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Review of the Indo-Pacific Flasherwrasses of the genus *Paracheilinus* (Perciformes: Labridae), with descriptions of three new species

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Abstract

The Indo-Pacific labrid fish genus *Paracheilinus* now contains 20 species. Most of the currently known species inhabit the mega-diverse East Indian region including *Paracheilinus angulatus*, *P. carpenteri*, *P. cyaneus*, *P. filamentosus*, *P. flavianalis*, *P. lineopunctatus*, *P. nursalim*, *P. rennyae*, *P. togeanensis*, *P. walton*, as well as three recent discoveries described as new species herein. Five species are known from the Red Sea and Indian Ocean, including *P. attenuatus* (Seychelles and Kenya), *P. hemitaeniatus* (Madagascar and South Africa), *P. mccoskeri* (Kenya, Comoro Islands and Arabian Gulf to Andaman Sea), *P. octotaenia* (Red Sea), and *P. piscilineatus* (Mauritius). The remaining two species, *P. bellae* and *P. rubricaudalis*, are mainly confined to Micronesia/Marshall Islands and PNG/Fiji/Vanuatu, respectively. Members of the genus are typically distinguished on the basis of their caudal-fin and dorsal-fin shapes, the presence or absence of elongate filamentous dorsal-fin rays, and, in particular, the color of terminal-phase (TP) males, including their dramatic nuptial-display patterns. *Paracheilinus paineorum* n. sp. is described from 8 specimens, 43.1–70.0 mm SL, collected in Indonesia (southwestern Flores, Sulawesi, Nusa Penida, East Borneo, and Seribu Islands) in depths of 10–65 m. It is closely related to the allopatric *P. filamentosus* and *P. xanthocirritus* n. sp., differing mainly in coloration (particularly the bright red dorsal-fin markings) and larger maximum size (to at least 70 mm SL). *Paracheilinus xanthocirritus* n. sp. is described from 12 specimens, 33.9–49.3 mm SL, collected in the South China Sea at the Anambas Islands of Indonesia and Brunei in depths of 15–25 m. In contrast to the closely related *P. paineorum* n. sp., TP males of this species have a mostly yellow dorsal fin lacking red markings. The two new species further differ from *P. filamentosus* by having a narrower interorbital and a shorter caudal peduncle. A third new species, *Paracheilinus alfiani*, n.

sp., is described on the basis of two specimens, 48.8 and 49.3 mm SL, from Lembata Island in the Lesser Sunda Islands of Indonesia. It is characterized by a rounded and relatively tall dorsal fin without elongate filamentous rays, a slightly rounded caudal fin, and distinctive TP male coloration. In addition to the new species descriptions, a diagnosis and color illustrations are included for all members of the genus. We also present a key to the species and a neighbor-joining tree of mitochondrial DNA sequences which clarifies the genetic relationships among species, revealing four discrete species complexes within the genus.

Key words: coral reef fishes, taxonomy, ichthyology, wrasses, DNA barcoding, phylogenetics.

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Introduction

Members of the Indo-Pacific labrid fish genus *Paracheilinus* are commonly known as flasherwrasses due to the spectacular display pattern of courting males. They commonly occur in aggregations consisting of numerous, much smaller and far less brilliant initial-phase fish and relatively few of the colorful terminal-phase males (Fig. 1). Courtship activities occur daily and generally commence about 1–2 hours before sunset. The neon-like "flasher" pattern is produced instantaneously during an impressive display in which the colorful median fins are fully erected, sometimes including a spectacular filamentous dorsal fin (which is characteristic of several species). Although peak "flashing" behavior occurs just prior to dusk, it is also seen throughout the day, particularly during

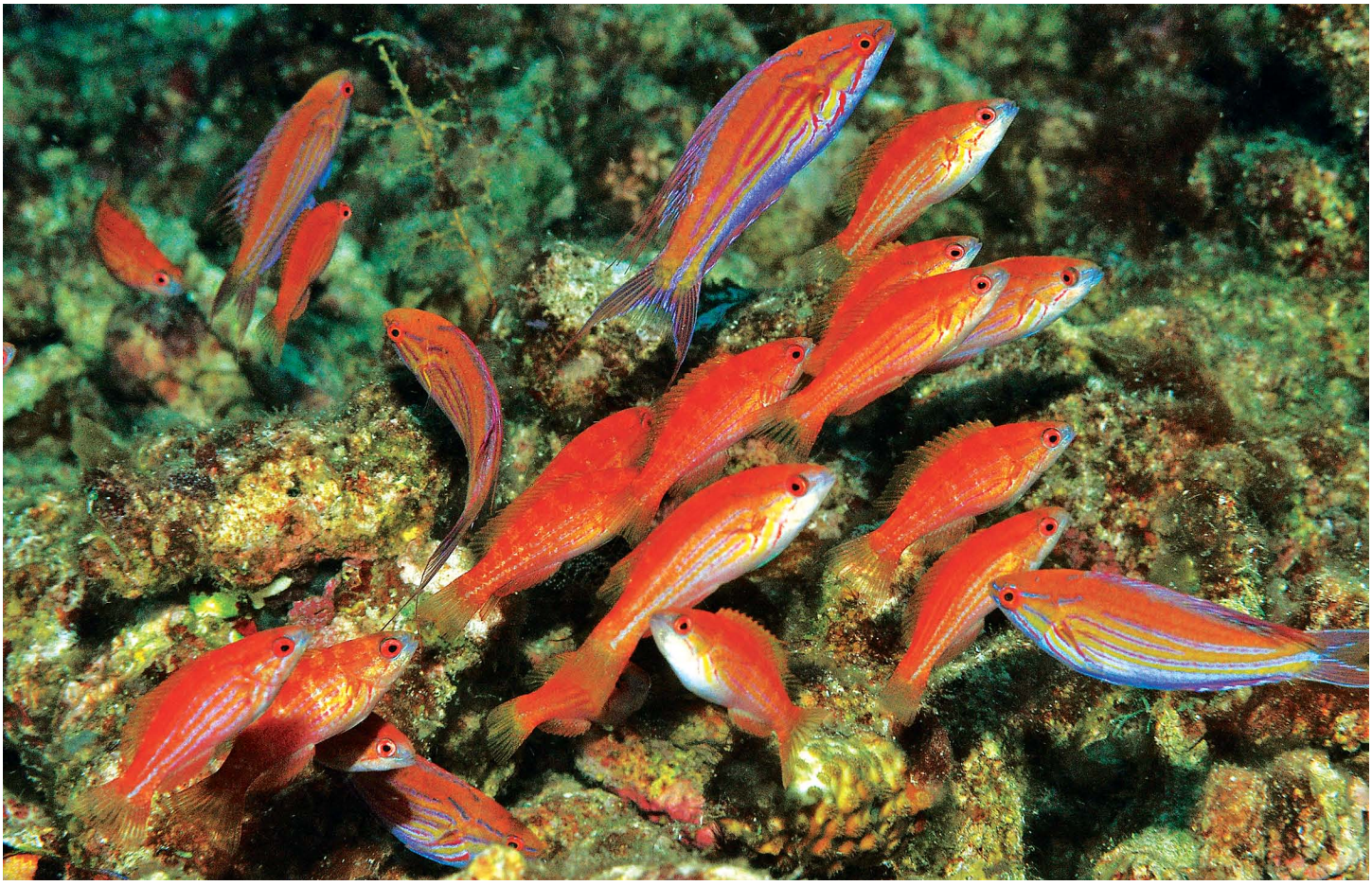


Figure 1. *Paracheilinus filamentosus*, underwater photograph of aggregation, showing mainly females (TP males upper center and far right and some at left), Tufi, Oro Province, Papua New Guinea (G.R. Allen).

agonistic encounters between both conspecific and congeneric males. Nuptial activity gradually ceases after sunset with individuals swimming slowly or hovering close to the bottom. Finally, as darkness descends, they retire into crevices, usually among rubble or low-profile corals.

These small (usually under 70 mm SL) fishes frequently form large aggregations of tens to hundreds of individuals which, during periods of moderate current, rise well above the bottom to feed on zooplankton. They typically inhabit rubble bottoms, or *Halimeda* algal beds, of outer-reef slopes. The usual depth range is about 5–70 m, but they are most abundant between about 15–40 m.

The genus, which now contains 20 species, has not been comprehensively reviewed. We therefore take this opportunity to summarize our knowledge of these interesting fishes, including descriptions of three new species. Although the genus is widely distributed in the Indo-western Pacific region, all but the four Indian Ocean species occur in the western Pacific Ocean. Indonesia, with 11 species, is by far the richest area. The four Indian Ocean species generally have allopatric distributions, but, in the western Pacific, two and occasionally three species may co-occur on reefs of Indonesia, Sabah (Malaysia), Brunei, and the Philippines. The genus was almost unknown until the use of scuba equipment by ichthyologists became prevalent in the 1970s. Moreover, the predilection of flasherwrasses for deeper reef environments, particularly seldom-collected relatively deep and featureless rubble bottoms, was also responsible for their lack of detection until recent decades. Fourmanoir (in Roux-Estève & Fourmanoir 1955) described the first member of the genus, *Paracheilinus octotaenia*, a Red Sea endemic species. Nineteen years later, the second species, *Paracheilinus filamentosus* Allen, 1974, was described from northern Papua New Guinea. Subsequently, divers, and especially underwater photographers, became more aware of their presence, resulting in the discovery of numerous additional species, with fully half of the twenty recognized species described since 1999 (Randall & Harmelin-Vivien 1977, Randall & Lubbock 1981, Cornic 1987, Randall 1988, Kuiter & Allen 1999, Randall 1999a, Randall & Allen 2003, Allen & Erdmann 2006, 2008, Allen, Erdmann & Yusmalinda 2013).

Fourteen of the currently known species inhabit the mega-diverse Indo-Australian Archipelago, including *P. angulatus* Randall & Lubbock, 1981; *P. carpenteri* Randall & Lubbock, 1981; *P. cyaneus* Kuiter & Allen, 1999; *P. filamentosus* Allen, 1974; *P. flavianalis* Kuiter & Allen, 1999; *P. lineopunctatus* Randall & Lubbock, 1981; *P. nursalim* Allen & Erdmann, 2008; *P. rennyae* Allen, Erdmann & Yusmalinda, 2013; *P. togeanensis* Kuiter & Allen, 1999; *P. walton* Allen & Erdmann, 2006; as well as the three recently discovered new species described herein. Four species are restricted to the Red Sea and western Indian Ocean: *P. attenuatus* Randall, 1999a; *P. hemitaeniatus* Randall & Harmelin-Vivien, 1977; *P. octotaenia* Fourmanoir, 1955; and *P. piscilineatus* (Cornic, 1987). *Paracheilinus mccoskeri* Randall & Harmelin-Vivien, 1977 ranges across the Indian Ocean from Kenya, the Comoro Islands, and the Persian Gulf to the eastern margin of the Andaman Sea. The remaining two species, *P. bellae* Randall, 1988 and *P. rubricaudalis* Randall & Allen, 2003, are mainly confined to the islands of western Oceania, i.e. Micronesia, Marshall Islands, and Japan for the former and Papua New Guinea to Fiji and Vanuatu for the latter.

Materials and Methods

Lengths given for specimens are standard length (SL), the straight-line distance from the front of the upper lip to the base of the caudal fin (the posterior end of the hypural plate). Head length (HL) is measured from the same median anterior point to the end of the opercular membrane, and snout length from the same point to the fleshy anterior edge of the eye. Body depth is the maximum depth and body width the greatest width just posterior to the gill opening. Eye diameter is the greatest fleshy diameter of the orbit and interorbital width the least bony width. Caudal-peduncle depth is the least depth; caudal-peduncle length is measured horizontally from the rear base of the last anal-fin ray to the caudal-fin base. Spines and rays are measured to their extreme base. Pectoral-fin ray counts include the uppermost rudimentary ray. Gill-raker counts were made on the first gill arch and include rudiments. The posterior lateral-line scale count includes the tubed scale on the caudal-fin base.

Proportional measurements for the new species are presented in tables as percentages of the standard length. Step-in measurements are provided in the text of the description rounded to the nearest 0.1. Data in parentheses in the species descriptions refer to the range for paratypes, if different from that of the holotype.

Type specimens of the three new species are deposited at the Museum Zoologicum Bogoriense, Cibinong, Java, Indonesia (MZB), United States National Museum of Natural History, Washington, D.C. (USNM), and Western Australian Museum, Perth (WAM). Other institutional abbreviations are as follows: AMS (Australian Museum, Sydney), BPBM (Bernice P. Bishop Museum, Honolulu, USA), MNHN (Muséum national d'Histoire naturelle, Paris), NCIP (Pusat Penelitian dan Pengembangan Oseanologi, Jakarta, Indonesia), and NMV (Museum Victoria, Melbourne, Australia).

Specimens of 17 of the 20 known species in the genus (all but *P. bellae*, *P. lineopunctatus*, and *P. togeanensis*) were sequenced for the cytochrome *c* oxidase I, subunit I (COI) mitochondrial DNA-barcoding marker (Ward *et al*. 2009) and the sequences were compared to evaluate relationships within the genus. In total, tissue samples (or completed COI sequences from other laboratories) were obtained from 22 of the male paratypes of the new species and from 46 individuals of other congeners (predominantly from the East Indian region) as follows (Table 1): six specimens of *P. cyaneus* from Raja Ampat in West Papua, four specimens of *P. filamentosus* from New

TABLE 1

Provenance of DNA barcode (mtDNA COI) sequences of *Paracheilinus* species
(MB denotes Indonesian Biodiversity Research Center (IBRC) vouchers)

species	voucher #	collection location	GenBank #	species	voucher #	collection location	GenBank #
P. alfiani	MB043401	Indonesia	KT253629	*P. mccoskeri*	MB040304	Myanmar: Mergui	KP187625
P. alfiani	MB043501	Indonesia	KT253630	*P. nursalim*	MB040701	Indonesia: Misool	KT253607
P. alfiani	MB043601	Indonesia	KT253631	*P. nursalim*	MB041001	Indonesia	KT253608
P. angulatus	MB040601	Philippines: El Nido	KF709102	*P. nursalim*	MB041002	Indonesia	KT253609
P. angulatus	MB040901	Brunei: Colombo Reef	KF709104	*P. nursalim*	MB042601	Indonesia	KT253617
P. angulatus	MB040902	Brunei: Colombo Reef	KP187629	*P. octotaenia*	TAU-RH-1080	Israel: Eilat	
P. angulatus	MB043802	Brunei: Colombo Reef	KP187638	*P. paineorum*	MB042101	Indonesia	KT253615
P. angulatus	MB044001	Brunei: Colombo Reef	KP187640	*P. paineorum*	MB042201	Indonesia	KT253616
P. angulatus	MB044005	Brunei: Colombo Reef	KP187643	*P. paineorum*	MB042701	Indonesia	KT253618
P. attenuatus	LIDMA2080-14	Kenya, aquarium trade		*P. paineorum*	MB042801	Indonesia	KT253619
P. carpenteri	MB040501	Brunei: Colombo Reef	KF709101	*P. paineorum*	MB042802	Indonesia	KT253620
P. carpenteri	MB043901	Brunei: Colombo Reef	KP187639	*P. paineorum*	MB042901	Indonesia	KT253621
P. carpenteri	MB044002	Brunei: Colombo Reef	KP187641	*P. paineorum*	MB043101	Indonesia	KT253622
P. carpenteri	MB044003	Brunei: Colombo Reef	KP187642	*P. paineorum*	MB043102	Indonesia	KT253623
P. cyaneus	MB040401	Indonesia: Raja Ampat	KP187626	*P. paineorum*	MB043103	Indonesia	KT253624
P. cyaneus	MB040402	Indonesia: Raja Ampat	KF709100	*P. piscilineatus*	MB043201	Mauritius	KT253625
P. cyaneus	MB040403	Indonesia: Raja Ampat	KP187627	*P. piscilineatus*	MB043202	Mauritius	KT253626
P. cyaneus	MB040404	Indonesia: Raja Ampat	KP187628	*P. piscilineatus*	MB043203	Mauritius	KT253627
P. cyaneus	MB041601	Indonesia: Raja Ampat	KF709108	*P. rennyae*	MB041401	Indonesia: SW Flores	KF709106
P. cyaneus	MB041701	Indonesia: Raja Ampat	KP187632	*P. rennyae*	MB041501	Indonesia: SW Flores	KF709107
P. filamentosus	MB042001	PNG: New Britain	KP187633	*P. rennyae*	MB042301	Indonesia: SW Flores	KP187635
P. filamentosus	MB042002	PNG: New Britain	KF709109	*P. rubricaudalis*	MB043301	Australia	KT253628
P. filamentosus	MB042003	PNG: New Britain	KF709110	*P. walton*	MB040101	Indonesia: Manokwari	KF709097
P. filamentosus	MB042004	PNG: New Britain	KP187634	*P. walton*	MB042401	Indonesia: Manokwari	KP187636
P. flavianalis	MB040801	Indonesia: SE Bali	KF709103	*P. xanthocirritus*	MB040201	Brunei	KT253605
P. flavianalis	MB041101	Indonesia: SW Flores	KF709105	*P. xanthocirritus*	MB040202	Brunei	KT253606
P. flavianalis	MB041201	Indonesia: SW Flores	KP187630	*P. xanthocirritus*	MB041801	Anambas	KT253610
P. flavianalis	MB041301	Indonesia: SW Flores	KP187631	*P. xanthocirritus*	MB041901	Anambas	KT253611
P. flavianalis	MB042501	Indonesia: SW Flores	KP187637	*P. xanthocirritus*	MB041902	Anambas	KT253612
P. hemitaeniatus	DSFSG509-11	South Africa	KF489687	*P. xanthocirritus*	MB041903	Anambas	KT253613
P. hemitaeniatus	DSFSG636-11	South Africa	KF489688	*P. xanthocirritus*	MB041904	Anambas	KT253614
P. mccoskeri	MB040301	Myanmar: Mergui	KF709098	*P. xanthocirritus*	MB043701	Brunei	KT253632
P. mccoskeri	MB040302	Myanmar: Mergui	KF709099	*P. xanthocirritus*	MB043801	Brunei	KT253633
P. mccoskeri	MB040303	Myanmar: Mergui	KP187624	*P. xanthocirritus*	MB044004	Brunei	KT253634

Britain in Papua New Guinea, two specimens of *P. walton* from Manokwari in West Papua, four specimens of *P. nursalim* from Raja Ampat in West Papua, four specimens of *P. mccoskeri* from the Mergui Archipelago Andaman Sea, four specimens of *P. carpenteri* from Brunei, five specimens of *P. flavianalis* (four from SW Flores and one from Nusa Penida in SE Bali), one specimen of *P. rubricaudalis* from Ribbon Reef in the Australia, six specimens of *P. angulatus* (five from Brunei and one from Palawan in the Philippines), three specimens of *P. rennyae* from Komodo in SW Flores, two sequences of *P. hemitaeniatus* from South Africa (from the DNA-barcode database BOLD), one sequence of *P. attenuatus* from Kenya (from BOLD), one sequence of *P. octotaenia* from the Red Sea (from Naama Kimmerling, pers. comm.), and three specimens of *P. piscilineatus* from Mauritius. The fairy wrasse *Cirrhilabrus humanni* was used as an outgroup. All of our specimens were fixed in 95% EtOH and stored in the Indonesian Biodiversity Research Center (IBRC) Laboratory in Denpasar, Bali, Indonesia.

