins is usually branched near the base and is counted as a single ray.

Counts of fin rays, tubed lateral-line scales, and gill rakers are based on 61 specimens and proportional measurements were taken for 26 specimens, 45.3–86.8 mm SL. Counts and proportions appearing in parentheses apply to the range for the paratypes if different from the holotype, followed by the mean value when referring to body proportions. Proportional measurements (expressed as percentage of the standard length) and counts for soft dorsal-fin rays, soft anal-fin rays, pectoral-fin rays, total gill rakers on the first arch, and tubed lateral-line scales are presented in Tables 1 & 2.

DNA sequences were obtained from 4 individuals of putative *Pomacentrus imitator* species from Fiji and 2 true *P. imitator* from the Coral Sea. In addition, we utilized DNA sequences from 3 individuals of *P. philippinus* from the Philippines and 19 individuals from other members of the western Pacific *P. philippinus* complex (see Allen *et al.* 2017), including *P. albiaxillaris*, *P. flavoaxillaris*, *P. magniseptus*, and *P. nigriradiatus* (GenBank accession numbers for 16S in Fig. 5; COI: KY463238–KY463251, KY463257–KY463264, MF828502–MF828506; CR: MF828507–MF828511, MF828542–MF828563). The specimens were fixed in 95% EtOH and stored at room temperature until tissues were processed for DNA extraction. Mitochondrial DNA was extracted using a 10% Chelex solution (Walsh *et al.* 1991). Portions of the 16S, cytochrome oxidase subunit I (COI), and control region loci were amplified via PCR using the primers 16Sar [5'-cgc ctg tt atc aaa aac at-3']/16Sbr [5'-ccg gtc tga act cag atc acg t-3'] (Westneat & Alfaro 2005), fish BCH [5'-taa act tca ggg tga cca aaa aa-3']/fish BCL [5'-tca acy aat cay aaa gat aty gg-3'] (Matt Craig, pers. comm.) and CRK [5'-agc tca gcg cca gag cgc cgg tct tgt aaa-3']/CRE [5'-cct gaa gta gga acc aga tg-3'] (Lee *et al.* 1995), respectively. The PCR reaction was carried out in 25 µL volumes, using 1 µL of template. Each reaction included 4 µL 10x PCR buffer (Applied Biosystems), 2.5 µL 10 mM dNTPs, 1.25 µL of each primer at 10 mM, 2 µL 25 mM MgCl₂ solution, 0.125 µL AmplyTaq Gold™ (Applied Biosystems), and 14.5 µL ddH₂O. The thermocycling profile included an initial denaturation of 94°C for 3 min, 35 cycles of 94°C for 30s, 53°C for 30s, and 72°C for 60s, with a final extension of 72°C for 2 min. The PCR reactions were checked on 1% agarose gels stained with ethidium bromide. The PCR product was sequenced at the UC Berkeley sequencing facility. Forward and reverse sequences were proofread using MEGA5 (Tamura *et al.* 2011), and then aligned using CLUSTALW with subsequent alignment by eye. Phylogenetic analyses were performed using Bayesian reconstruction methods in BEAST v1.7 (Drummond & Rambaut 2007) with the concatenated alignment of the three loci. The model that best fit the data for each locus was chosen using jModeltest 0.1.1 (Guindon & Gascuel 2003, Posada 2008), while all other priors were left as the default values in BEAUTi (Drummond & Rambaut 2007). All BEAST analyses were run for a total of 500 million generations and sampled every 5000 generations. Convergence and the consequent proportion of burn-in were assessed using Tracer v.1.5 (available from <http://beast.bio.ed.ac.uk/>). Genetic distances from concatenated data were generated using Patristic (Fourment & Gibbs 2006).

Pomacentrus flavioculus, n. sp.

Yelloweye Damselfish

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Figures 1, 2, 4A; Tables 1 & 2.

Pomacentrus philippinus (non Evermann & Seale) Allen 1975: 218 & 225, lower figure (in part, Fiji).

Pomacentrus imitator (non Whitley) Allen 1991: 147, lower figure (in part, Fiji and Tonga); Randall 2005: 379 (Fiji and Tonga).

Holotype. WAM P.30151-001, 72.4 mm SL, Fiji, Lau Archipelago, Vatoa Island, 19° 48' S, 178° 15' W, A.D. Lewis, 14 June 1986.