Mitochondrial DNA was extracted using a 10% Chelex solution (Walsh *et al*. 1991). A portion of the cytochrome *c* oxidase subunit I (COI) region was amplified via PCR using the following primers: FishBCL (5'-TCAACYAATCAYAAAGATATYGGCAC-3'), FishBCH (5'- TAAACTTCAGGGTGACCAAAAAATCA-3'), jgLCO (5'-TITCIACIAAYCAYAARGAYATTGG-3'), and jgHCO (5'-TAIACYTCIGGRTGICCRAARAAYCA-3')(Geller *et al*. 2013). The PCR reaction was carried out in 25 µL volumes, using 1 µL of template. Each reaction included 2.5 µL (10xPCR buffer Gold), 2.5 µL (8mM dNTPs), 2 µL (25 mM $MgCl_2$ solution), 1.25 µL of each primer at 10 µM, 0.125 µL AmplyTaq-Gold™ (Applied Biosystems) and PE Amplitaq (5units/µL) (red taq) and 14.5 µL ddH_2O.

The thermocycling profile for COI 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. PCR reactions were checked on 1% agarose gels stained with ethidium bromide. The PCR product was sequenced at the University of California Berkeley sequencing facility, with all sequences accessioned in GenBank (Table 1). Forward and reverse sequences were proofread in MEGA5, then aligned using ClustalW (Tamura *et al*. 2011). Two methods were used to generate tree reconstructions: neighbor joining using MEGA5 (Tamura *et al*. 2011) and MRBAYES 3.2 (Ronquist & Hulsenbeck 2003). Neighbor joining was used to assess the model of best fit for the nucleotide substitutions. The Bayesian Information Criterion (BIC) was used to rank the Tamura Nei (TrN) model with a discrete Gamma distribution (TrN+G) to derive the best fit to the data. This model assumes different rates of transitions and transversions as well as different nucleotide frequencies, and was chosen as the appropriate model as determined by JModelTest 0.1.1 (Posada 2008, Guindon & Gascuel 2003). Bootstrap support was determined using 1000 bootstrap replicates in MEGA5. For the Bayesian analysis, we used a Markov Chain Monte Carlo (MCMC) approach with four chains. Analyses were run for 10,000,000 generations with an initial burn-in of 250,000 generations. After 10,000,000 generations, the resulting tree was checked for convergence using the TRACER program (Rambaut & Drummond 2007).

Genus *Paracheilinus* Fourmanoir, 1955

Paracheilinus Fourmanoir in Roux-Estève & Fourmanoir, 1955: 100 (type species: *Paracheilinus octotaenia* Fourmanoir, by original designation).

Diagnosis. Dorsal-fin rays IX (rarely VIII or X),11; anal-fin rays III,9 (rarely 8 or 10); pectoral-fin rays 14 (rarely 13 or 15); principal caudal-fin rays 13, the median 11 branched; lateral-line interrupted, the pored scales 14–17 + 4–10; median predorsal scales 5 (rarely 4 or 6); rows of scales on cheek 2; gill rakers on first branchial arch 12–18; branchiostegal rays 5; vertebrae 25; body depth 2.9–4.1 in SL; scleral cornea of eye over pupil divided nearly vertically into two continuous roundish portions; snout short, 3.3–5.1 in HL; mouth small and oblique, maxilla nearly reaching a vertical at front edge of eye; three pairs of curved canine teeth anteriorly in upper jaw, progressively more laterally projecting, third (posteriormost) pair much the largest; single pair of

canine teeth anteriorly in lower jaw, very strongly curved laterally; side of jaws with single row of small close-set conical teeth; no canine tooth at corner of mouth; no teeth on palate; ventral margin and corner of preopercle thin and membranous, posterior margin with a finely serrate bony edge (serrae may be reduced to a few in large individuals), except upper part covered by a large scale; scales on head and chest large; snout, chin, and interorbital space naked; dorsal and anal-fin spines slender, progressively longer posteriorly, in some species dorsal-fin soft rays elongated into long filamentous extensions; caudal fin varying from emarginate or truncate to rounded, lanceolate, or lunate with or without lobes with long filamentous extensions; pelvic fins inserted below lower pectoral-fin base, longest ray not reaching origin of anal fin; an elongate axillary scale above and adjacent to each pelvic fin, and a large median scaly process consisting of two elongate pointed scales extending from base of pelvic fins.

Color patterns. Like most other labrid fishes, flasherwrasses are characterized by female-to-male (protogynous) sex reversal and exhibit different juvenile, female, and male color patterns. Young individuals first become sexually mature as females or, less frequently, as small males, both referred to as initial-phase (IP) fish. IP males usually spawn in aggregations. Both male and female IP individuals are capable of transforming to the usually larger and more colorful terminal-phase male (TP), which then typically defends a harem of females. The color patterns of TP males, particularly the color patterns associated with their nuptial displays, are diagnostic for species.

Twelve of the species have basic male-stripe patterns that fall into two categories, which we refer to as patterns A and B. We refer to the horizontal linear marks, mostly on the sides, as stripes and oblique or thicker lines, often on the head and curved marks on fins as bands. Pattern A is illustrated in Figure 2A and is present in its basic form in *P. angulatus*, *P. filamentosus*, *P. paineorum*, *P. togeanensis*, and *P. xanthocirritus*. The pattern consists of three bands (usually red or blue) on the head: two originating from the posterior edge of the eye and extending to the opercle margin, and one originating on the upper lip and passing along the lower edge of the eye to the lower opercle margin. The body pattern consists of two primary stripes that run along the middle portion of the side to the caudal peduncle and several shorter, secondary stripes or bands. The first is a short band originating at the upper opercle margin, the second is a stripe positioned on the anterior half of the side between the two primary stripes. Finally, there are two short bands below the lowermost primary stripe that extend obliquely downward along the side of the breast and abdominal region. A variation of pattern A is found in *P. cyaneus*, *P. nursalim*, and *P. walton* (Fig. 2B). In addition to the basic pattern described above, these species have scattered small dark spots (sometimes in horizontal rows) on the side of the body in the spaces between the other stripes and bands. This pattern is especially evident in females and young males (Fig. 3). Another variation of pattern A is evident in *P. alfiani*, in which the two primary stripes are somewhat expanded and diffuse on the posterior half of the body (see species description).

Pattern B is present in *P. flavianalis*, *P. mccoskeri*, and *P. rubricaudalis* (Fig. 2C). The pattern consists of a series of anterior bands: a short band from the front of the eye to the snout tip, a band from the upper lip, passing along the lower edge of the eye to the lower opercular edge and continued onto the side of the breast to above the pelvic fins, and another upward-slanting band from the upper rear corner of the eye to the opercular edge and continued for a short distance on the adjacent upper body. There are three stripes (usually red or blue) on the body: the uppermost primarily along the posterior half, extending to the upper caudal peduncle; the middle one a short stripe just above the upper pectoral-fin base, extending from the opercle edge to about the level of the anterior anal-fin rays; and the lowermost from the lower pectoral-fin base to the lower caudal peduncle.

The remaining species have their own distinctive color patterns, although certain trends are evident. For example, four of the species, i.e. *P. bellae*, *P. lineopunctatus*, *P. octotaenia*, and *P. rennyae*, possess pin-striped patterns, essentially consisting of a series of narrow stripes (usually red, purple or blue), horizontal rows of spots (i.e. broken lines), or vermiculations on the side of the body. One species from the western Indian Ocean, *P. hemitaeniatus*, possesses a unique pattern in which most of the stripes are confined to the anterior half of the body. The remaining two species, *P. attenuatus* and *P. piscilineatus*, both from the western Indian Ocean, have individual patterns that incorporate an unusual peculiarity of the middle head stripe, which extends as an arc over the pectoral-fin base, then continuing, in the former species, along most of the length of the body as the lowermost body stripe and, in the latter species, as a prominent blue stripe to the base of the caudal fin.

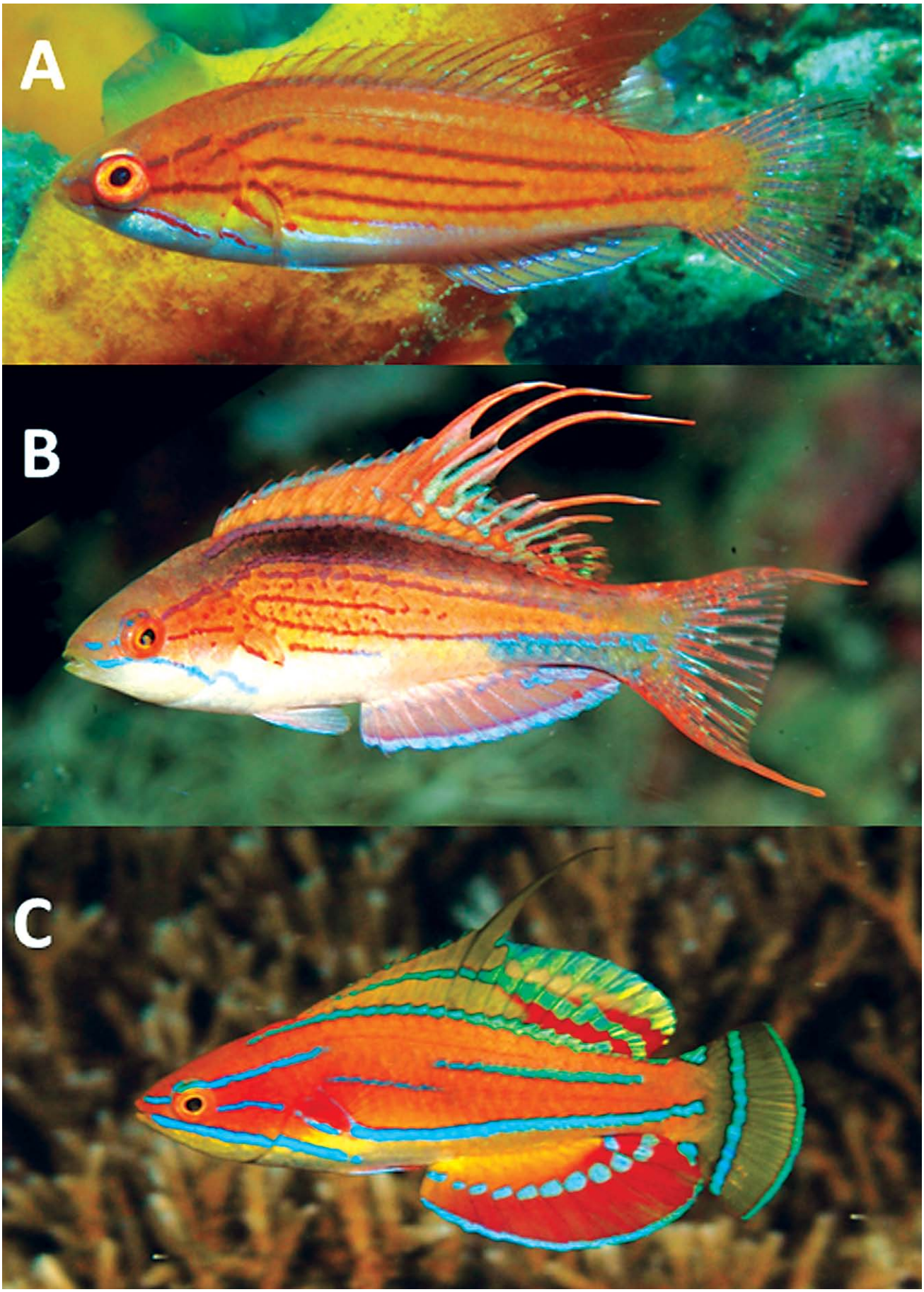


Figure 2. Genus *Paracheilinus*, basic stripe patterns on head and body of TP males: A) pattern A (*P. paineorum*, not nuptial display), B) pattern A variation (*P. nursalim*, not nuptial display), and C) pattern B (*P. mccoskeri* nuptial display)(G.R. Allen).

Figure 3. *Paracheilinus walton*, showing TP male (not nuptial display) at left, approximately 40 mm SL, and a probable female at right, approximately 30 mm SL, Cenderawasih Bay, West Papua, Indonesia (G.R. Allen).

Nuptial-display color patterns. The color patterns displayed by courting nuptial males are diagnostic for species (Fig. 4) and particularly useful for separating closely related species. During the display, spectacular neon-like colors are flashed while the median fins are fully erected, followed by bursts of rapid, erratic swimming in the immediate vicinity of the much smaller, dull-colored females. The head and body stripes, as well as the fin margins, become electric blue and the fin coloration is greatly intensified. Species possessing dorsal-fin filaments are especially spectacular, with these normally drab appendages often transformed to vivid blue-white or yellow-white hues. Additionally, most species exhibit a brilliant blue band along the upper back or even, in the case of *P. cyaneus*, the entire forehead and back assume a glowing, blue-green color. These displays are further enhanced by the erected, intensely colorful dorsal and anal fins (usually red, yellow, or orange, or a combination), often ornamented with electric-blue bands, stripes, or rows of blue spots.

Female and juvenile coloration. Juveniles and IP individuals are usually reddish or red-orange, grading to white on the ventral portion of the head and body (Fig. 1). Females generally show the basic adult pattern, although it is much duller and inconspicuous compared to the TP male pattern. Both juveniles and IP fish may exhibit narrow dark stripes and about six, broad, diffuse darkish bars on the body that can be quickly switched on or off. Females of species that possess elongate dorsal filaments usually show initial development of these structures (Fig. 3). Small individuals of *P. attenuatus* (under about 30 mm SL) are exceptional within the genus in having an eye-sized ocellus basally at the middle of the dorsal fin, and an additional smaller spot dorsally on the caudal peduncle.

Hybridization. Individuals presumed to be hybrids, such as those in Figure 5, are frequently seen in areas inhabited by more than one species of *Paracheilinus*. This phenomenon, which was previously noted by Kuiter & Allen (1999) and Allen & Erdmann (2012), is likely the result of the highly synchronized spawning behavior, occurring daily just prior to sunset, regardless of species. It is common to see males of more than one species on the same reef and in close proximity, vigorously pursuing large mixed-species groups of initial-phase females. Putative hybrids are generally recognizable on the basis of combinations of features (derived from the presumed parents) related to color pattern and the shape of the dorsal and caudal fins. Kuiter & Allen (1999) illustrated the following presumed hybrids (approximate location in parentheses): *P. angulatus* x *P. cyaneus* (Derawan Island, Kalimantan, Indonesia), *P. angulatus* x *P. paineorum* (reported as *P. filamentosus*; Derawan Island, Kalimantan), *P. paineorum* (reported as *P. filamentosus*) x *P. flavianalis* (Bali, Indonesia). Additionally, our recent investigations in Indonesia have documented four other presumed hybrids, including *P. cyaneus* x *P. nursalim* (Kaimana region, West Papua; Fig. 5C), *P. paineorum* x *P. togeanensis* (Lembeh Strait, northern Sulawesi; Fig. 5B), *P. rennyae* x *P. paineorum* (southwestern Flores), and *P. alfiani* x *P. paineorum* (Lembata Island; see *P. alfiani* description below). A probable hybrid *P. angulatus* x *P. lineopunctatus* was observed by the first author at Anilao, Luzon, Philippines (Fig. 5A).

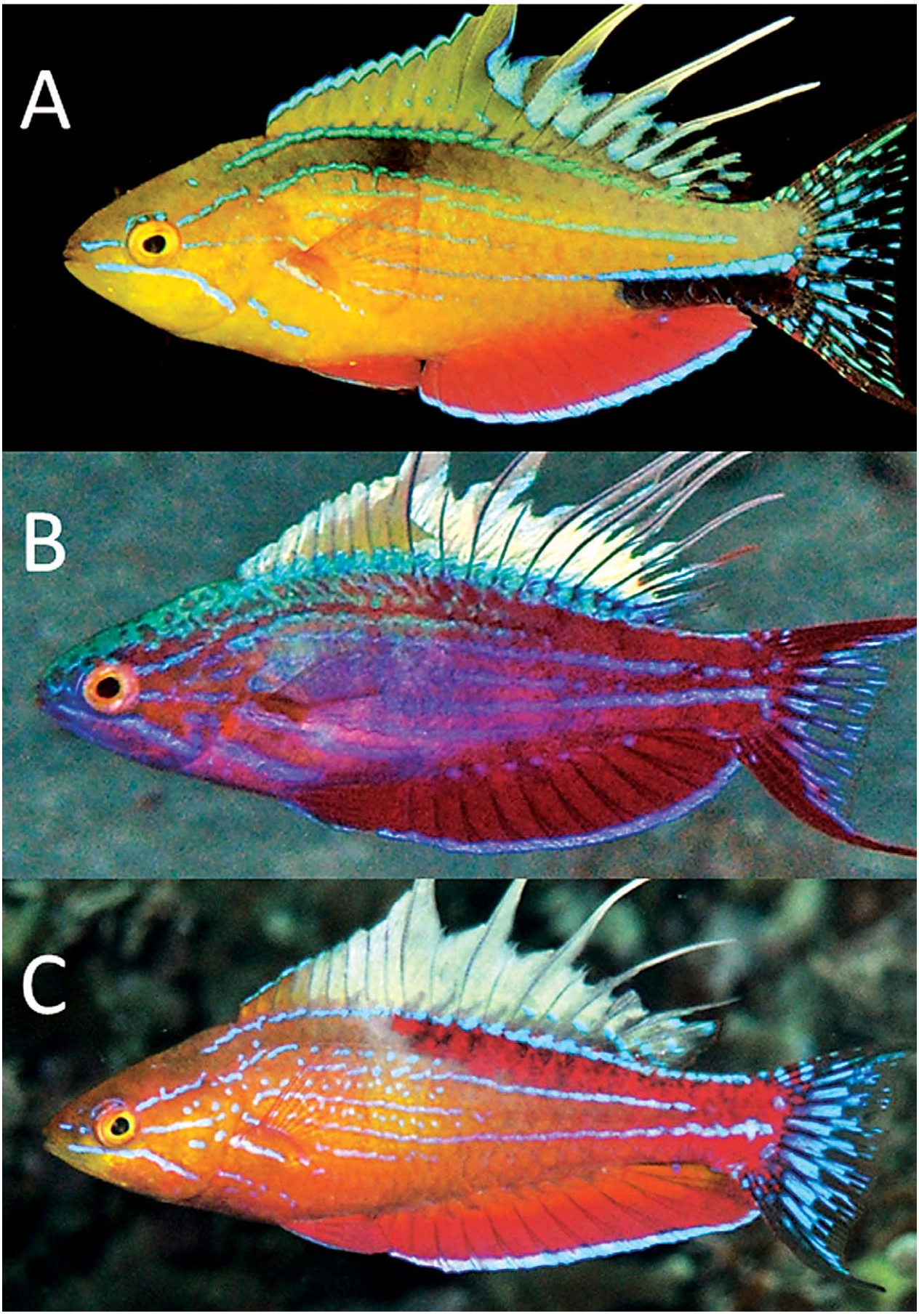


Figure 4. Genus *Paracheilinus*, nuptial-male display patterns in a set of closely related species in the *filamentosus* group: A) *P. nursalim*; B) *P. cyaneus*; and C) *P. walton* (G.R. Allen).

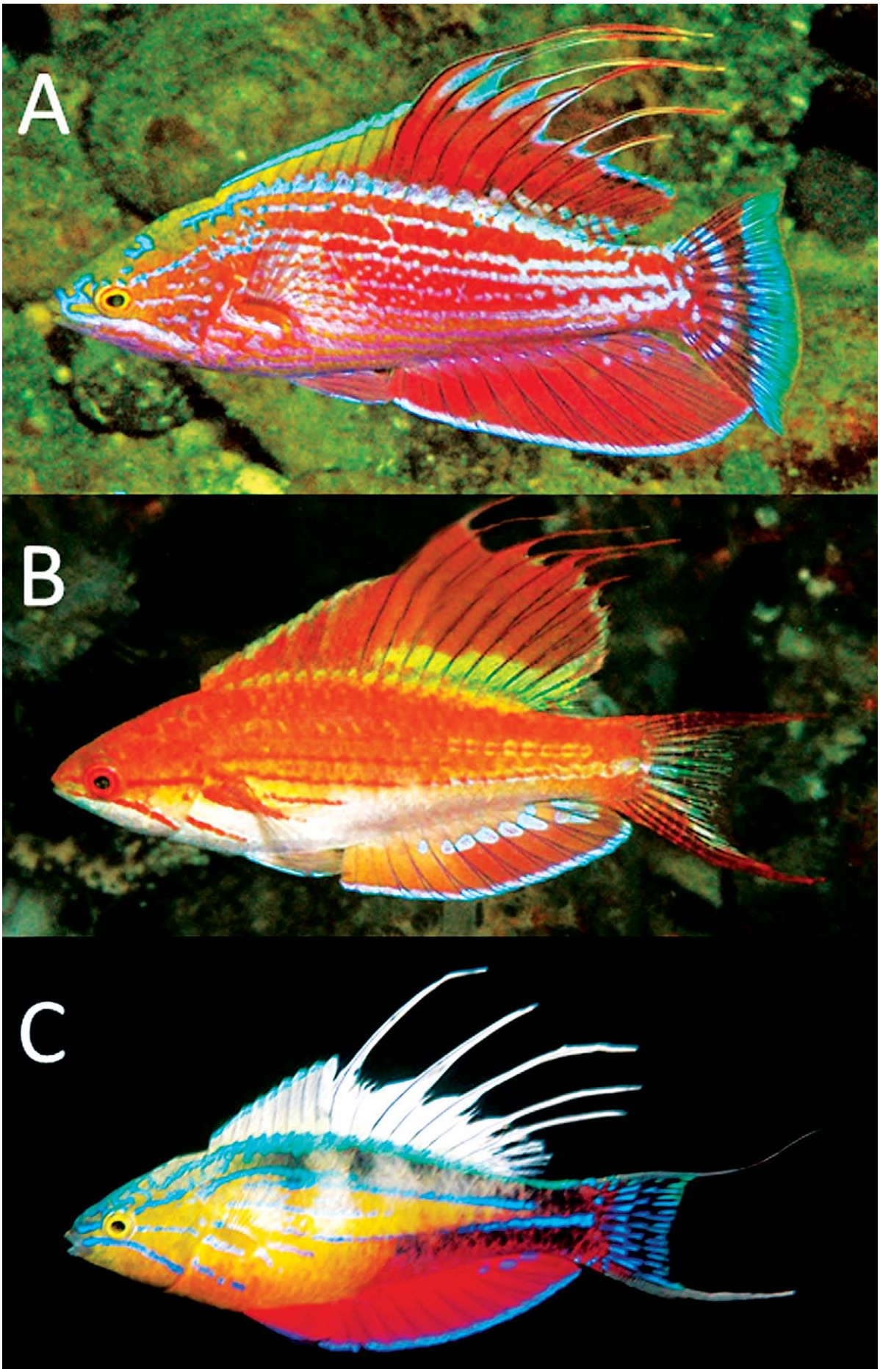


Figure 5. Genus *Paracheilinus*, nuptial-male display, examples of hybridization: A) *P. angulatus x P. lineopunctatus;* B) *P. paineorum* x *P. togeanensis*; and C) *P. cyaneus* x *P. nursalim*; all fish approximately 55 mm SL (G.R. Allen).

Diagnostic features and intrageneric relationships. The most important features for identification of *Paracheilinus* species include the shape of the dorsal fin (particularly the presence or absence of elongate, filamentous fin rays), the shape of the caudal fin (rounded, truncate, lunate, or lanceolate), and color pattern, especially of the nuptial-display pattern of TP males. Although diagnostic in TP males, caudal-fin shape can be misleading in smaller individuals: males less than about 35–40 mm SL in species which develop a strongly lunate fin frequently have a truncate caudal fin.

The genus is divisible into four main groups based on morphology and color pattern, which generally matches the genetic relationships discussed in a later section. The *filamentosus* group is characterized by many, almost always four or more, filamentous dorsal-fin rays in TP males and a strongly lunate or forked caudal fin and comprises *P. bellae*, *P. cyaneus*, *P. filamentosus*, *P. nursalim*, *P. paineorum*, *P. walton*, and *P. xanthocirritus*. The species within this group, as in the other three groups, are readily separable on the basis of coloration, especially the nuptial-display pattern (Fig. 4). Other potential members of the *filamentosus* group are *P. lineopunctatus* and *P. togeanensis*, although these species lack either a forked caudal fin (rounded in *P. lineopunctatus*) or filamentous dorsal-fin rays (*P. togeanensis*). Unfortunately, we do not have genetic samples for these two species which are difficult to obtain.

The *mccoskeri* group is characterized by a rounded caudal fin and a single filamentous extension of the soft dorsal fin in TP males, sometimes with one to three additional filamentous dorsal-fin rays. Members of this group comprise *P. carpenteri*, *P. flavianalis*, *P. mccoskeri*, and *P. rubricaudalis*. The *angulatus* group, which contains *P. alfiani*, *P. angulatus* and *P. rennyae*, lacks filamentous dorsal-fin rays, has either a rounded (*P. alfiani* and *P. rennyae*) or moderately lunate (*P. angulatus*) caudal fin, and has either a rounded (*P. alfiani* and *P. rennyae*) or angular dorsal-fin profile (*P. angulatus*). Finally, the western-Indian-Ocean group contains all but one of the species from this region, comprising *P. attenuatus*, *P. hemitaeniatus*, *P. octotaenia*, and *P. piscilineatus* (*P. mccoskeri* is also found in the area, but is not included). Caudal-fin shape and color patterns differ between the species in the group, and most lack filamentous dorsal-fin rays, although *P. attenuatus* has a single hair-like extension of the first soft dorsal-fin ray.

Taxonomic placement of *Paracheilinus*. Randall (1999b) included *Paracheilinus* in the tribe Cirrhilabrini of the labrid subfamily Cheilininae. The tribe contains six genera, including *Cirrhilabrus* Temminck & Schlegel, 1845; *Conniella* Allen, 1983; *Paracheilinus*; *Pseudocheilinops* Schultz, 1960; *Pseudocheilinus* Bleeker, 1862; and *Pteragogus* Peters, 1855. Members of the tribe share the unique character of a double pupil resulting from an oblique vertical division of the scleral cornea into two near-equal parts (Springer & Randall 1974), an apparent adaption for close vision in detecting small prey. Allen (1974) discussed the apparent close relationship between *Paracheilinus* and *Cirrhilabrus*.

Cirrhilabrus are very similar to *Paracheilinus* in size, general appearance, and exhibit remarkably similar behavior and habitat preference. The two genera commonly mingle in rubble or *Halimeda* algal beds. Similar to *Paracheilinus*, the TP males of *Cirrhilabrus* are extremely colorful and flash nuptial colors to smaller, often dull-colored females 1–2 hours prior to sunset. The small initial-phase *Cirrhilabrus* females are sometimes courted by males of *Paracheilinus*, and consequently often appear in the background of photographs of courting males. Based on their synchronous courtship behavior and close morphology, one might expect occasional inter-generic hybrids, but none have been observed to date. The main morphological difference between the two genera is in the number of dorsal-fin spines and pectoral-fin rays (usually 9 and 14 respectively in *Paracheilinus* vs. 11 and 15 or 16 in *Cirrhilabrus*). In addition, the margin of the preopercle is serrate in *Cirrhilabrus* compared to smooth in *Paracheilinus*. Small juveniles (under about 25 mm SL) of the two genera are generally similar in appearance, except those of *Cirrhilabrus* usually possess a dark spot or saddle dorsally on the caudal peduncle, which is generally absent in *Paracheilinus* (except *P. attenuatus*); in addition, most species of *Cirrhilabrus* have juveniles with a prominent white spot on the tip of the snout, while juvenile *Paracheilinus* have distinctive white eyebrow-like marks over the dorsal scleral surface of each eye. The monotypic genus *Conniella* from offshore reefs of northwestern Australia is essentially identical to *Cirrhilabrus*, except it lacks pelvic fins and the internal supporting structure (i.e. pelvic girdle).

Key to the Species of the Genus *Pseudocheilinus*, based on TP male characters

1a. Adults without elongate filamentous dorsal-fin ray(s) 2

1b. Adults with 1–9 elongate filamentous dorsal-fin ray(s) 8

2a. Caudal fin rounded 3

2b. Caudal fin truncate, emarginate, or lunate 5

3a. Outer margin of caudal fin narrowly blue in life with single blue band near base; pair of blue bands across interorbital/forehead; no orange zone posteriorly on dorsal and anal fins; body stripes uninterrupted (no rows of spots or broken lines)(Red Sea) .....***P. octotaenia***

3b. Outer margin of caudal fin broadly yellow in life; no blue bands across interorbital/forehead; orange zone posteriorly on dorsal and anal fins; some body stripes usually interrupted (may form rows of spots or broken lines) 4

4a. Anterior dorsal fin yellow-orange to about second spine; basal two-thirds of caudal fin reddish with double band of blue spots; conspicuous blue markings along base of anal fin; about 10 broken or complete greyish-to-blue stripes on side of body (Komodo Islands & SW Flores, Indonesia) .....***P. rennyae***

4b. Anterior dorsal fin yellow-orange to about sixth spine; basal two-thirds of caudal fin purple to blue without double band of blue spots; no blue markings along base of anal fin; color pattern of side not as in 4a (Lembata Island, Indonesia) .....***P. alfiani*, n. sp.**

5a. Caudal fin truncate or slightly emarginate (Mauritius) .....***P. piscilineatus***

5b. Caudal fin moderately to deeply lunate 6

6a. Posterior dorsal-fin and anal-fin rays elongated, forming sharply pointed profile on each fin (Philippines & northern Borneo, eastern margin of South China Sea) .....***P. angulatus***

6b. Posterior dorsal-fin and anal-fin rays not elongated, forming more or less rounded profile on each fin 7

7a. Posterior half of dorsal fin noticeably tall and rounded, longest dorsal-fin soft rays about equal to head length; dark body stripes not mainly confined to anterior half of body (Tomini Bay to North Sulawesi, Indonesia) .....***P. togeanensis***

7b. Posterior half of dorsal fin not noticeably tall and rounded, longest dorsal-fin soft rays less than head length; dark body stripes mainly confined to anterior half of body (KwaZulu-Natal, South Africa & south-western Madagascar) .....***P. hemitaeniatus***

8a. Caudal fin lanceolate (longest rays in middle portion of fin); soft portion of dorsal fin rounded except for single, uniformly thin, hair-like filamentous first ray (Seychelles & Kenya) .....***P. attenuatus***

8b. Caudal fin not lanceolate, either rounded or deeply lunate; filamentous rays of soft dorsal fin not thin and hair-like, each generally broad at base and tapering to a thin point 9

9a. Caudal fin rounded 10

9b. Caudal fin lunate (or truncate in smaller males <40 mm SL) 14

10a. Four or more narrow stripes on side of body; 2–8 elongate filamentous dorsal-fin rays 11

10b. Three narrow stripes on side of body, middle one on anterior half of body and slightly oblique; usually a single elongate filamentous extension of soft dorsal fin (except *P. flavianalis* with 1–4) 12

11a. Four narrow blue-to-reddish stripes along side of body, short middle two on anterior half of body; 2–4 elongate filamentous dorsal-fin rays (southern Japan, Taiwan, Palau, Philippines, Brunei, & Kalimantan & Sulawesi, Indonesia) .....***P. carpenteri***

11b. Numerous (more than four) purplish-to-reddish stripes or vermiculated lines along side of body; 5–8 elongate filamentous dorsal-fin rays (Philippines) .....***P. lineopunctatus***