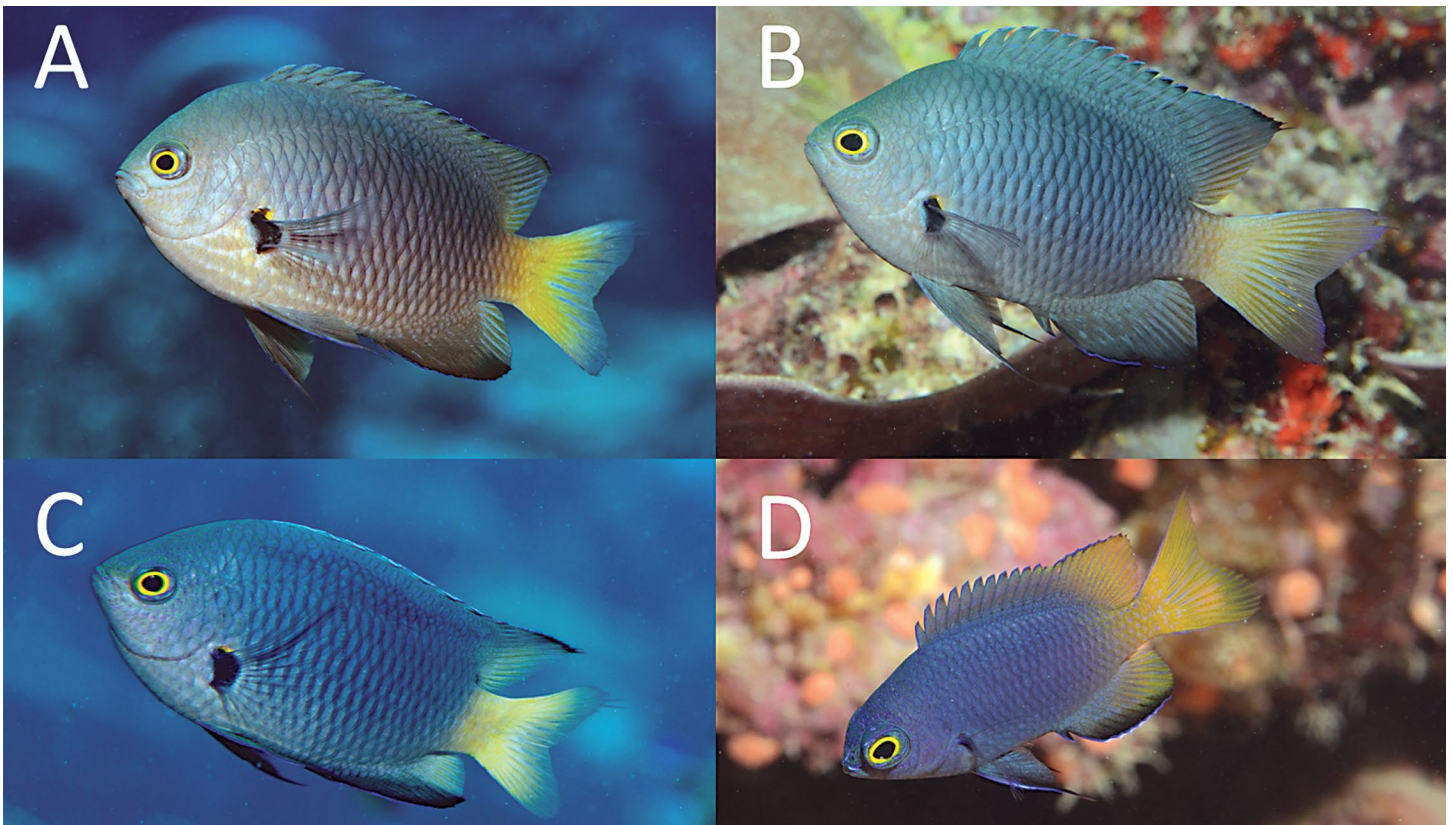


Figure 1. *Pomacentrus flavioculus*, Lau Archipelago, Fiji, underwater photographs: A) approx. 70 mm SL, B) approx. 55 mm SL, C) subadult, approx. 45 mm SL, D) juvenile, approx. 20 mm SL (G.R. Allen).

Paratypes. ROM 48799, 12 specimens, 31.1–76.2 mm SL, Fiji, Great Astrolabe Reef, 18° 37.084' S, 178° 30.344' E, rotenone, A. Emery *et al.*, 24 March 1983; ROM 48802, 37 specimens, 27.1–76.4 mm SL, Fiji, Yasawa Goup, Nanuyasawatu Island, 16° 43.011' S, 177° 36.114' E, rotenone, A. Emery *et al.*, 29 April 1983; ROM 90814, 10 specimens, 25.8–72.1.0 mm SL, Fiji, Great Astrolabe Reef, 18° 43.793' S, 178° 32.284' E, rotenone, A. Emery *et al.*, 2 April 1983; ROM 90820, 16 specimens, 17.1–77.8 mm SL, Fiji, Great Astrolabe Reef, Dravuni Island, 18° 45.447' S, 178° 31.217' E, rotenone, A. Emery *et al.*, 28 March 1983; USNM 275233, 25 specimens, 32.8–68.0 mm SL, Fiji, Naviti Island, 17° 06' S, 177° 13' E, 17–24 m, rotenone, V. Springer *et al.*, 28 May 1982; USNM 333945, 21 specimens, 58.0–86.8 mm SL, Tonga, Tongatapu, Atata Island, 21° 02' 08" S, 175° 12' 22" W, 15–20 m, rotenone, J.T. Williams *et al.*, 22 October 1993; USNM 337921, 8 specimens, 57.7–73.3 mm SL, Tonga, Vava'u Group, Luamoko Island, 18° 40' 55" S, 174° 06' 09" W, 21–31 m, rotenone, J.T. Williams *et al.*, 15 November 1993; WAM P.30147-001, 10 specimens, 31.7–72.8 mm SL, Fiji, Great Astrolabe Reef, Vuro Island, 19° 52' S, 178° 30' E, 5–15 m, rotenone, R. Bolin *et al.*, 8 May 1965.

Diagnosis. A species of the pomacentrid genus *Pomacentrus* with the following combination of characters: dorsal-fin rays usually XIII,14; anal-fin rays usually II,14–15; pectoral-fin rays 17–18; tubed lateral-line scales usually 16–18; total gill rakers on first arch usually 23–24; body depth 1.6–2.1 (mean 1.9) in SL; scales absent on preorbital and suborbital bones; color in life generally bluish gray with blackish scale margins producing network pattern; caudal fin and adjacent caudal peduncle dull yellow; intense black spot covering pectoral-fin base, including axil, its upper margin narrowly orange; eye with bright yellow ring around pupil and narrow blue stripe (often interrupted) on dorsal scleral surface.