12a. Anal fin yellow; 1–3 elongate filamentous dorsal-fin rays (southern & eastern Indonesia & reefs off northwestern Australia) .....***P. flavianalis***

12b. Anal fin mostly red; single filamentous extension of soft dorsal fin (mostly first ray) 13

13a. Caudal fin mainly yellow-brown to brownish; body depth 3.0–3.4 in SL; pelvic fins 2.1–2.4 in HL (Kenya, Comoro Islands, Persian Gulf, Maldive Islands, Chagos Archipelago, & Andaman Sea) .....***P. mccoskeri***

13b. Caudal fin mainly bright red; body depth 3.4–3.6 in SL; pelvic fins 1.8–2.0 in HL (Fiji, Vanuatu, Great Barrier Reef, Coral Sea, & Papua New Guinea) .....***P. rubricaudalis***

14a. Body relatively slender, depth 3.6–3.7 in SL; numerous narrow blue stripes and wavy lines on body (Palau, Yap, Chuuk, & Marshall Islands) .....***P. bellae***

14b. Body depth 2.9–3.5 in SL; relatively few blue stripes on body (usually only two running full-length of body plus several short bands) 15

15a. Stripe pattern A (see Fig. 2A & B) 16

15b. Stripe pattern B (see Fig. 2C) 18

16a. No row of blue spots on anal fin; stripes relatively thick in nuptial display; background color of body maroon to violet red; central caudal fin without elaborate blue markings, instead a narrow blue posterior (Papua New Guinea, Solomon Islands, & northern Great Barrier Reef) .....***P. filamentosus***

16b. Row of blue spots basally on anal fin; stripes relatively thin in nuptial display; background color of body bright red to yellow or orange; central caudal fin with elaborate blue markings 17

17a. Dorsal fin as in Figure 6A, with bright red area over last few dorsal-fin spines, first few soft rays (except basal portion), and filamentous rays; anterior dorsal fin yellow or orange, posterior fin and base mostly pale bluish (central Indonesia, from Java Sea east to Komodo & Sulawesi) .....***P. paineorum*, n. sp.**

17b. Dorsal fin as in Figure 6B, yellow to yellow orange, including filamentous rays, with irregular dark area on posterior fin, and bluish basal band (southeastern South China Sea) .....***P. xanthocirritus*, n. sp.**

18a. Prominent rectangular black patch on ventral third of caudal peduncle (southern Raja Ampat to Kaimana, West Papua, Indonesia) ..... ***P. nursalim***

18b. No black patch on ventral third of caudal peduncle 19

19a. Dorsal part of head and anterior body bright blue-green; anal fin deep burgundy red rimmed with blue (West Papua, Halmahera, Sulawesi, & Kalimantan, Indonesia) ..... ***P. cyaneus***

19b. Head and anterior body reddish orange to yellow; anal fin orange or yellowish rimmed with blue (Cenderawasih Bay to Ayau Atoll, West Papua, Indonesia) ..... ***P. walton***

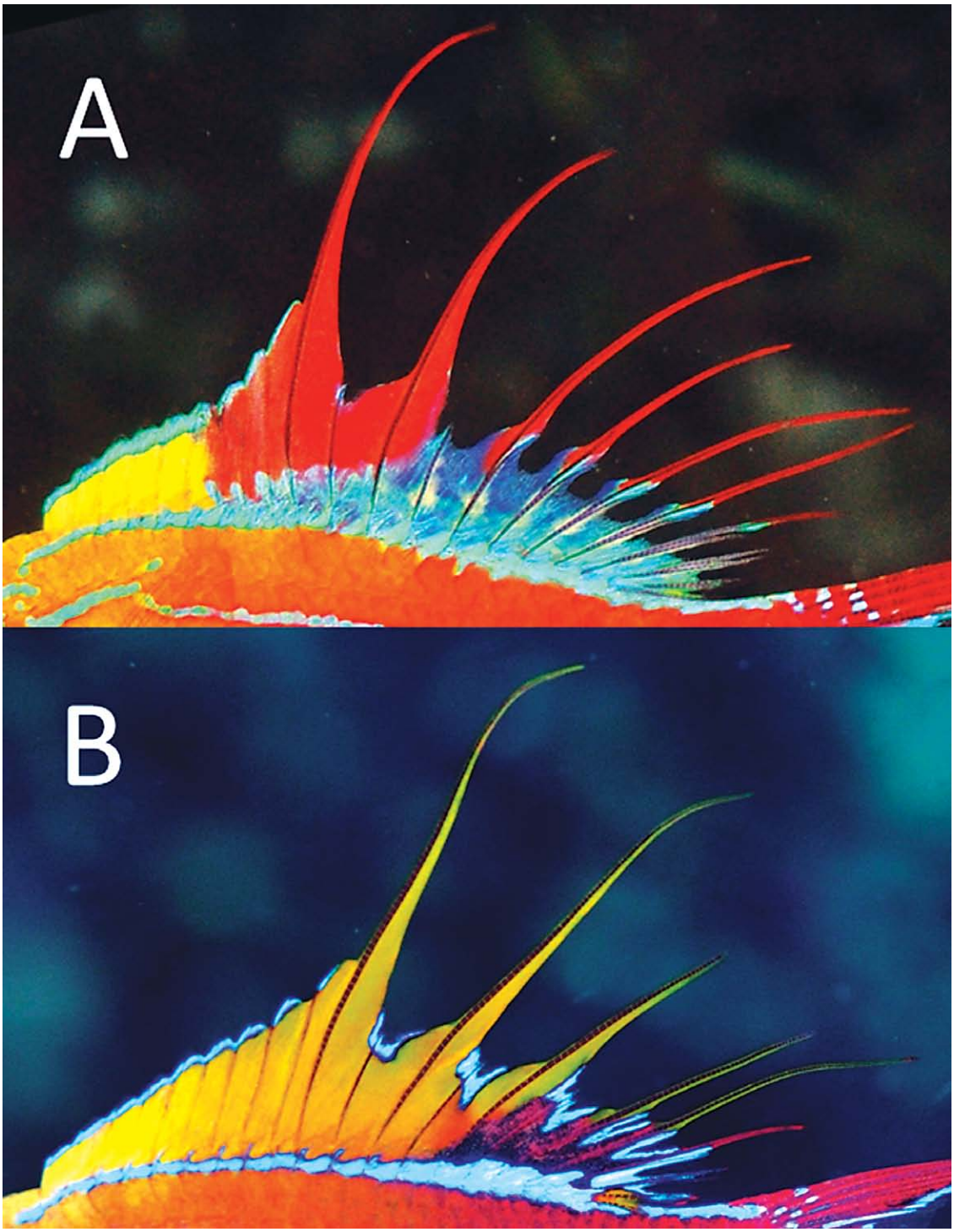


Figure 6. Dorsal fin coloration of nuptial-male display: *Paracheilinus paineorum* (A) vs. *Paracheilinus xanthocirritus* (B) (G.R. Allen).

Paracheilinus alfiani, n. sp.

Figures 7–9; Table 2.

Holotype. MZB 22244, male, 49.3 mm SL, Waru Waruwuntun, 08° 16.398’ S, 123° 32.746’ E, Lembata Island, Lesser Sunda Islands, Indonesia, 18–22 m, spear, R. Alfian, May 14, 2014.

Paratypes. WAM P.34276-001, male, 48.8 mm SL, collected with holotype.

Diagnosis. Pored lateral-line scales 15 + 5–6; gill rakers on first branchial arch 13–14; body depth 3.1–3.2 in SL; head length 3.1–3.2 in SL; snout length 3.8–3.9 in HL; eye diameter 4.2–4.4 in HL; interorbital width 4.2–4.4 in HL; least depth of caudal peduncle 2.2–2.4 in HL; caudal-peduncle length 1.8 in HL; dorsal fin of both sexes without elongate filamentous rays; longest dorsal-fin soft ray of TP male 4.3–4.4 in SL; pelvic fin length 1.6–1.8 in HL; caudal fin of both sexes slightly rounded (truncate in preserved specimens); maximum size to at least 49.3 mm SL; color of TP males generally orange on head and anterior body, grading to reddish or purplish posteriorly (except broad, purple-edged, median orange zone); head and body pink ventrally; stripe pattern a variation of pattern A with purple-to-reddish stripes and bands on head and body with two primary stripes expanded and diffuse on posterior half of body; dorsal and anal fins mainly burgundy red to purplish with yellow-orange sections anteriorly (on dorsal fin) and posteriorly, and narrow blue outer margins; caudal fin mainly blue to purple with broad outer margin of yellow; pelvic fins purple to burgundy red; pectoral fins translucent. Peak nuptial-display pattern features a large white patch behind pectoral fin, linked dorsally with tapered stripe of neon blue at level of anterior lateral line, continuing to caudal-fin base.

Description. Dorsal-fin rays IX; anal-fin rays III,9; pectoral-fin rays (including upper rudimentary ray) 14; lateral-line interrupted, pored scales 15 + 4 (15 + 5 or 6); scales above lateral line to origin of dorsal fin 2; scales below lateral line to origin of anal fin 6; median predorsal scales 5; median preventral scales 5 (4); transverse scale rows on cheek 2; circumpeduncular scales 14; gill rakers 13 (14); pseudobranchs 12.

Body depth 3.2 (3.1) in SL; body width 2.2 (2.1) in body depth; head length 3.2 (3.1) in SL; snout length 3.9 (3.8) in HL; eye diameter 4.2 (4.4) in HL; interorbital width 4.4 (4.2) in HL; least depth of caudal peduncle 2.4 (2.2) in HL; caudal-peduncle length 1.8 in HL.

Mouth small, oblique, maxilla not reaching vertical at front edge of eye, its length 4.4 (4.7) in HL; three pairs of curved canine teeth anteriorly in upper jaw, progressively more laterally projecting, third (posteriormost) pair largest; single pair of canine teeth anteriorly in lower jaw, very strongly curved laterally; side of jaws with single row of small close-set conical teeth; no canine tooth at corner of mouth; no teeth on palate; fleshy flap on side of lower lip; gill rakers short, longest about one-third length of longest gill filaments on first gill arch; posterior nostril an oval opening about 2–3 times larger than cephalic sensory pores, about level with fleshy upper edge of eye and slightly anterior to vertical at anterior bony edge of eye; anterior nostril much smaller, forming an oblique slit a short distance in front of posterior nostril and slightly more dorsal in position, without noticeable fleshy rim; cephalic sensory system consisting of nine pores posterior and ventral along edge of eye, two supraocular pores, five occipital pores, a single mid-interorbital pore, three small pores on side of snout, four mandibular pores, and five preopercular pores.

Head scaled except for anterior occipital region, interorbital space, snout, and chin; a row of pointed scales on base of dorsal and anal fins; basal half of caudal fin with large scales; axillary scale of pelvic fin slightly shorter than pelvic spine; midventral scaly process of pelvic fins slightly longer than pelvic spine.

Free ventral margin of preopercle extending forward to vertical at center of eye, vertical posterior margin to level of lower edge of pupil; exposed bony edge of preopercle smooth without serrations.

Origin of dorsal fin above third lateral-line scale, predorsal length 3.1 (3.0) in SL; dorsal-fin spines progressively longer, first 5.5 in paratype in HL (damaged in holotype), and ninth 2.4 in HL; soft portion of dorsal fin gently rounded without filamentous rays, longest (third) ray 4.4 (4.3) in SL; origin of anal fin below base of first dorsal-fin soft ray, preanal length 1.7 (1.8) in SL; first anal-fin spine 3.4 (3.8) in HL; second anal-fin spine 2.9 (3.1) in HL; third anal-fin spine 2.7 (2.9) in HL; longest (penultimate) anal-fin soft ray 4.2 in SL; caudal fin truncate (preserved) to slightly rounded (when live and fin fully expanded), 4.6 (4.7) in SL; pectoral-fin length 1.5 (1.4) in HL; pelvic-fin length 1.6 (1.8) in HL.

Figure 7. *Paracheilinus alfiani*, nuptial-male display (peak pattern below), approx. 50 mm SL, Lembata Island, Indonesia (N. DeLoach).

Color of TP male in life. (from video clips) Head and anterior body generally orange, grading to reddish or purplish posteriorly (except broad, purple-edged, median orange zone); head and body pink ventrally; pattern of narrow purple to brownish stripes on anterior body; dorsal and anal fins mainly burgundy red to purplish with narrow blue outer margin; caudal fin mainly blue to purple with broad outer yellow margin; pelvic fins purple to burgundy red; pectoral fins translucent.

Male nuptial coloration. (Fig. 7) Head and anterior body generally orange, orange continued posteriorly as broad zone initially, gradually tapering nearly to a point at caudal-fin base; upper and lowermost portions of side

purplish brown and pinkish respectively; several narrow brown to purplish stripes on head and body; dorsal and anal fins mainly burgundy red with purple rays, except anterior (to about sixth dorsal-fin spine) and posterior (last 1 or 2 rays) parts of dorsal fin and posteriormost portion of anal fin yellow orange; narrow blue margin on both dorsal and anal fins; row of triangular blue spots (increasing in size posteriorly, largest about two-thirds pupil size) along base of dorsal fin; caudal fin purplish to blue on basal two-thirds with broad yellow outer margin; pelvic fins burgundy red with purple rays; pectoral fins translucent. A dramatic color change occurs at peak nuptial display (Fig. 7, lower) in which body assumes a dark purplish hue (particularly noticeable along upper back) with a large, bright white patch just behind pectoral fin, linked above to a tapered stripe of neon blue at level of anterior lateral line, which continues to caudal-fin base.

Color of IP in life. (from video clips) Head and body reddish or red-orange, grading to white on ventral aspect, with reddish-to-bluish stripes mostly paralleling those of TP males. Initial-phase fish of *filamentosus* group mostly similar in appearance (Fig. 1).

Color of holotype in alcohol. (Fig. 8) After several months in alcohol, pale whitish to pale tan; broken purplish stripe from rear margin of eye to pectoral-fin base and similar stripe just above, extending onto anterior dorsal part of body; broad charcoal-colored zone on upper side below soft dorsal fin; slightly yellowish mid-lateral stripe, tapering posteriorly on rear half of body; lower side mainly whitish with numerous fine melanophores; dorsal and anal fins whitish with purple spines and rays; caudal-fin rays purple on basal two-thirds and translucent whitish on outer margin; pelvic fins purple; pectoral fins translucent.

Distribution and habitat. The new species is currently known only from the type locality on the northern coast of Lembata Island in the Lesser Sunda Group of Indonesia (Fig. 9). Interestingly, despite extensive survey effort by the authors in both Maumere Bay and the Alor region (100 km west and east of the type locality, respectively), *P. alfiani* has not been recorded outside of Lewaling Bay in northern Lembata Island. A similar phenomenon of a highly restricted local range is also found in *P. rennyae*, which is currently only known from southern Komodo Islands and nearby southern Flores. *Paracheilinus alfiani* is generally found on sloping, low profile bottoms with branching hard and soft corals (predominantly *Sarcophyton* and *Xenia*) in depths of about 20 m. It was observed in large mixed aggregations with *P. paineorum* and *P. flavianalis*. A number of suspected hybrids, most likely *P. alfiani* x *P. paineorum*, with the colors of *P. alfiani* and the filamentous rays of *P. paineorum* (Fig. 10), were also observed in the area.

Etymology. The species is named in honor of dive guide Rahmad "Yann" Alfian, the collector of the holotype.

Remarks. The new species belongs in the *angulatus* group, based primarily on the absence of elongate filamentous dorsal-fin rays, the absence of a strongly lunate caudal fin (in this case rounded), and close genetic affinity. Notably however, *P. angulatus* is easily distinguished by sharply pointed dorsal-fin and anal-fin outlines and a moderately lunate caudal-fin shape (and is allopatric, from northern Indonesia and Philippines). The new species is most similar in appearance to two other Indonesian species: *P. rennyae* and *P. togeanensis* (placement

Figure 8. *Paracheilinus alfiani*, preserved holotype, MZB 22244, male, 49.3 mm SL, Lembata Island, Indonesia (G.R. Allen).

TABLE 2

Proportional measurements of male type specimens
of *Paracheilinus alfiani*, n. sp.
as percentages of the standard length

	holotype	paratype
	MZB 22244	WAM P.33899
Standard length (mm)	49.3	48.8
Body depth	31.5	32.3
Body width	14.2	15.1
Head length	31.0	32.1
Snout length	7.9	8.5
Orbit diameter	7.5	7.4
Interorbital width	7.1	7.6
Upper jaw	7.1	6.8
Depth of caudal peduncle	13.2	14.5
Length of caudal peduncle	16.8	18.1
Predorsal distance	32.3	33.8
Preanal distance	58.9	55.8
Prepelvic distance	34.3	35.7
Length of dorsal-fin base	51.8	53.2
First dorsal-fin spine	2.2 (damaged)	5.9
Last dorsal-fin spine	13.2	13.2
Longest dorsal-fin soft ray	22.6	23.1
Length of anal-fin base	25.5	27.3
First anal-fin spine	9.2	8.5
Second anal-fin spine	10.7	10.4
Third anal-fin spine	11.4	11.3
Longest anal-fin soft ray	23.9	23.9
Caudal-fin length	22.0	21.5
Pectoral-fin length	20.1	22.3
Pelvic fin-spine length	10.5	11.8
Pelvic fin length	19.1	17.8

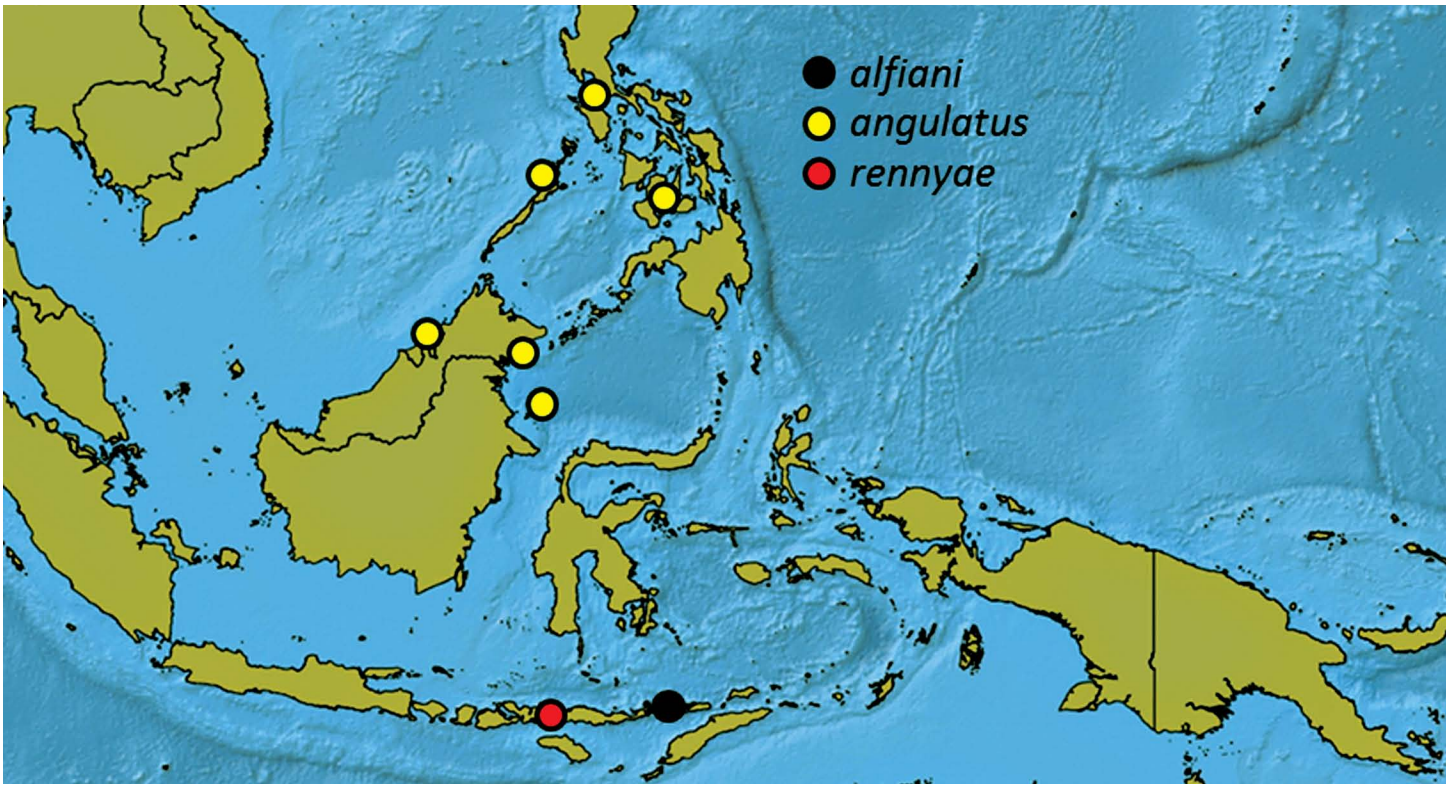


Figure 9. Geographic distribution of the *angulatus* group of *Paracheilinus* in the East Indies.

of the latter is uncertain without any genetic sequences). The three species share a rounded dorsal-fin profile without elongate filamentous rays (note that several western Indian Ocean species share this character but are distant geographically and genetically and have very different color patterns). *Paracheilinus togeanensis* is easily distinguished by its lunate caudal fin and color pattern. *Paracheilinus alfiani* shares body and fin shape with its close relative *P. rennyae*, however the color patterns of TP males of the two species are considerably different: in particular, the numerous thin broken stripes on the side of *P. rennyae* vs. the relatively few stripes of *P. alfiani* and the patch of yellow-orange on the anterior dorsal fin of *P. rennyae* occupies only the first two spinous membranes, compared to over six membranes on *P. alfiani*.

Figure 10. Probable *Paracheilinus alfiani* x *P. paineorum* hybrid, nuptial-male display, approx. 55 mm SL, Lembata Island, Indonesia (N. DeLoach).

Paracheilinus angulatus Randall & Lubbock, 1981

Figures 7 & 11–13.

Paracheilinus angulatus Randall & Lubbock 1981: 26, pl. 2D (type locality: Mactan Island, Cebu, Philippines); Kuiter & Tonozuka 2004: 497, 4 figs. (Philippines & northern Indonesia); Michael 2009; 279, 2 figs. (northern Indonesia & Philippines); Kuiter 2010: 111, 5 figs. (Philippines & northern Indonesia); Allen & Erdmann 2012: 705 (Brunei, Malaysia (Sabah), Kalimantan, & Philippines).

Material examined. Batangas, Luzon, Philippines: BPBM 22526 (paratype), 59.9 mm SL. Brunei: WAM P.33128-004, 40.2 mm SL; WAM P.34267-003, 47.2 mm SL.

Diagnosis. Pored lateral-line scales 17 + 6–7; gill rakers on first branchial arch 15–17; body depth 3.2–3.3 in SL; head length 3.1–3.3 in SL; snout length 4.0–4.3 in HL; eye diameter 4.0–4.1 in HL; interorbital width 3.8–4.3 in HL; least depth of caudal peduncle 2.1–2.2 in HL; caudal peduncle length 1.6–1.9 in HL; dorsal and anal fins gradually increasing in height posteriorly with pointed posterior tips; no filamentous dorsal-fin rays; longest dorsal-fin soft ray of TP male 3.3–4.1 in SL; pelvic fin length 1.6–1.9 in HL; caudal fin of TP males emarginate to moderately lunate; maximum size to at least 60.0 mm SL; color of TP males overall orange-red with bluish stripes in pattern A on head and body; dorsal fin mainly crimson red except orange covering first few spinous membranes; anal fin with sky-blue outer margin and two rows of bluish-to-lavender spots basally, outermost row confined to rear section of fin and continuous with cluster of blue spots along posterior margin.

Remarks. *Paracheilinus angulatus* occurs in the East Indian region at the Philippines (Palawan, Cebu, and Luzon) and northern Borneo, including Brunei, Malaysian Sabah and Indonesian Kalimantan (Fig. 9), in depths of 10–40 m (Allen & Erdmann 2012). The TP males of this distinctive species differs from all other congeners in having the combination of a sharply angular and pointed profile of the dorsal and anal fins, no filamentous dorsal-fin rays, and an emarginate to lunate caudal fin (Figs. 11–13). Despite this unique combination of morphological characters, we include *P. alfiani* and *P. rennyae* in the same *angulatus* group based on the shared character of no

Figure 11. *Paracheilinus angulatus*, nuptial-male display, approx. 55 mm SL, Anilao, Luzon, Philippines (G.R. Allen).

Figure 12. *Paracheilinus angulatus*, TP male (not nuptial display), approx. 50 mm SL, Anilao, Luzon, Philippines (G.R. Allen).

filamentous dorsal-fin rays, apparently the defining character since this group of three allopatric species have very close mtDNA lineages, most likely indicating very recent evolutionary divergence. Other species that are missing the elongate filamentous dorsal-fin rays comprise *P. togeanensis* (genetic placement unknown) and three western Indian Ocean congeners that are only distantly related (*P. hemitaeniatus*, *P. octotaenia,* and *P. piscilineatus*).

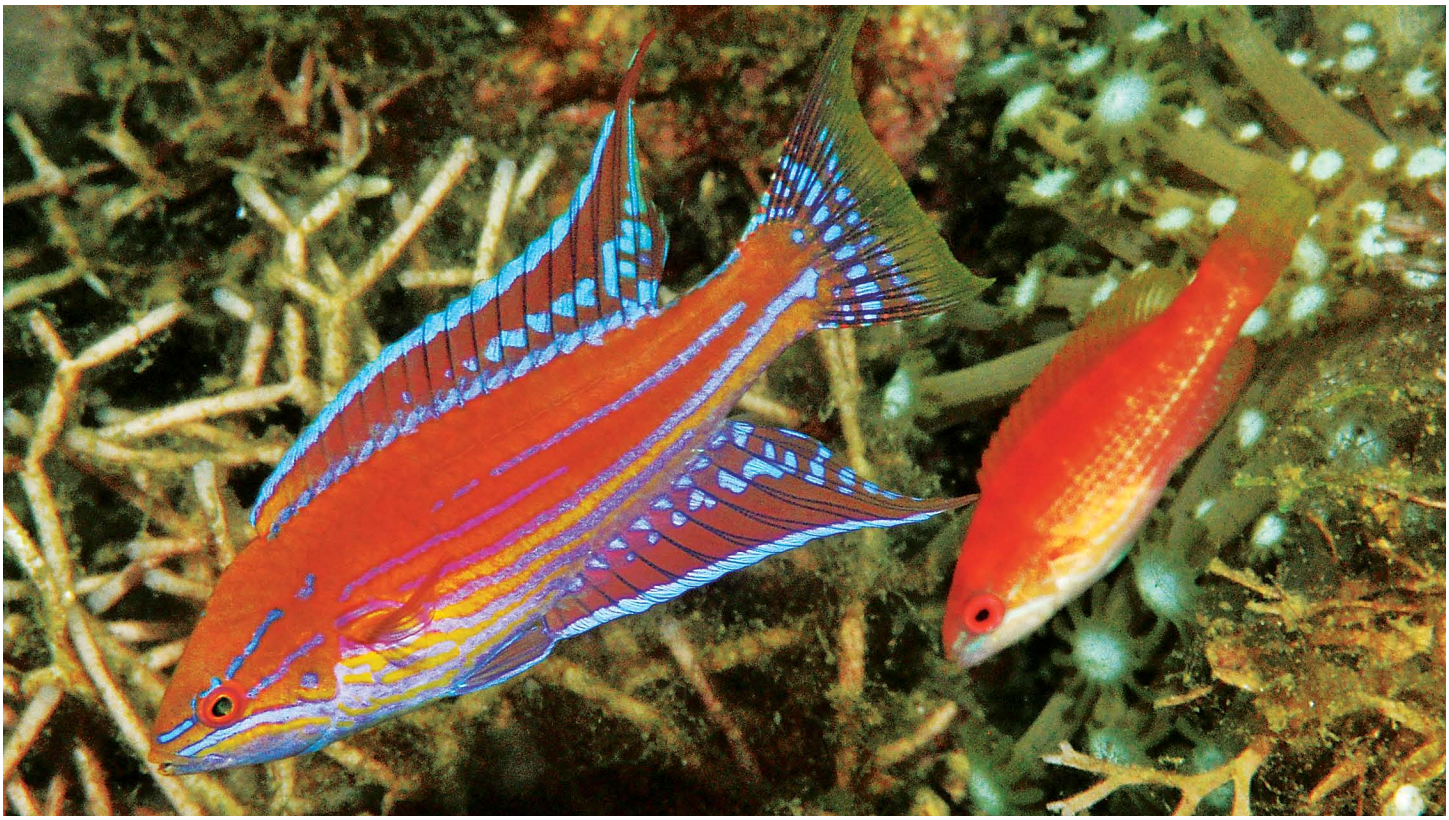


Figure 13. *Paracheilinus angulatus*, nuptial-male display at left, approx. 55 mm SL, and female at right, approx. 35mm SL, Anilao, Luzon, Philippines (G.R. Allen).

Paracheilinus attenuatus Randall, 1999

Figures 14–16.

Paracheilinus mccoskeri [*non* Randall & Harmelin-Vivien] Randall & van Egmond 1994: 58, fig. 45 (St. Francois Atoll, Amirante Islands, Seychelles).

Paracheilinus attenuatus Randall 1999a: 34, figs. 2–3 (type locality: St. François Atoll, Amirante Islands, Seychelles); Michael 2009; 280, 1 fig. (Seychelles & Kenya); Kuiter 2010: 118, 4 figs. (Seychelles & off Kenya).

Material examined. St. François Atoll, Amirante Islands, Seychelles: BPBM 35614 (holotype), 59.5 mm SL; BPBM 35506 (paratype), 35.4 mm SL; USNM 352065 (paratype), 37.6 mm SL.

Diagnosis. Pored lateral-line scales 15–18 + 5–7; gill rakers on first branchial arch 12–14; body depth 3.2–3.6 in SL; head length 2.9–3.1 in SL; snout length 3.9–4.1 in HL; eye diameter 3.4–4.5 in HL; interorbital width 3.6–4.0 in HL; least depth of caudal peduncle 2.2–2.4 in HL; caudal peduncle length 1.6–1.9 in HL; 4–6 (rarely 3) soft dorsal-fin and anal-fin profile of both IP and TP phases rounded, with a single filamentous extension of first dorsal-fin soft ray in both phases (but much longer in TP); longest dorsal-fin soft ray of TP male 1.6–1.7 in SL; pelvic fin length 1.6–1.8 in HL; caudal fin of juvenile truncate, IP caudal fin outline lanceolate with rounded central projection, but becoming prominently pointed lanceolate in TP males; maximum size to at least 65.8 mm SL; juveniles (up to about 30 mm SL) mainly reddish orange with 4 or 5 blue stripes on side of body, distinctive eye-sized, blue-edged, black spot at base of middle dorsal fin and second similar spot about one-half size of first on upper caudal peduncle, iris bright red; IP reddish orange grading to yellow or white ventrally with three complete long lavender-to-bluish body stripes, iris bright red; TP males generally pale orange to yellow with three bold lavender-to-blue stripes on side of body, three similar stripes across posterior head from rear edge of eye, the middle stripe sometimes extending over the pectoral-fin base in a continuous arc connecting to the lower body stripe, lowermost head stripe continued as a short oblique extension across side of thorax; dorsal-fin background yellow with broad wedge-shaped, blue-edged red zone posteriorly, single elongate filamentous dorsal-fin ray orange to red; anal fin yellow basally and red to orange distally, with irregular rows of blue-to-lavender spots at base and mid-fin with a blue-to-lavender outer margin.

Figure 14. *Paracheilinus attenuatus*, initial phase, 37.6 mm SL, St. François Atoll, Amirante Islands, Seychelles (J.E. Randall).

Figure 15. *Paracheilinus attenuatus*, upper: TP male holotype, BPBM 35614, 59.5 mm SL, St. François Atoll, Amirante Islands, Seychelles (J.E. Randall); lower: nuptial-male display in aquarium, approx. 50 mm SL, Kenya (K. Kohen).

Figure 16. *Paracheilinus attenuatus*, developmental changes in the same individual in the aquarium, upper: intermediate phase adult male, approximately 45 mm SL; lower: earlier appearance as late initial phase, approximately 35 mm SL, import from Kenya (H. Tanaka).