Description. Dorsal-fin rays XIII,14 (2 with XIII,13); anal-fin rays II,14 (II,13–15), all dorsal- and anal-fin soft rays branched, last to base; pectoral-fin rays 18 (15–18), lowermost 1–2 rays and uppermost pair unbranched; pelvic-fin rays I,5; principal caudal-fin rays 15, median 13 branched; upper procurrent caudal-fin rays 6 (6–7) and lower procurrent caudal-fin rays 6, posterior pair segmented; scales in longitudinal series 27; tubed lateral-line scales 16 or 17 (15–18); posterior midlateral scales with a pore or deep pit (in continuous series) 8 (7–8); scales above lateral line to origin of dorsal fin 3; scales above lateral line to base of middle dorsal spine 1.5; scales below lateral line to origin of anal fin 9; gill rakers 7+16 (6–8+15–18), total rakers 23 (22–25); pseudobranch filaments 14 (13–15); total vertebrae 26 (8 specimens).

Body ovate, depth 1.9 (1.6–2.1, 1.9) in SL, and compressed, width 2.9 (2.3–3.3, 2.9) in body depth; HL 3.6 (3.2–3.6, 3.4) in SL; dorsal profile of head evenly rounded from dorsal-fin origin to snout; snout shorter than orbit, length 3.6 (3.3–4.2, 3.7) in HL; orbit diameter 3.1 (2.6–3.5, 3.0) in HL; interorbital space convex, width 3.0 (2.7–3.2, 2.9) in HL; caudal-peduncle depth 1.7 (1.7–2.1, 1.8) in HL; caudal-peduncle length 2.5 (2.0–2.8, 2.4) in HL.

Mouth terminal, small, and oblique, forming an angle of about 35–40° to horizontal axis of head and body; maxilla reaching a vertical about even with anterior edge of pupil, upper-jaw length 3.3 (3.1–3.6, 3.3) in HL; teeth of jaws uniserial posteriorly, becoming biserial at front of jaws with addition of slender buttress teeth in spaces between main row of larger teeth; teeth incisiform to conical, about 40–42 in main row of each jaw of holotype (excluding buttress teeth). Tongue triangular with rounded tip, set far back in mouth. Gill rakers long and slender, longest on lower limb near angle, about two-thirds length of longest gill filaments. Nostril round with slightly raised rim, level with lower edge of pupil and about midway between anterior edge of eye and upper lip.

Opercle ending posteriorly in flat spine, tip obtuse, barely projecting from beneath a large scale; rear margin of preopercle with 20 tiny serrae on left side of holotype (17–27); preorbital with single serra separated by rounded notch from suborbital series; lower edge of suborbital smooth or with one or more tiny serrae.

Scales finely ctenoid; head scaled except lips and tip of snout; preorbital (lacrimal) and suborbital scaleless; scaly sheath at base of dorsal and anal fins, averaging about two-thirds pupil width at base of dorsal fin and about the same width at base of anterior part of anal fin, tapering in width on anteriormost and posteriormost sections; column of scales on each membrane of dorsal and anal fins narrowing distally, those on spinous portion of dorsal fin progressively longer, reaching at least two-thirds distance to spine tips on posterior membranes, and covering as much as half of soft portion of dorsal and anal fins; small scales on caudal fin extending about 60–70% of distance to posterior margin; small scales on basal 30–35% of pectoral fins; a cluster of several scales forming a median process, extending posteriorly from between base of pelvic fins, its length 54–72% that of pelvic-fin spine; axillary scale above base of pelvic-fin spine, its length 56–75% length of pelvic-fin spine.

Origin of dorsal fin over third or fourth tubed lateral-line scale, predorsal distance 2.6 (2.5–2.7, 2.5) in SL; base of soft portion of dorsal fin contained about 1.8 times in base of spinous portion; dorsal-fin spines gradually increasing in length to last spine; first dorsal-fin spine 4.2 (3.1–5.2, 3.9) in HL; seventh dorsal-fin spine 2.1 (1.7–2.3, 2.0) in HL; last dorsal-fin spine 1.9 (1.5–2.0, 1.7) in HL; membranes of spinous portion of dorsal fin moderately incised between spine tips; seventh dorsal-fin soft ray longest, 1.1 (1.0–1.4, 1.2) in HL; first anal-fin spine 3.8 (3.2–4.8, 3.9) in HL; second anal-fin spine 1.8 (1.5–2.0, 1.8) in HL; longest (ninth) anal soft ray 1.3 (1.1–1.8, 1.3) in HL; caudal fin moderately forked with rounded to moderately angular lobes, its length 2.6 (2.3–3.4, 2.9) in SL; posterior margin of caudal fin frequently with short filamentous extensions (abraded or absent in preserved specimens); fourth pectoral-fin ray longest, 2.9 (2.6–3.1, 2.9) in HL; pelvic-fin spine 1.6 (1.4–2.0, 1.6) in HL; first soft ray of pelvic fin forming filamentous tip, 2.8 (2.5–3.2, 2.8) in SL.

Color in life. (Fig. 1) Body of adult overall bluish gray with blackish scale margins producing a network pattern, grading to pale yellowish on caudal peduncle; head bluish gray dorsally, grading to brownish on cheek and lower opercle, usually with scattered blue markings, including small spots on nape, interorbital, and snout, streaks below eye, and sometimes larger, faint spots on cheek and opercle; eye with bright yellow ring around pupil and a narrow blue stripe (often interrupted) on dorsal scleral surface; dorsal fin mainly dark bluish gray with fine blue outer margin, except posterior edge of fin translucent to slightly yellowish; anal fin bluish gray with broad black outer margin from fin origin to posterior apex, posterior edge of fin translucent yellowish; caudal fin pale yellow, grading to translucent on posterior margin; pelvic fins gray to blackish with narrow blue anterior margin; pectoral fins translucent with dusky gray rays, intense black spot covering base, including axil, its upper margin narrowly orange. Small juveniles generally blue, grading to yellow on caudal peduncle with bright blue spot or streak on most scales; spinous portion of dorsal fin grayish with narrow blue outer margin, soft portion yellow; anal fin bluish with blue-edged, broad, black outer margin anteriorly, posterior half of fin yellowish; caudal fin yellow; pelvic fins dusky gray with blue anterior margin; blue markings on head and yellow ring around pupil similar to adult; dark spot on uppermost pectoral-fin base with blackish to dark blue spot covering upper two-thirds of base.

Color in alcohol. (Fig. 2) Generally brown with darker brown scale margins, grading to tan on caudal peduncle, and lighter brown on head and thorax; dorsal and anal fins mainly dark brown; caudal fin pale tan; pectoral fins semitranslucent with black spot covering base, including axil; pelvic fins blackish.



Figure 2. *Pomacentrus flavioculus*, preserved holotype, WAM P.30151-001, 72.4 mm SL, Vatoa Island, Lau Archipelago, Fiji (G.R. Allen).

Etymology. The new species is named *flavioculus* (Latin: yellow eye) with reference to the diagnostic yellow ring that encircles the pupil.

Distribution. The new species is known only from Fiji and Tonga (Fig. 3), where it is commonly encountered in depths of about 4–30 m. It occurs on both outer reefs and in lagoons, usually adjacent to steep coral formations with abundant ledges and overhangs.

Comparisons. The new species is a member of the *Pomacentrus philippinus* species complex, which contains 7 species in the western Pacific Ocean (Fig. 3), and at least three additional undescribed species that range as far

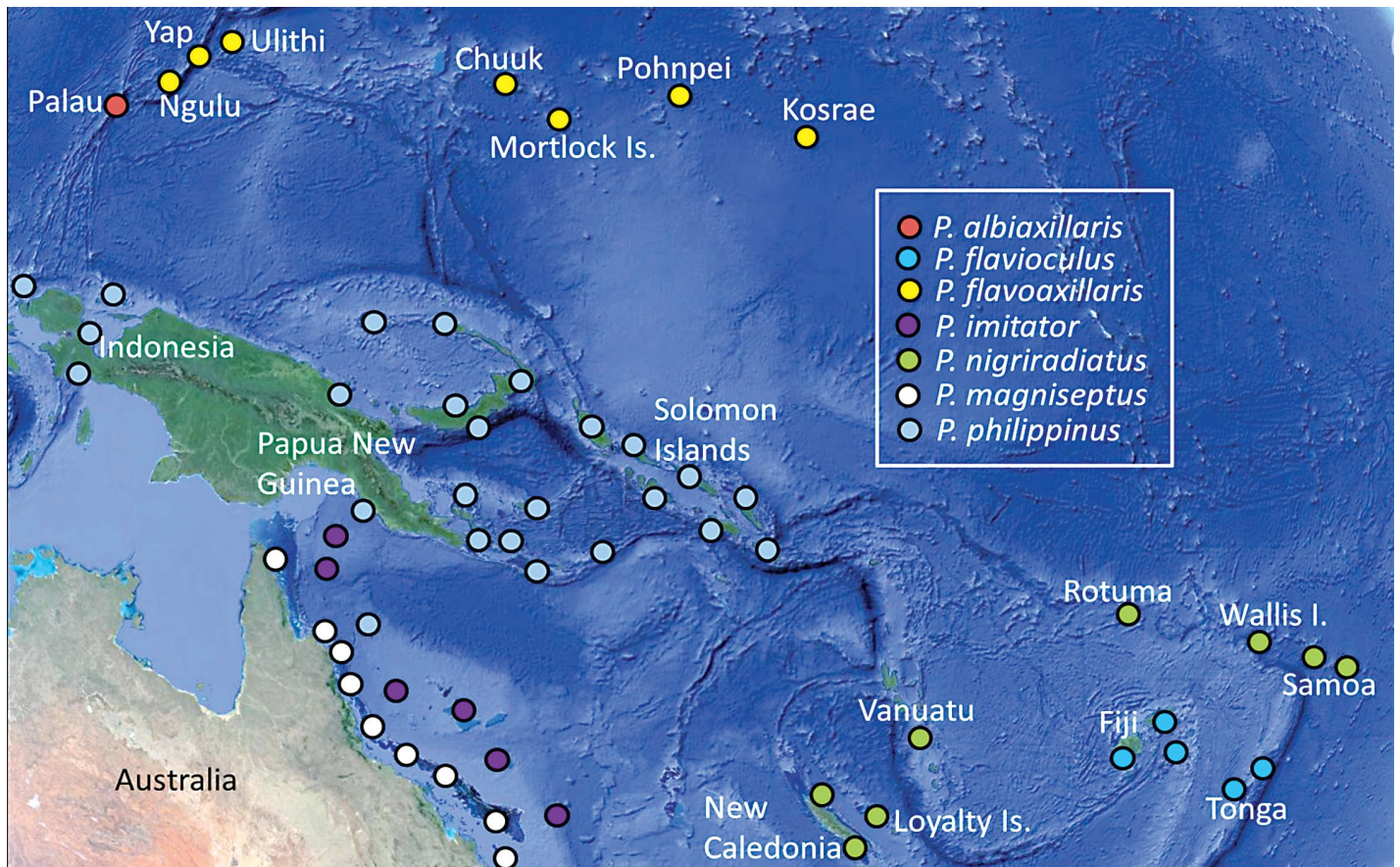


Figure 3. Map of the western Pacific Ocean region with distributions of the *Pomacentrus philippinus* species complex.