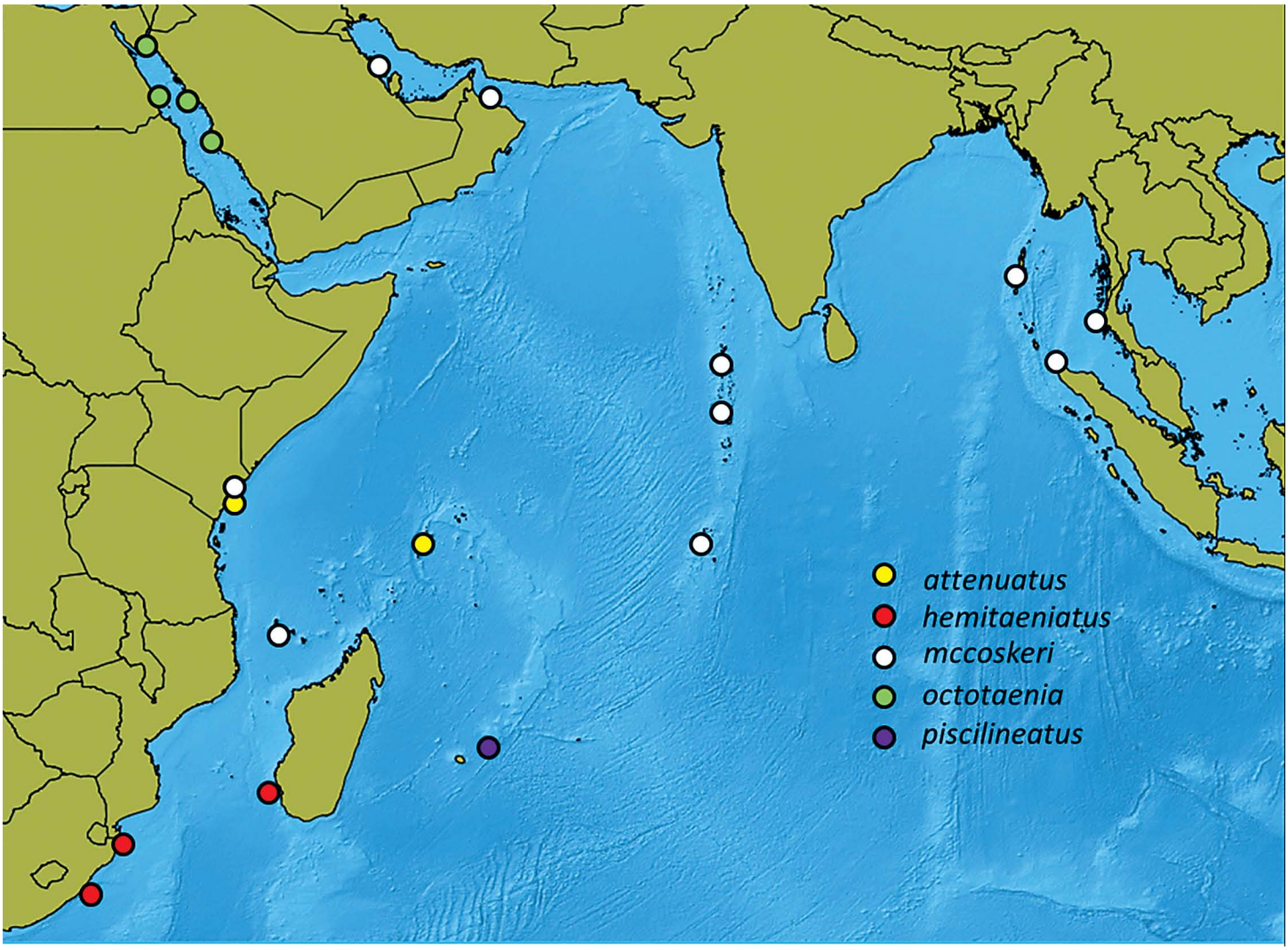


Figure 17. Geographic distribution of *Paracheilinus* species in the Indian Ocean.

Remarks. *Paracheilinus attenuatus* is currently known from six type specimens collected at St. François Atoll, Amirante Islands, Seychelles, and numerous fish exported from Kenya by the aquarium trade (including a single paratype). The known depth range is 28–50 m (Randall 1999a). The TP males of this species are distinguished from their congeners by a rounded dorsal fin with a single hair-like filament, a lanceolate caudal fin, and their distinctive color pattern. It is the only member of the genus with ocelli as part of the juvenile markings and the only member with a lanceolate caudal fin.

The species is part of the western-Indian-Ocean group, which comprises four of the five species from the region, i.e. *P. attenuatus*, *P. hemitaeniatus*, *P. octotaenia*, and *P. piscilineatus*. The remaining regional species, *P. mccoskeri*, is widespread in the northern and central Indian Ocean and belongs to another species-complex, more closely allied with western Pacific species. The Indian Ocean species of *Paracheilinus* are mostly allopatric in distribution (Fig. 17), except for in Kenya, where *P. mccoskeri* apparently overlaps with *P. attenuatus*.

The western-Indian-Ocean group form a related set of mtDNA lineages, however they are not particularly close to each other; nevertheless, as a group they are genetically distant from the other large species complexes that make up the other Indo-Pacific members of the genus. The grouping is mostly allied by geographic location; they are not very similar in appearance, each having a quite distinctive pattern of colors and markings and very different caudal-fin shapes, lateral stripe patterns, and nuptial male displays. The primary shared feature of their morphology is that three of the four have no elongate filamentous dorsal-fin rays in TP males (and only a single filament in *P. attenuatus*).

Paracheilinus bellae Randall, 1988

Figures 18–19.

Paracheilinus bellae Randall 1988: 222, pl. II D & pl. III H (type locality: Bigej-Mack Reef, Kwajalein Atoll, Marshall Islands); Myers 1999: 193 (Kwajalein Atoll); Michael 2009; 280, 2 figs. (Kwajalein Atoll); Kuiter 2010: 110, 2 figs. (Palau, Yap, Chuuk, Marshall Islands, & Iriomote, Japan).
Paracheilinus filamentosus [*non* Allen] Myers 1999: 193 & Plate 115H (Palau).

Material examined. Kwajalein Atoll, Marshall Islands: BPBM 28751 (holotype), 51.0 mm SL; BPBM 28764 (paratype), 46.6 mm SL; USNM 278976 (paratype), 51.8 mm SL.

Diagnosis. Pored lateral-line scales 15 + 5–6; gill rakers on first branchial arch 13–14; body depth 3.6–3.7 in SL; head length 3.2–3.3 in SL; snout length 3.7–3.9 in HL; eye diameter 4.3–4.8 in HL; interorbital width 4.3–4.5 in HL; least depth of caudal peduncle 2.2–2.3 in HL; caudal peduncle length 1.6 in HL; 3–6 (frequently 5) elongate filamentous dorsal-fin rays in TP male, longest dorsal-fin soft ray 1.7–1.8 in SL; pelvic fin length 1.6–1.7 in HL; caudal fin of TP male deeply lunate; maximum size to at least 51.8 mm SL; TP male coloration overall bluish to light purple with yellow to reddish stripes and vermiculations on side of body; dorsal fin largely greenish white; head adorned with bright blue and yellow bands or vermiculations and prominent blue stripe along base of dorsal fin; anal fin mainly burgundy red with sky-blue margin; caudal fin with dark red elongate lobes and blue central region basally; pelvic fins burgundy red with bluish anterior edge.

Remarks. *Paracheilinus bellae* is mainly restricted to the islands of Micronesia, including Palau, Yap, Saipan, Chuuk, and the Marshall Islands (Fig. 18). The only report from outside this region is from Iriomote Island, Japan (Kuiter 2010). The known depth range is 15–31 m. The species clearly belongs to the *filamentosus* group of species, based on its many elongate filamentous dorsal-fin rays, deeply lunate caudal fin, and stripe pattern (no tissue for genetic analysis is available). It differs from the other members of this group on the basis of its narrower body (body depth 3.6–3.7 in SL) and the distinctive color pattern of the TP male (Fig. 19).

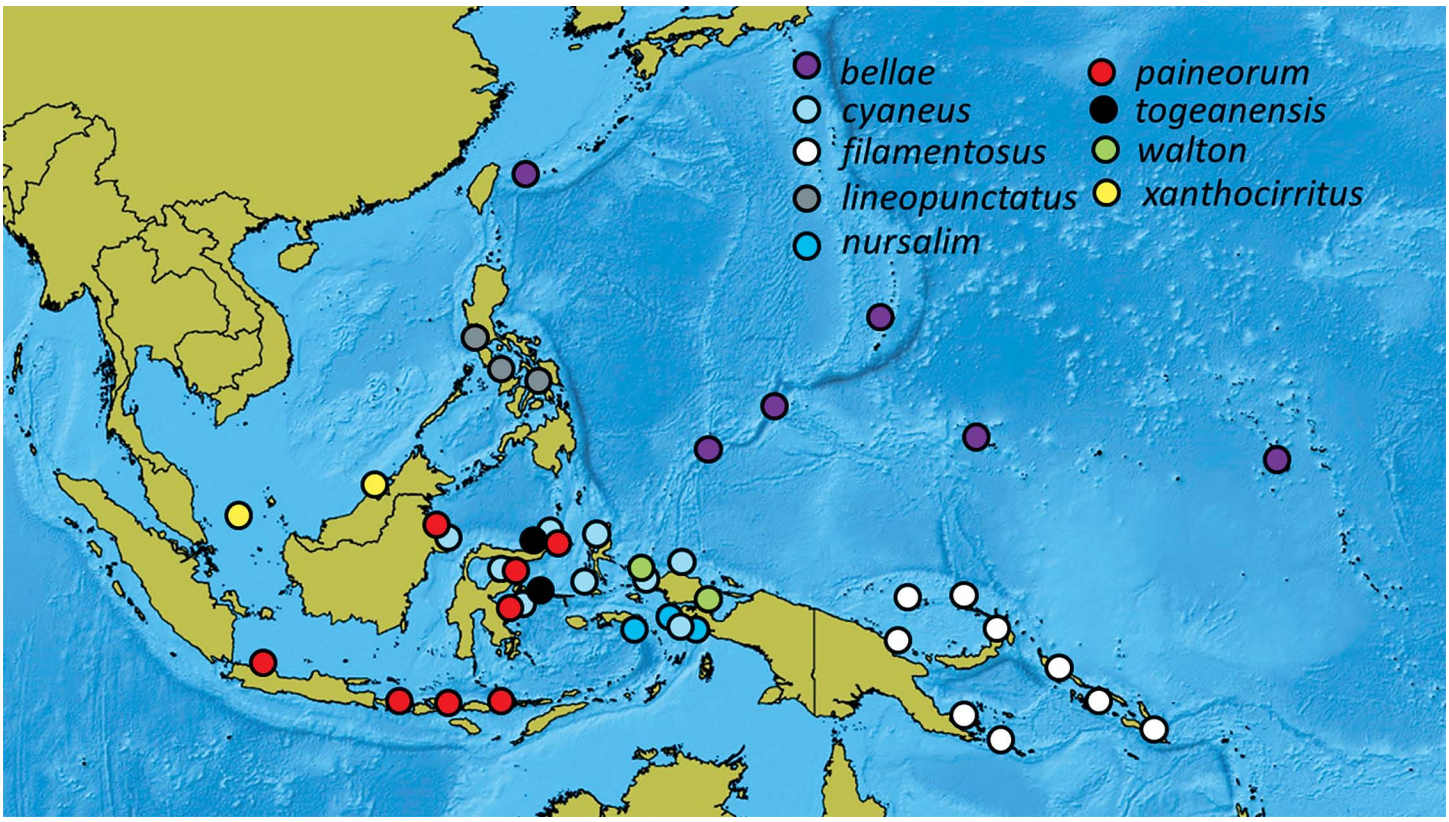


Figure 18. Geographic distribution of the *filamentosus* group of *Paracheilinus* in western Pacific Ocean.

Figure 19. *Paracheilinus bellae*, upper: nuptial-male display, approx. 50 mm SL, Palau (K. Nishiyama, courtesy H. Tanaka); lower: TP male holotype, BPBM 28751, 51.0 mm SL, Kwajalein Atoll, Marshall Islands, Micronesia (J.E. Randall).

At the time the species was described it was known from only the type location in Kwajalein Atoll. Since then it has been photographed at other locations. Myers (1999) reported that *P. bellae* was replaced in Palau by *P. filamentosus*, but the documentation of *P. bellae* in Palau suggests that the reports of *P. filamentosus* in Palau by Kuiter & Tonozuka (2004) and numerous subsequent internet sources (who mistakenly cite Westneat (2001, p. 3452) as the source) are misidentified *P. bellae*. The photographs from Palau, by Kazuhiko Nishiyama (Fig. 19 upper) and by Hiroshi Nagano (Myers 1999, Plate 115H), show *P. bellae*.

Paracheilinus carpenteri Randall & Lubbock, 1981

Figures 20–21.

Paracheilinus carpenteri Randall & Lubbock 1981: 24, pl. 2A, B (type locality: Mactan Island, Cebu, Philippines); Myers 1999: 193, pl. 115 F & G (Indonesia south to Bali to Flores (erroneous listing), Philippines, Taiwan to S. Japan, Palau); Michael 2009; 281, 4 figs. (Philippines to S. Japan, & Palau); Kuiter 2010: 114, 5 figs. (Philippines to S. Japan, & Palau); Allen & Erdmann 2012: 705 (Brunei & Philippines); Nishiyama & Motomura 2012: 232, 14 figs. (12 figs. from southern Japan, 2 figs. from Philippines).

Material examined. Mactan Island, Philippines: BPBM 22424 (holotype), 39.0 mm SL; BPBM 22116 (paratype), 52.0 mm SL; BPBM 21156 (paratypes), 2 specimens, 35.0–36.8 mm SL; USNM 219334 (paratypes), 12 specimens, 17.6–36.5 mm SL. Caban Island, Batangas, Luzon, Philippines: AMS I.20697-001 (paratype), 32.3 mm SL; BPBM 22465 (paratypes), 10 specimens, 21.6–65.8 mm SL. Brunei: WAM P.33128-005, 12 specimens, 19.0–35.5 mm SL.

Diagnosis. Pored lateral-line scales 14–17 + 4–6; gill rakers on first branchial arch 14–17; body depth 3.0–3.3 in SL; head length 3.0–3.3 in SL; snout length 3.7–4.1 in HL; eye diameter 3.2–4.6 in HL; interorbital width 4.0–4.3 in HL; least depth of caudal peduncle 2.1–2.3 in HL; caudal peduncle length 1.7–1.9 in HL; 2–4 elongate filamentous dorsal-fin rays in TP males, longest dorsal-fin soft ray 1.9–2.7 in SL; pelvic fin length 2.0–2.4 in HL; caudal fin of TP male rounded; maximum size to at least 65.8 mm SL; color of TP males overall orange to brownish orange-red with a pair of blue stripes extending most of length of body and notably two shorter stripes on anterior body in between; a pair of thin blue stripes behind eye and third thicker band from upper jaw, passing under lower margin of eye to edge of opercle, continuing across side of thorax; dorsal fin and filamentous rays yellowish to dull orange to brown (frequently brighter on anterior half of fin) with narrow blue outer margin (some populations with bright red filamentous rays and distal portion of soft dorsal fin), a blue band running along base of fin, a blue band breaking into spots through middle of fin, and frequently a dusky-to-black zone posteriorly, filling area between blue bands; anal fin yellow-orange to burgundy red except a zone of more yellowish at base below a blue band or series of spots or rectangular blocks; caudal fin dusky to blackish basally divided by a bluish

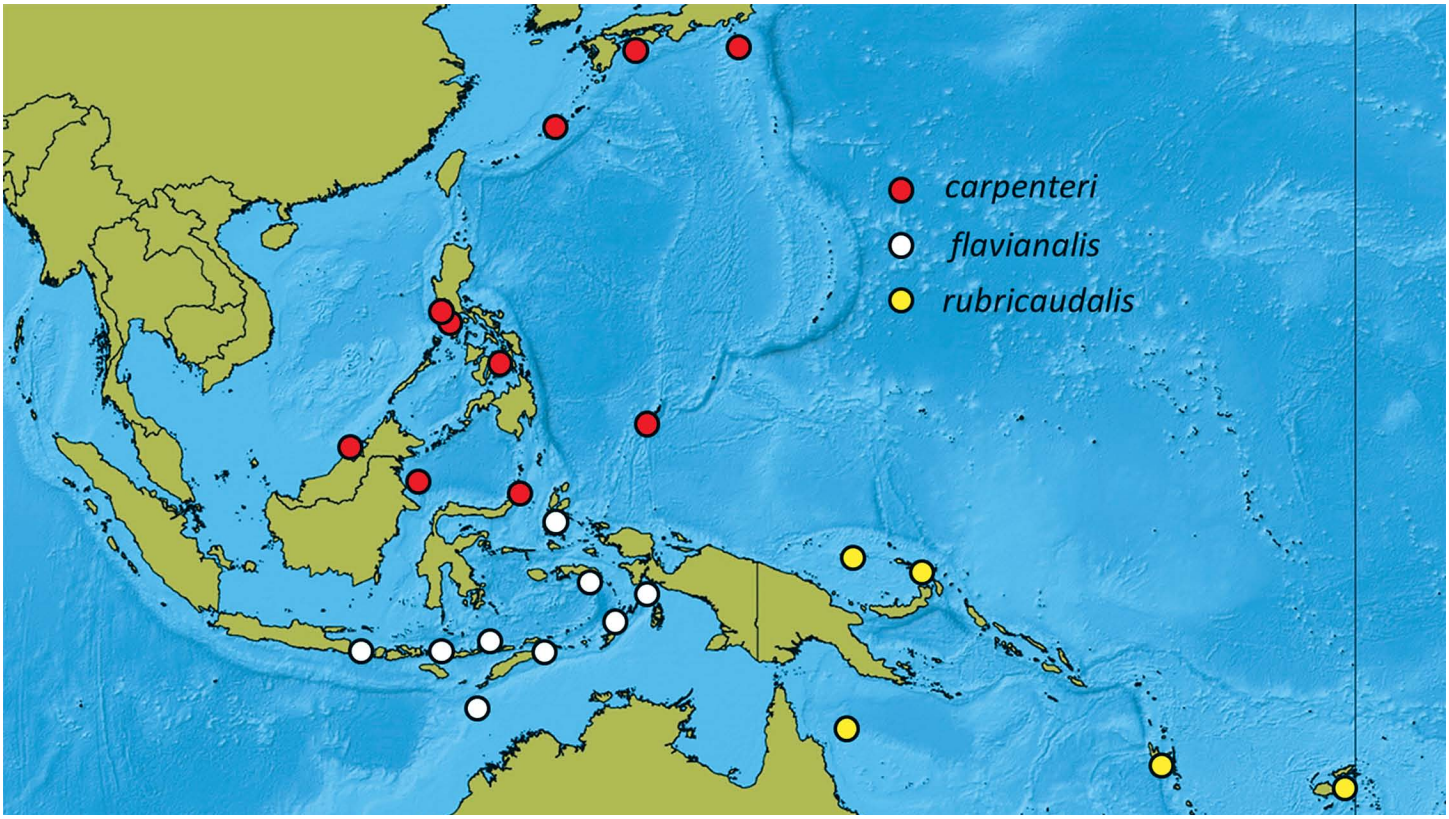


Figure 20. Geographic distribution of the western Pacific members of the *mccoskeri* group of *Paracheilinus*.