TABLE 1

Proportional measurements of selected type specimens of *Pomacentrus flavioculus*, n. sp.
as percentages of the standard length

| | holotype | | | | paratypes | | | | | |
|-----------------------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|--------------|----------------|----------------|
| | WAM P.30151 | USNM 333945 | USNM 333945 | USNM 333945 | WAM P.30147 | WAM P.30147 | WAM P.30147 | ROM 48799 | WAM P.30147 | WAM P.30147 |
| Standard length (mm) | 72.4 | 86.8 | 76.9 | 70.9 | 66.6 | 63.5 | 61.9 | 58.6 | 55.4 | 49.4 |
| Body depth | 53.7 | 53.4 | 56.4 | 60.7 | 51.5 | 51.3 | 53.3 | 51.7 | 50.9 | 54.6 |
| Body width | 18.8 | 18.9 | 18.8 | 19.3 | 16.2 | 17.2 | 18.6 | 19.0 | 15.8 | 17.1 |
| Head length | 28.2 | 31.1 | 30.1 | 28.8 | 28.4 | 28.2 | 29.4 | 29.3 | 29.0 | 30.5 |
| Snout length | 7.7 | 8.8 | 7.9 | 8.7 | 7.7 | 7.5 | 7.1 | 7.9 | 7.7 | 7.8 |
| Orbit diameter | 9.0 | 8.9 | 9.9 | 9.7 | 9.8 | 9.3 | 10.2 | 10.0 | 10.4 | 11.7 |
| Interorbital width | 9.5 | 9.7 | 10.5 | 10.3 | 10.0 | 9.6 | 10.1 | 9.9 | 9.9 | 10.9 |
| Caudal-peduncle depth | 16.6 | 15.1 | 16.2 | 16.8 | 15.8 | 15.4 | 16.3 | 15.5 | 15.8 | 15.5 |
| Caudal-peduncle length | 11.4 | 12.4 | 11.9 | 11.5 | 12.1 | 12.4 | 12.1 | 10.4 | 11.6 | 14.3 |
| Upper jaw length | 8.6 | 8.5 | 9.3 | 8.8 | 8.3 | 9.0 | 8.8 | 8.6 | 8.8 | 9.5 |
| Predorsal length | 38.4 | 39.1 | 40.7 | 41.7 | 37.9 | 37.3 | 40.5 | 38.7 | 38.8 | 40.2 |
| Preanal length | 65.0 | 69.0 | 67.5 | 67.6 | 66.0 | 65.2 | 69.5 | 66.5 | 65.9 | 66.3 |
| Prepelvic length | 38.9 | 43.5 | 43.9 | 41.8 | 37.4 | 38.1 | 38.8 | 40.0 | 38.1 | 38.2 |
| Length dorsal-fin base | 64.1 | 64.3 | 65.0 | 66.2 | 65.0 | 65.4 | 64.8 | 65.3 | 63.6 | 65.0 |
| Length anal-fin base | 29.9 | 29.4 | 29.8 | 31.6 | 28.8 | 29.5 | 30.2 | 30.0 | 28.4 | 29.1 |
| Length pectoral fin | 34.5 | 33.3 | 34.6 | 38.0 | 34.3 | 37.4 | 36.2 | 32.6 | 32.6 | 36.0 |
| Length pelvic fin | 36.4 | 34.1 | 35.1 | 36.9 | 37.7 | 33.0 | 38.3 | 38.3 | 35.0 | 37.0 |
| Length pelvic-fin spine | 17.2 | 15.6 | 17.6 | 18.7 | 18.4 | 20.2 | 18.3 | 17.3 | 18.7 | 18.0 |
| Length first dorsal spine | 6.7 | 8.2 | 7.3 | 7.9 | 7.9 | 7.9 | 7.9 | 7.7 | 7.1 | 6.9 |
| Length second dorsal spine | 13.5 | 16.5 | 13.3 | 16.7 | 14.6 | 14.1 | 15.0 | 15.4 | 13.6 | 13.4 |
| Length seventh dorsal spine | 15.1 | 17.4 | 16.8 | 18.6 | 16.7 | 16.9 | 17.2 | 17.0 | 16.3 | 16.6 |
| Length longest dorsal ray | 24.7 | 22.6 | 23.4 | 24.2 | 23.5 | 28.3 | 28.9 | 20.4 | 26.4 | 26.0 |
| Length first anal spine | 7.5 | 7.4 | 7.5 | 7.6 | 7.9 | 7.9 | 7.0 | 8.4 | 6.7 | 7.3 |
| Length second anal spine | 15.3 | 15.5 | 17.0 | 17.3 | 16.7 | 16.0 | 17.1 | 17.7 | 14.7 | 16.3 |
| Length longest anal ray | 21.4 | 21.6 | 22.1 | 23.0 | 25.3 | 22.2 | 24.8 | 23.6 | 22.8 | 19.0 |
| Length caudal fin | 39.1 | 29.2 | 31.3 | 36.4 | 33.4 | 37.4 | 38.2 | 35.2 | 40.8 | 42.9 |
| Caudal concavity | 10.3 | 8.0 | 8.1 | 12.3 | 7.3 | 8.5 | 8.1 | 11.9 | 12.2 | 13.1 |

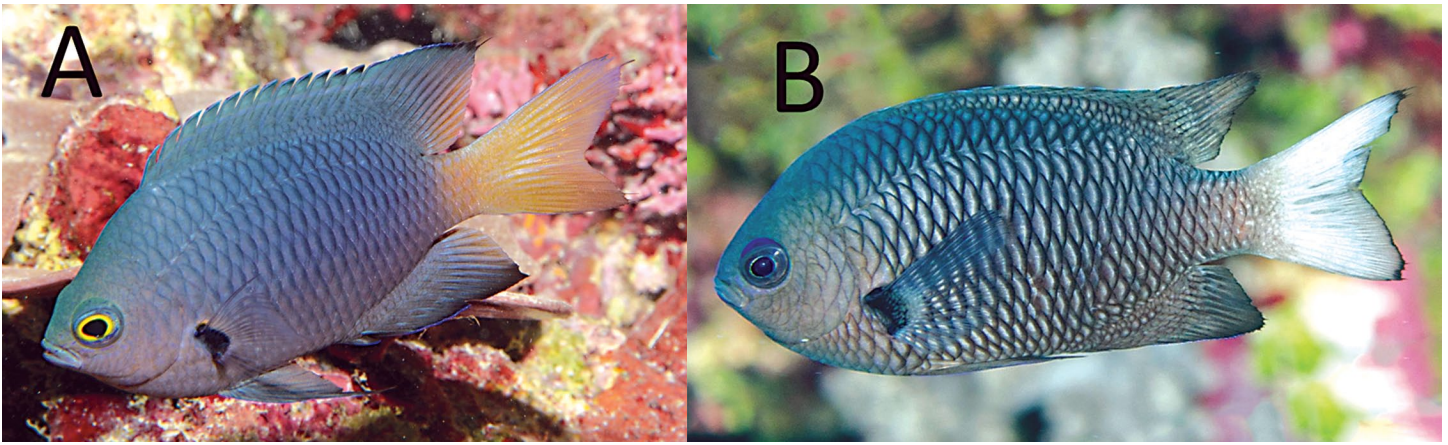


Figure 4. Comparison of adult color patterns, approx 60–70 mm SL: A) *Pomacentrus flavioculus*, Fiji (G.R. Allen), B) *P. imitator*, Coral Sea (I. Shaw).

west into the Indian Ocean as the Maldive Islands. *Pomacentrus flavioculus* is closely related to *P. imitator* from the Coral Sea, and was formerly misidentified as this species by both Allen (1991) and Randall (2005). However, the new species clearly differs from *P. imitator* on the basis of several color-pattern features (Fig. 4), including a bright yellow ring that encircles the pupil, a more uniform body color (vs. contrasting pale scale centers and dark scale margins), a yellowish caudal fin (vs. whitish), and a small orange marking immediately above the large black spot that covers the pectoral-fin base (absent in *P. imitator*). Although the two species share most meristic

TABLE 2
Frequency distribution of soft dorsal-fin, anal-fin, total gill-raker, pectoral-fin-ray, and lateral-line scale counts for members of the *Pomacentrus philippinus* species complex

| Species | Soft dorsal-fin rays | | | | | Soft anal-fin rays | | | | Total gill-rakers | | | | |
|--------------------------------|----------------------|----|----|----|--|--------------------|----|----|--|-------------------|----|----|----|----|
| | 12 | 13 | 14 | 15 | | 13 | 14 | 15 | | 21 | 22 | 23 | 24 | 25 |
| <i>P. albiaxillaris</i> | 1 | 11 | 42 | 2 | | 4 | 48 | 4 | | 7 | 25 | 22 | 22 | |
| <i>P. flavioculus</i> , n. sp. | | 2 | 59 | | | 1 | 40 | 20 | | 4 | 30 | 26 | 1 | |
| <i>P. flavoaxillaris</i> | | 2 | 23 | 1 | | 1 | 24 | 1 | | | 6 | 8 | 2 | |
| <i>P. imitator</i> | | | 9 | 1 | | | 3 | 7 | | 1 | | 8 | 1 | |
| <i>P. magniseptus</i> | | 1 | 18 | 4 | | 1 | 15 | 4 | | 1 | 4 | 13 | 5 | |
| <i>P. nigriradiatus</i> | | 1 | 24 | 17 | | | 16 | 26 | | | 7 | 20 | 14 | |
| <i>P. philippinus</i> | | 2 | 5 | 1 | | | 5 | 3 | | | 1 | 6 | 1 | |

| Species | Pectoral-fin rays | | | | | Lateral-line scales | | | | |
|--------------------------------|-------------------|----|----|----|--|---------------------|----|----|----|----|
| | 16 | 17 | 18 | 19 | | 15 | 16 | 17 | 18 | 19 |
| <i>P. albiaxillaris</i> | 1 | 25 | 85 | | | 1 | 2 | 32 | 71 | 4 |
| <i>P. flavioculus</i> , n. sp. | 5 | 28 | 90 | | | 4 | 43 | 63 | 11 | |
| <i>P. flavoaxillaris</i> | 2 | 5 | 43 | 2 | | | | 16 | 9 | |
| <i>P. imitator</i> | | 8 | 12 | | | | 2 | 7 | 10 | |
| <i>P. magniseptus</i> | | 1 | 44 | 1 | | | 1 | 8 | 31 | 4 |
| <i>P. nigriradiatus</i> | | 6 | 70 | 10 | | | | 19 | 53 | 3 |
| <i>P. philippinus</i> | | 1 | 11 | | | | 1 | 6 | 8 | |