Figure 21. *Paracheilinus carpenteri*, nuptial-male display, upper: approx. 50 mm SL, Anilao, Luzon, Philippines (G.R. Allen); lower: approx. 50 mm SL, northern Sulawesi, Indonesia (M.V. Erdmann).

to reddish band, then yellow-brown to brownish-green on outer portion with narrow blue band, often underlined by red, at margin; pelvic fins orange red with narrow blue anterior margin.

Remarks. The distribution of *P. carpenteri* (Fig. 20) currently includes Palau, southern Japan (Izu Islands, Kochi, Kagoshima, and Okinawa), Taiwan (Fish Database of Taiwan 2016), Philippines (Luzon, Mindoro, Siquijor Island, and Cebu), Indonesia (North Sulawesi and northeastern Kalimantan), and Brunei, in 12–40 m depth (Kuiter 2010, Allen & Erdmann 2012). Populations or individuals in parts of the range, particularly Japan, Palau, and the photograph from Sulawesi (Fig. 21, lower), can have bright red filamentous rays and outer portions of the soft dorsal fin (e.g. usually, but not always, red in Japanese photos of Nishiyama & Motomura 2012).

This species is one of the three allopatric Pacific Ocean members of the *mccoskeri* group based on its rounded caudal fin and filamentous dorsal-fin rays (although it has more than the other members) in TP males, as well as genetic affinity. It is remarkably similar in coloration to the Indian Ocean *P. mccoskeri*, but differs from all its relatives in having two instead of one short stripe anteriorly between the two long body stripes and more than one, usually 2 to 4, filamentous dorsal-fin rays.

Paracheilinus cyaneus Kuiter & Allen, 1999

Figures 4B, 18, & 22–23.

Paracheilinus cyaneus Kuiter & Allen 1999: 121 (type locality: Banggai Island, Sulawesi, Indonesia); Kuiter & Tonozuka 2004: 499, 6 figs. (eastern Sulawesi, Indonesia); Michael 2009; 283, 2 figs. (Sulawesi, Indonesia); Kuiter 2010: 107, 5 figs. (Kalimantan to West Papua, Indonesia); Allen & Erdmann 2012: 705 (Kalimantan to West Papua, Indonesia).

Material examined. Banggai Islands, Sulawesi, Indonesia: NCIP 6167 (holotype), 52.2 mm SL; WAM P. 31498-001 (paratype), 48.7 mm SL. Raja Ampat Islands, West Papua Indonesia: WAM P.32247-002, 50.3 mm SL; WAM P.33027–016, 46.4 mm SL.

Diagnosis. Pored lateral-line scales 14 + 5; gill rakers on first branchial arch 14; body depth 2.9–3.1 in SL; head length 3.1–3.3 in SL; snout length 4.3 in HL; eye diameter 4.2 in HL; interorbital width 4.4–4.7 in HL; least depth of caudal peduncle 2.0–2.3 in HL; caudal peduncle length 1.5–1.8 in HL; 5–8 (usually 8) elongate filamentous dorsal-fin rays in TP males, longest dorsal-fin soft ray 2.2–2.4 in SL; pelvic fin length 1.8–2.0 in HL; caudal fin of TP male deeply lunate; maximum size to at least 52.5 mm SL; juveniles (under about 20 mm SL) pinkish with broad zone of yellow along middle of side; color of TP males overall orange red to burgundy red with reddish-to-bluish stripes on head and body in pattern A; nuptial-display pattern with several sky-blue stripes and bands on head and body, anterior body strongly suffused with green to bluish and broad zone of same color dorsally on head and along base of dorsal fin; dorsal fin turquoise to bluish white with wedge-shaped yellow-to-light brown area on middle of spinous part of fin, filamentous fin rays yellowish white to pink; anal and pelvic fins dark red with blue margin, central portion of caudal fin with elaborate blue markings.

Remarks. *Paracheilinus cyaneus* is widely distributed in eastern Indonesia including West Papua (western Bird's Head Peninsula and Raja Ampat Islands), Halmahera, Sulawesi (Banggai Islands, Togean Islands, and Lembeh Strait), and northeastern Kalimantan (Derawan Island), at depths of 6–35 m (Fig. 18). It questionably occurs in the southern Philippines where it has been reported as "*P. filamentosus*" (Randall & Lubbock 1981; based on BPBM 22508 and USNM 219009; identification cannot be confirmed due to lack of color notes and/or tissue samples). It is sympatric with other members of the complex in many places, i.e. with *P. paineorum* in the west at Sulawesi and Kalimantan, with *P. togeanensis* in Sulawesi, with *P. walton* (Yapen Island) at the northern

Figure 22. *Paracheilinus cyaneus*, nuptial-male display, approx. 50 mm SL, Raja Ampat Islands, West Papua, Indonesia (G.R. Allen).

part of the Bird's Head Peninsula of West Papua, and with *P. nursalim* (Misool, Raja Ampat Islands) to the south of the Peninsula. The species are all readily separated by their nuptial-display pattern.

Paracheilinus cyaneus clearly belongs to the *filamentosus* group of species, based on its many elongate filamentous dorsal-fin rays and deeply lunate caudal fin in TP males, as well as shared mitochondrial DNA sequences with several others from that species complex.

Figure 23. *Paracheilinus cyaneus*, upper: TP male (not nuptial display), approx. 40 mm SL; lower: juveniles about 20 mm SL, Raja Ampat Islands, West Papua, Indonesia (G.R. Allen).

Paracheilinus filamentosus Allen, 1974

Figures 1, 18, & 24–26; Table 4.

Paracheilinus filamentosus Allen 1974: 452 (type locality: Kranket Island, Madang, Papua New Guinea); Randall & Lubbock 1981: 26, Pl. 2C (Papua New Guinea, Manado, & Philippines [latter two incorrect]); Kuiter & Tonozuka 2004: 494, no figs. are this species (Palau, Indonesia (both erroneous) to Solomon Islands); Michael 2009; 284, one fig. from PNG (Palau, Philippines, Indonesia (all erroneous), New Guinea, & Solomon Islands); Kuiter 2010: 106, figs. B & C are this species (widespread western Pacific [incorrect]); Allen & Erdmann 2012: 706 (Kalimantan, Java to West Papua, Indonesia, Brunei, Malaysia, Philippines, Palau (all erroneous), Papua New Guinea, & Solomon Islands).

Material examined. Madang, Papua New Guinea: AMS I.16994-001 (holotype), 62.6 mm SL; AMS I.16995-001 (paratypes), 4 specimens, 19.3–29.1 mm SL; WAM P.30375-003, 4 specimens, 34.2–43.0 mm SL; WAM P.30376-001, 8 specimens, 27.7–54.3 mm SL; WAM P.30623-004, 3 specimens, 37.6–45.1 mm SL. Manus Island, Papua New Guinea: WAM P.27824–065, 35.2 mm SL; WAM P.27825-002, 13 specimens, 21.0–47.3 mm SL; WAM P.27826–020, 78.0 mm SL. Bougainville, Papua New Guinea: WAM P.28160-003, 18 specimens, 14.2–39.4 mm SL. Rabaul, New Britain, Papua New Guinea: WAM P.28180-003, 18 specimens, 32.7–49.1 mm SL. Solomon Islands: AMS I.17479-001, 53.5 mm SL; AMS I.17496-001 (paratypes), 11 specimens, 28.9–57.0 mm SL; BPBM 14658 (paratypes), 6 specimens, 34.5–65.0 mm SL.

Diagnosis. Pored lateral-line scales 15–17 + 5–10; gill rakers on first branchial arch 12–16; body depth 3.0–3.3 in SL; head length 2.9–3.2 in SL; snout length 3.7–4.8 in HL; eye diameter 3.6–4.9 in HL; interorbital width 4.0–4.6 in HL; least depth of caudal peduncle 1.9–2.5 in HL; caudal peduncle length 2.0–2.4 in HL; 4–6 elongate filamentous dorsal-fin rays in TP males, longest dorsal-fin soft ray 1.9–2.0 in SL; pelvic fin length 1.9–2.0 in HL; caudal fin of TP male deeply lunate; maximum size to at least 78.0 mm SL; IP fish reddish orange dorsally grading to yellowish and white ventrally with several lavender stripes along head and body, iris bright red; color of TP male generally reddish orange to yellowish and white ventrally, with reddish-to-bluish-lavender stripes on head

Figure 24. *Paracheilinus filamentosus*, IP female, approx. 35 mm SL, Duke of York Islands, New Britain, Papua New Guinea (G.R. Allen).

Figure 25. *Paracheilinus filamentosus*, TP males (not nuptial display), approx. 55 mm SL, Tufi, Oro Province, Papua New Guinea (G.R. Allen).

and body in pattern A; dorsal and anal fins burgundy or maroon with sky-blue margins; caudal fin with maroon-to-violet-red lobes and narrow blue dorsal, ventral, and posterior margins; pelvic fins maroon to violet red with blue anterior margin; nuptial-display pattern largely maroon to reddish with sky-blue stripes and bands on head and body (these may be merged anteriorly), brownish orange on forehead, bright yellowish-to-whitish dorsal fin including filamentous rays, sometimes with bluish-green zone along base, and mainly yellow on anterior (spinous) portion of fin; nuptial-male display from the Solomon Islands includes an entirely yellow dorsal fin and a yellowish head (Fig. 26).

Remarks. *Paracheilinus filamentosus* is currently known from northeastern Papua New Guinea (Hermit and Ninigo Islands, Madang, Manus Island, Bismarck Archipelago, Milne Bay Province, and Bougainville), the far northern Great Barrier Reef of Australia, and the Solomon Islands (Fig. 18). The usual depth range is 5–35 m (Allen & Erdmann 2012). The prior literature (listed in the synonymy) included most other members of the *filamentosus* group in a highly variable nominal "*P. filamentosus*" found widespread throughout the western Pacific Ocean. The species complex is now split into a set of species as follows: *P. bellae* (mainly Micronesia), *P. cyaneus* (eastern Indonesia), *P. filamentosus* (Papua New Guinea and Solomon Islands), *P. nursalim* (southern West Papua, Indonesia), *P. paineorum* (central Indonesia), *P. walton* (Cenderawasih Bay to Ayau Atoll, West Papua, Indonesia), and *P. xanthocirritus* (southeastern South China Sea). *Paracheilinus lineopunctatus* (Philippines) and *P. togeanensis* (Tomini Bay and North Sulawesi) are possibly members of this complex (but the former has a rounded caudal fin and the latter has no filamentous dorsal-fin soft rays in TP males), although corroborating genetic evidence is unavailable.

The *filamentosus* group is characterized by TP males with numerous (almost always four or more) filamentous soft dorsal-fin rays and a deeply lunate caudal fin. The members of this species complex are morphologically very similar and cannot be differentiated by meristics and morphology. TP male coloration, particularly the nuptial-display pattern, is the most reliable means of identification. In addition, most of the species can be identified by location, since they exhibit fully allopatric distributions (Fig. 18), with the notable exception that in northern Indonesia *P. cyaneus* overlaps broadly with *P. paineorum* and overlaps more narrowly at the range edges with *P. togeanensis*, *P. walton*, and *P. nursalim*. The salient differences between *P. filamentosus* and its most similar congeners, *P. paineorum* and *P. xanthocirritus*, are discussed under the descriptions for those species and the nuptial-male color differences are summarized in Table 4.

Figure 26. *Paracheilinus filamentosus*, nuptial-male display, upper: approx. 55 mm SL, Manus Island, Papua New Guinea (G.R. Allen); lower: approx. 55 mm SL, Russell Group, Solomon Islands (R.C. Steene).

Paracheilinus flavianalis Kuiter & Allen, 1999

Figures 20 & 27.

Paracheilinus flavianalis Kuiter & Allen 1999: 123, figs. 4–7 (type locality: Scott Reef, NW Shelf of Australia); Kuiter & Tonozuka 2004: 496, 7 figs. (southern Indonesia to NW Australia); Michael 2009: 287, 4 figs. (southern Indonesia to NW Australia); Kuiter 2010: 115, 4 figs. (southern Indonesia to NW Australia); Allen & Erdmann 2012: 707 (Bali & Sulawesi to southwest Papua, Indonesia & Scott & Hibernia Reefs, NW Shelf of Australia).

Material examined. Scott Reef, Western Australia: WAM P.30836–007 (holotype), 42.8 mm SL. Bali, Indonesia: NCIP 6167 & 6170 (paratypes), 2 specimens, 46.2–48.2 mm SL; NMV A20059 (paratypes), 2 specimens, 50.0–50.3 mm SL. Seringapatam Reef, Western Australia: WAM P.31194-001 (paratypes), 14 specimens, 20.2–34.7 mm SL. Kaimana region, West Papua, Indonesia: WAM P. 32789-003, 2 specimens, 46.1–50.4 mm SL; WAM P. 32792-003, 2 specimens, 45.5–48.0 mm SL.

Diagnosis. Pored lateral-line scales 15–16 + 4–7; gill rakers on first branchial arch 13–15; body depth 3.0–3.5 in SL; head length 2.7–3.1 in SL; snout length 4.1–5.1 in HL; eye diameter 3.0–4.0 in HL; interorbital width 4.0–4.9 in HL; least depth of caudal peduncle 2.2–3.0 in HL; caudal peduncle length 1.6–2.5 in HL; 1–3 (often 1) elongate filamentous dorsal-fin rays in TP males, longest dorsal-fin soft ray 1.8–2.6 in SL; pelvic fin length 1.9–2.6 in HL; caudal fin of TP male rounded; maximum size to at least 53.0 mm SL; color of TP male overall orangish red to yellowish ventrally with red-to-bluish stripes and bands on head and body in pattern B, body can be bright yellow in nuptial display (Fig. 27); dorsal fin yellowish to orange with midline blue stripe or broken into row of blue spots, in nuptial display the soft dorsal-fin can become broadly white or bluish with a thick blue margin, the distal part of the central portion of the dorsal fin and the elongate filamentous ray(s) are bright red; anal fin yellow to yellow orange with narrow, sky-blue outer margin, variable development of a row of blue spots or lines midway out on the fin, from one or two posteriorly to almost a full stripe; caudal fin yellow-brown to dusky green to dark with a narrow blue band about one-third out from base and a narrow sky-blue margin; pelvic fins yellow to yellowish orange with a narrow sky-blue anterior margin.

Remarks. *Paracheilinus flavianalis* is known from southern and eastern Indonesia (Lesser Sunda Islands (Bali eastward), Molucca Islands, Halmahera, Raja Ampat Islands, and the southern coast of the Bird's Head Peninsula of West Papua), Timor Leste, and the Northwest Shelf of Australia (Scott, Seringapatam, and Hibernia reefs)(Fig. 20). The normal depth range is 6–35 m (Allen & Erdmann 2012).

One of three allopatric species in the *mccoskeri* group in the western Pacific Ocean, the other two being *P. carpenteri* and *P. rubricaudalis*. *Paracheilinus flavianalis* closely resembles the allopatric *P. mccoskeri* which is found widely in the Indian Ocean, differing primarily in TP male coloration and in often having more than one filamentous dorsal-fin soft ray. The primary color differences are a mostly yellow anal fin vs. a prominently red distal two-thirds of the anal fin in *P. mccoskeri*, and a distinctive red patch on the distal portion of the mid-dorsal fin extending onto the filamentous ray(s) vs. yellow to brownish for the same area on TP males of *P. mccoskeri*. The prolonged filaments of the dorsal fin are evident at a smaller size in *P. flavianalis* (31.4 mm SL versus about 38 mm SL) and Indonesian TP males often have 2 or 3 filaments vs. only one in *P. mccoskeri*.

The allopatric *P. carpenteri* is found to the north of the range of *P. flavianalis*, primarily in northern Indonesia, Philippines, and northward to Japan. It shares most of the TP male color patterns of *P. flavianalis*, especially those *P. carpenteri* populations with red dorsal-fin filaments, although the two species can be reliably separated by two short mid-anterior stripes (vs. one) and a bright red anal fin in all TP males of *P. carpenteri*. The third Pacific member of the species complex, *P. rubricaudalis*, is well-separated geographically (found only far to the east in Papua New Guinea and eastwards into the islands of the South Pacific), and can be distinguished by its TP male coloration, i.e. a red caudal fin, absence of blue spots midway on the dorsal fin and/or anal fin, as well as a single soft-dorsal-fin filamentous extension in TP males (often containing more than one elongated fin ray).