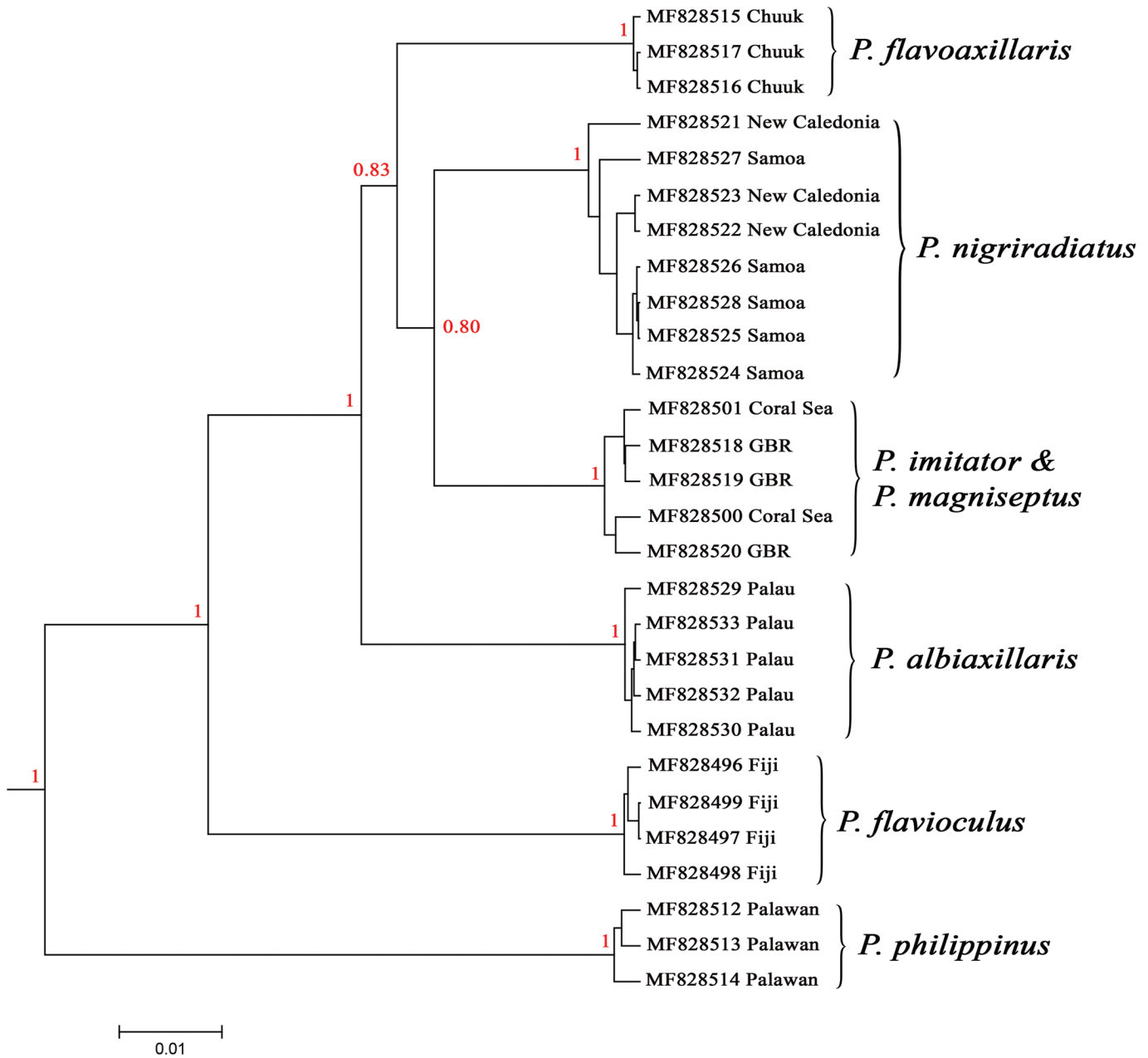


Figure 5. Maximum Credibility Tree generated from concatenated mitochondrial DNA data set of 16S, COI, and control region loci from species in the *Pomacentrus philippinus* complex. Numbers on the nodes indicate posterior probability for Bayesian Inference methods. Genbank accession numbers for 16S and collection locality are listed for each individual (*P. imitator* specimens comprise the two sequences from the Coral Sea and *P. magniseptus* specimens comprise the three sequences from the Great Barrier Reef, abbreviated as GBR). The scale bar refers to substitutions per site.

and morphological features, *P. flavioculus* usually has 14 anal-fin rays (in about two-thirds of specimens) while a similar proportion of *P. imitator* have 15 anal-fin rays (Table 2). In addition, *P. flavioculus* usually has a greater preanal distance (62.5%–71.3%, mean 66.9% SL vs. 60.0%–63.7% SL) and almost always possesses a longer pelvic-fin spine (mean 18.0% SL vs. range of 14.2–17.4% SL).

Genetic analysis. We resolved relationships within the *P. philippinus* species complex using a concatenated alignment of mtDNA segments, including 587 base-pairs of 16S, 657 base-pairs of COI, and 404 base-pairs of the control region. A phylogenetic tree obtained from BEAST (Fig. 5) shows the species of the complex form a monophyletic set of lineages with generally high interspecific divergences (except one case) and low intraspecific genetic distances of less than 1%. The new species diverged by an average pairwise genetic distance of 8.4% from *P. imitator* from the type location of the Coral Sea, about the same divergence as from several other members of the complex, and greater than the divergence between several other members of the complex (Table 3).

Interestingly, two of the species in the complex share mitochondrial DNA sequences, i.e. *P. magniseptus* from the Great Barrier Reef and *P. imitator* from the adjacent Coral Sea. Despite the similarity of their mtDNA sequences, the two species show distinctly different color patterns (compare Figs. 6 and 4B) and are allopatric, occupying a different set of reefs along the Queensland coastline. It is not uncommon among reef-fish species complexes, especially those with colorful color patterns associated with reproductive adults, to have members that share mtDNA lineages, indicating that the evolution of phenotypic changes have apparently outpaced the rate of mtDNA divergence, or some residual degree of hybridization and gene flow exists between populations (reviewed in Victor [2015]). These sibling-species pairs usually diverge in color pattern, and sometimes in meristics, behaviors, and habitat preferences (although rarely morphology). Classic examples of Indo-Pacific reef-fish species complexes that have species with very different color patterns, but sharing mtDNA lineages, include species complexes within the wrasse genera *Cirrhilabrus* (Allen *et al.* 2015, Tea *et al.* 2016, Victor 2016) and *Paracheilinus* (Allen *et al.* 2016).

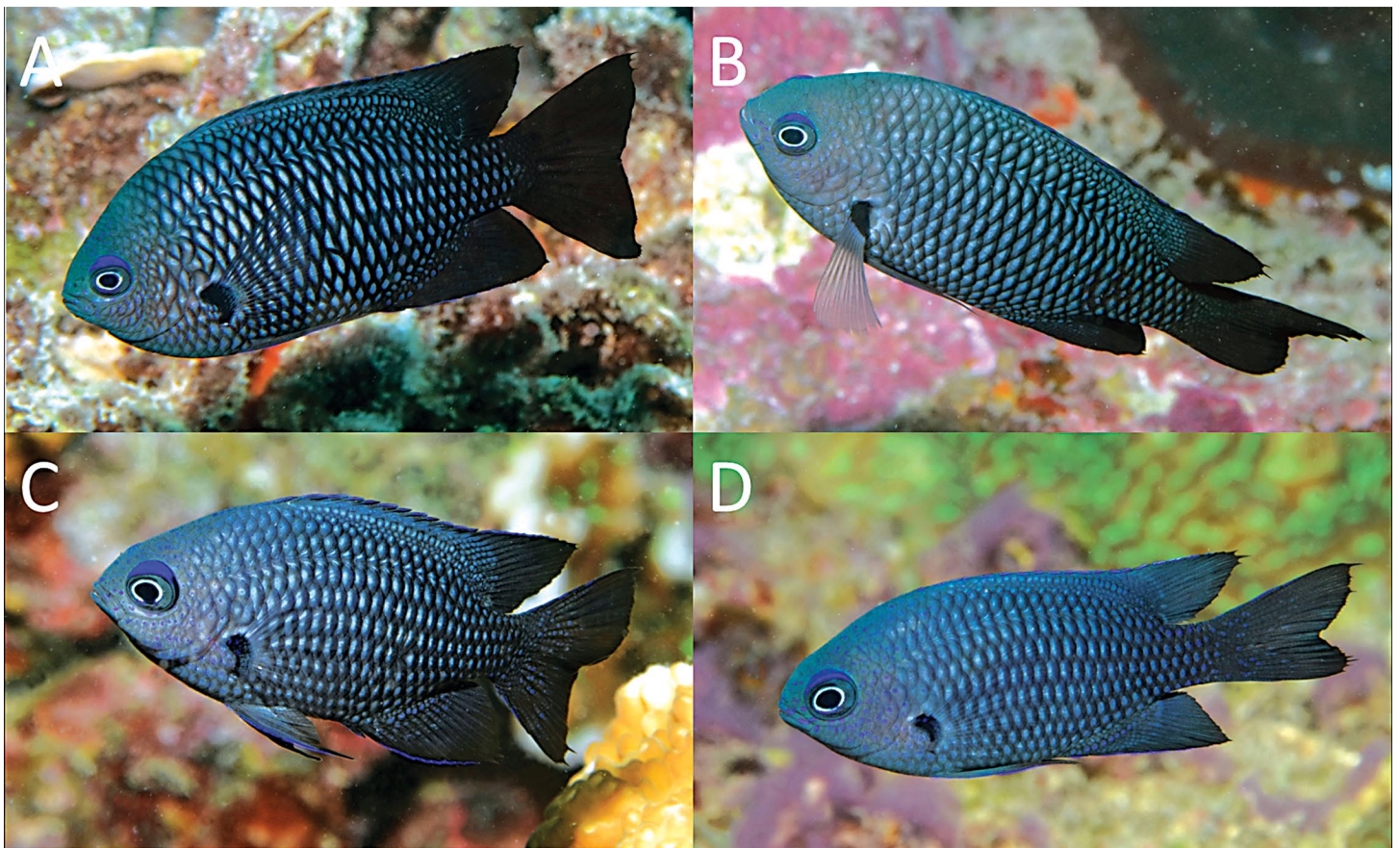


Figure 6. *Pomacentrus magniseptus*, underwater photographs, Pixie Reef, Great Barrier Reef, Queensland, Australia: A) approx. 70 mm SL; B) approx. 55 mm SL; C) approx. 45 mm SL; and D) approx. 35 mm SL (G.R. Allen).

TABLE 3

Average interspecific pairwise genetic distance matrix for concatenated mitochondrial DNA sequences for the *Pomacentrus philippinus* species complex in the western Pacific Ocean

| Species | Location | 1 | 2 | 3 | 4 | 5 | 6 |
|--|-----------------------|-------|-------|-------|-------|-------|---|
| 1 <i>P. flavoaxillaris</i> | Chuuk | | | | | | |
| 2 <i>P. nigriradiatus</i> | Samoa & New Caledonia | 0.047 | | | | | |
| 3 <i>P. imitator</i> & <i>P. magniseptus</i> | Coral Sea & GBR | 0.047 | 0.040 | | | | |
| 4 <i>P. albiaxillaris</i> | Palau | 0.054 | 0.054 | 0.054 | | | |
| 5 <i>P. flavioculus</i> , n. sp. | Fiji | 0.084 | 0.084 | 0.084 | 0.084 | | |
| 6 <i>P. philippinus</i> | Palawan | 0.116 | 0.116 | 0.116 | 0.116 | 0.116 | |

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