Figure 27. *Paracheilinus flavianalis*, nuptial-male display; upper: approx. 50 mm SL, Triton Bay, West Papua, Indonesia (G.R. Allen); lower: approx. 60 mm SL, Bali, Indonesia (R.H. Kuiter).

Paracheilinus hemitaeniatus Randall & Harmelin-Vivien, 1977

Figures 17 & 28–29.

Paracheilinus hemitaeniatus Randall & Harmelin-Vivien 1977: 338, fig. 4 (type locality: Tuléar, Madagascar); Randall & Lubbock 1981: 28, fig. 1 (Tuléar, Madagascar); Kuiter 2010: 110, 4 figs. (Madagascar & KwaZulu-Natal, South Africa).

Material examined. Tuléar, Madagascar: BPBM 19599 (holotype), 67.6 mm SL; BPBM 19600 (paratype), 29.2 mm SL.

Diagnosis. Pored lateral-line scales 16 + 5–6; gill rakers on first branchial arch 14–16; body depth 3.3–4.1 in SL; head length 2.9–3.3 in SL; snout length 3.7–3.8 in HL; eye diameter 3.1–4.3 in HL; interorbital width 3.7–3.9 in HL; least depth of caudal peduncle 2.1–2.4 in HL; caudal peduncle length 1.5–1.9 in HL; no elongate filamentous dorsal-fin rays in TP males, longest dorsal-fin soft ray 4.2 in SL; pelvic fin length 1.7–1.9 in HL; caudal fin of TP male deeply lunate; maximum size to at least 67.6 mm SL; IP reddish orange grading to white ventrally with narrow white irregular lines dorsally on head and numerous faint purplish stripes on the anterior half of the body alternating with yellow; TP male generally pink with bluish-to-violet head, grading to white ventrally; three bluish-to-purplish bands radiating from rear eye, middle one loosely connecting to thick band sometimes circumscribing yellow patch at pectoral-fin base; about 10 dark-blue-to-purplish stripes or alternating broken lines on side, confined to anterior half of body, most above level of pectoral-fin base; dorsal fin mostly pinkish to yellow with crimson edging; anal and pelvic fins yellowish; caudal fin pinkish to reddish, bordered upper and lower by yellowish bands continuing as bright yellow dorsal and ventral trailing filaments; nuptial display presently undocumented.

Remarks. *Paracheilinus hemitaeniatus* was known on the basis of only three specimens collected at Tuléar, southwestern Madagascar in 1972 (Fig. 14). More recently, the species has been photographed and collected in South Africa by Dennis King at the Protea Banks (30°49.897’ S, 30° 28.974’ E), off Port Shepstone on the KwaZulu-Natal south coast and at Sodwana Bay near the Mozambique border. The known depth range is 20–50 m (Kuiter 2002, 2010). The species can be distinguished from congeners by the combination of a rounded dorsal fin without elongate filamentous rays, a deeply lunate caudal fin in TP males, and the color pattern, especially the absence of stripes on much of the posterior body, the patch of yellow ringed with purple at the pectoral fin base, and especially long yellow filaments extending from the caudal-fin lobes in the TP males. It is a member of the western-Indian-Ocean group based on its geographic range and genetic affinities.

Figure 28. *Paracheilinus hemitaeniatus*, TP male, approx. 50 mm SL, KwaZulu-Natal, South Africa (D. King).

Figure 29. *Paracheilinus hemitaeniatus*, TP male, approx. 60 mm SL (right) and IP female, approx. 35 mm SL (left), KwaZulu-Natal, South Africa (D. King).

Figure 30. *Paracheilinus lineopunctatus*, TP male (not nuptial display), approx. 55 mm SL, Batangas, Luzon, Philippines (R. Myers).

Paracheilinus lineopunctatus Randall & Lubbock, 1981

Figures 18 & 30–31.

Paracheilinus lineopunctatus Randall & Lubbock 1981: 21, pl. 1B (type locality: Mactan Island, Cebu, Philippines)*;* Michael 2009: 287, 3 figs. (Philippines & Okinawa [latter erroneous]); Kuiter 2010: 113, 5 figs. (Philippines); Allen & Erdmann 2012: 707, upper fig. only (Philippines, Taiwan, Ryukyu Islands, southern Japan (latter three erroneous]).

Material examined. Mactan Island, Philippines: BPBM 22506 (holotype), 38.8 mm SL; BPBM 22114 (paratypes), 6 specimens, 25.3–48.7 mm SL; USNM 219335 (paratypes), 4 specimens, 26.5–51.2 mm SL. Caban Island, Batangas, Luzon, Philippines: AMS I.20696-001 (paratype), 33.2 mm SL; BPBM 22447 (paratypes), 5 specimens, 32.4–38.0 mm SL. Sumilon Island, Philippines: BPBM 22507 (paratype), 50.2 mm SL.

Diagnosis. Pored lateral-line scales 14–17 + 5–6; gill rakers on first branchial arch 12–16; body depth 3.0–3.4 in SL; head length 2.8–3.1 in SL; snout length 3.1–4.0 in HL; eye diameter 3.1–4.4 in HL; interorbital width 3.9–4.4 in HL; least depth of caudal peduncle 2.1–2.3 in HL; caudal peduncle length 1.6–1.9 in HL; 5–8 (frequently 6–7) elongate filamentous dorsal-fin rays in TP males, longest dorsal-fin soft ray 2.0–2.2 in SL; pelvic fin length 1.8–2.0 in HL; caudal fin of TP male rounded; maximum size to at least 51.2 mm SL; color of TP male overall orange-red to violet with dense bluish-to-purplish stripes, reticulations, and scattered irregular small spots on side; dorsal fin reddish orange on spinous portion to yellow or pinkish blue on soft dorsal fin with yellowish or pinkish elongate filamentous dorsal-fin rays; anal, caudal, and pelvic fins pink to reddish with purple fin-rays and narrow bluish or whitish margins; nuptial-male display color pattern includes sky-blue head, body, and dorsal-fin base, with two prominently contrasting large burgundy patches on head, one just behind eye (extending across thorax), and second in center of body, continuous with burgundy anal and caudal fins and a small dark burgundy wedge at base of most posterior portion of soft dorsal fin; dorsal fin bright blue to blue-green near base grading to bright white elongate filamentous dorsal-fin rays.

Remarks. *Paracheilinus lineopunctatus* is known only from the Philippines, in the Visayas Group and southern Luzon (Fig. 18). Listings from Taiwan and southern Japan are apparently incorrect; the Taiwanese record in the Fish Database of Taiwan is from an aquarium-trade specimen (K.T. Shao, pers. comm). The depth range is about 18–40 m (Allen & Erdmann 2012).

This species is distinguished from congeners by the combination of numerous (up to eight) elongate filamentous dorsal-fin rays along with a rounded caudal fin in TP males (and, independently, the unique color pattern). In the absence of any genetic material, we tentatively assign the species to the *filamentosus* group, presuming the numerous filamentous rays are more significant than the rounded caudal fin, which is typical of other groups. Allen & Erdmann (2012, p.707, bottom) erroneously identified two photographs of possible *P. lineopunctatus* x *P. angulatus* hybrids as this species.

Figure 31. *Paracheilinus lineopunctatus*, nuptial-male display, approx. 55 mm SL, Anilao, Luzon, Philippines (G.R. Allen).

Paracheilinus mccoskeri Randall & Harmelin-Vivien, 1977

Figures 2C, 17 & 32–33.

Paracheilinus mccoskeri Randall & Harmelin-Vivien 1977: 332, figs. 4–7 (type locality: north of Morone, Grande Comore Island, Comoro Islands); Randall & Lubbock 1981: 23, pl. 1C (Comoros, Maldives, & Andaman Sea); Winterbottom *et al*. 1989: 55 (Chagos Archipelago); Randall 1992: 131 (Maldives); Debelius 1993: 225 (Indian Ocean); Randall 1995: 287 (Persian Gulf & Gulf of Oman); Carpenter *et al*. 1997: 199 (Persian Gulf); Kuiter & Tonozuka 2004: 497, 2 figs. (Indian Ocean); Michael 2009: 289, 3 figs. (Gulf of Oman, Comoros, Maldives, Similan Islands, Sumatra); Kuiter 2010: 116, 5 figs. (Indian Ocean); Allen & Erdmann 2012: 708, 2 figs. (East Africa to Andaman Sea & western Sumatra).

Material examined. Comoro Islands: AMS I.18604-001 (paratype), 40.8 mm SL; BPBM 19728 (paratypes), 7 specimens, 26.6–55.0 mm SL; USNM.215274 (paratypes), 2 specimens, 32.5–41.2 mm SL. Pulau Weh, Sumatra, Indonesia: WAM P.31523-002, 46.3 mm SL.

Diagnosis. Pored lateral-line scales 15–17 + 5–9; gill rakers on first branchial arch 13–15; body depth 3.0–3.4 in SL; head length 2.9–3.1 in SL; snout length 3.6–4.1 in HL; eye diameter 3.3–4.1 in HL; interorbital width 4.1–4.4 in HL; least depth of caudal peduncle 2.1–2.3 in HL; caudal peduncle length 1.7–1.9 in HL; single elongate filamentous dorsal-fin ray in TP males, longest dorsal-fin soft ray 1.2–1.9 in SL; pelvic fin length 2.1–2.4 in HL; caudal fin of TP male rounded; maximum size to at least 55.7 mm SL; TP male orange-red with blue stripes on head and body in pattern B; dorsal fin orange anteriorly with orange-to-dusky filament on first soft ray, thin blue stripe, often broken, midway out on fin expanding to a pattern of large blue spots consolidating near margin, basal portion of soft dorsal fin with variable-length bright red area; anal fin prominently red (in most populations proximal third yellow to orange and separated by a row of large blue spots breaking into multiple rows posteriorly), with thin blue-to-violet margin; caudal fin yellow-brown to dusky with blue or reddish band near basal portion of fin and thin blue posterior margin, sometimes with red underlining; pelvic fins yellowish, sometimes reddish on outer portion, with a narrow blue anterior margin and sometimes additional blue spots. Males in nuptial display can switch to a bright yellow body and a prominently contrasting white soft dorsal fin and red anal fin.

Remarks. *Paracheilinus mccoskeri* has the most extensive distribution of any species in the genus, being widely distributed in the Indian Ocean, including Kenya, Comoro Islands, the Persian Gulf (Jana Island, Saudi Arabia), Oman, Chagos Archipelago, Maldives, Andaman Sea (Andaman Islands, western Thailand), and Sumatra (westernmost extremity at Pulau Weh)(Fig. 17). The known depth range is 6–50 m (Allen & Erdmann 2012).

This species is the only Indian Ocean member of the *mccoskeri* group, closely related to three Pacific Ocean species: *P. carpenteri* from the Philippines and South China Sea, *P. flavianalis* from Indonesia and northwestern Australia, and *P. rubricaudalis* from Papua New Guinea, Vanuatu, and Fiji. The group is united by a rounded caudal fin and relatively few elongate filamentous dorsal-fin rays in the TP male (a single filament in *P. mccoskeri* and *P. rubricaudalis*, an additional 1 to 3 in the others). *Paracheilinus mccoskeri* can be separated from *P. carpenteri* by a single mid-anterior stripe (vs. double), from *P. flavianalis* by having a mostly red anal fin (vs. yellow), and from *P. rubricaudalis* by having blue spotting on the soft dorsal fin (vs. usually none) and usually no red caudal fin.

Figure 32. *Paracheilinus mccoskeri*, IP female, approx. 35 mm SL, DNA-confirmed ID, aquarium trade (B.C. Victor).

Figure 33. *Paracheilinus mccoskeri*, nuptial-male display, approx. 55 mm SL, Surin Islands, Thailand, Andaman Sea (G.R. Allen).

Figure 34. *Paracheilinus mccoskeri*, nuptial-male displays (with *Rabaulichthys stigmaticus* at right), Similan Islands, Thailand, Andaman Sea (Satoshi Kunihiro).

Paracheilinus nursalim Allen & Erdmann, 2008

Figures 2B, 4A, 18 & 35–36.

Paracheilinus nursalim Allen & Erdmann 2008: 181 (type locality: Triton Bay, West Papua, Indonesia); Michael 2009: 284, 1 fig. (Bird's Head Peninsula, Indonesia); Kuiter 2010: 109, 4 figs. (West Papua, Indonesia); Allen & Erdmann 2012: 708, 3 figs. (West Papua, Indonesia).

Material examined. Triton Bay and Fakfak Peninsula, West Papua, Indonesia: NCIP 6327 (holotype), 50.1 mm SL; AMS I.44190-001 (paratypes), 2 specimens, 42.2–46.7; BPBM 40658 (paratypes), 2 specimens, 44.8–47.2 mm SL; NCIP 6328 (paratypes), 3 specimens, 41.9–46.8 mm SL; WAM P.32788-001 (paratypes) , 2 specimens, 42.6–49.2 mm SL; WAM P. 32789-004 (paratype), 43.4 mm SL; WAM P. 32792-004 (paratypes), 2 specimens, 27.2– 42.9 mm SL; WAM P.32794-001 (paratype), 39.4 mm SL; WAM P.32795-001 (paratype), 51.0 mm SL; WAM P.32813-004, 41.6 mm SL WAM P.32948-001, 46.3 mm SL; USNM 390775 (paratypes) 4 specimens, 20.6–47.9 mm SL.

Diagnosis. Pored lateral-line scales 11–16 + 3–10 (usually 16 + 5–7); gill rakers on first branchial arch 12–15 (usually 12–13); body depth 2.9–3.5 in SL; head length 2.8–3.3 in SL; snout length 3.8–4.9 in HL; eye diameter 3.0–4.2 in HL; interorbital width 4.2–5.3 in HL; least depth of caudal peduncle 2.0–2.5 in HL; caudal peduncle length 1.5–2.3 in HL; 4–6 (rarely 3) elongate filamentous dorsal-fin rays in TP males, longest dorsal-fin soft ray 1.8–2.1 in SL; pelvic fin length 1.6–1.8 in HL; caudal fin of TP male deeply lunate, rounded in initial phase; maximum size to at least 50.1 mm SL; IP fish reddish orange grading to white on abdomen with numerous faint purple-to-bluish stripes, iris reddish orange (Fig. 35); TP male pink to pumpkin orange grading to white on abdomen and lower head, dusky on upper head and body with mostly reddish stripes (blue on snout and under eye) on head and body in a variation of pattern A (Fig. 2B); median fins mostly orangish pink with thick blue edges on dorsal and anal fins; nuptial-male display pattern largely yellow grading to yellow-orange ventrally,

Figure 35. *Paracheilinus nursalim*, IP fish, approx. 35 mm SL, Triton Bay, West Papua, Indonesia (G.R. Allen).

with thin blue stripes in a variation of pattern A, with a pair of contrasting rectangular blackish patches, one on upper side below spinous dorsal fin and second on lower third of caudal peduncle; dorsal fin mostly yellow with thin blue edge grading to bright white on elongate filamentous rays; anal fin and pelvic fins red with thick sky-blue edge; caudal fin translucent with rays highlighted in blue except for upper and lowermost rays with greatly elongated filaments that are bright white (Fig. 36).

Remarks. *Paracheilinus nursalim* is known only from the western Bird's Head Peninsula of West Papua, Indonesia, ranging from southeastern Misool (Raja Ampat Islands) southeastward to Triton Bay, West Papua, spanning a distance of approximately 450 km (Fig. 18). In this restricted range, only two other congeners, *P. cyaneus* and *P. flavianalis*, are sympatric with *P. nursalim*. A single male individual was photographed in nuptial colors in Ambon Bay (approximately 500 km west of the Bird's Head Peninsula) by William Tan in 2015 (pers. comm.); further investigations are needed to determine if a viable population exists in Ambon or if this simply represents a vagrant individual. The depth range extends from 5 m to at least 50 m, but it is most abundant from about 20–35 m (Allen & Erdmann 2012).

With numerous elongate filamentous dorsal-fin rays and a deeply lunate caudal fin in the TP male, this species is clearly a member of the *filamentosus* group, and it is also genetically close to other members of the species complex. It is most similar in appearance to *P. cyaneus* and *P. walton*, which share the stripe pattern A variation characterized by irregular rows of small dark spots on the side of the body in the spaces between the main stripes, especially evident in the initial phase and non-nuptial TP males (Figs. 35 and 2B respectively). Indeed, *P. nursalim* shares mtDNA haplotypes with *P. walton*. The distinctive TP male nuptial displays are the most reliable means of separating the three species; although *P. walton* can share the yellow body (but typically more orange) and bright white dorsal-fin filaments, the prominent rectangular black patches on the back and lower caudal peduncle are specific to *P. nursalim*. Instead, *P. walton* has a bright red band under the soft dorsal fin and a yellow-to-orange anal fin (vs. bright red). *P. cyaneus* is easily distinguished by a blue and red body in the TP male nuptial display.

Figure 36. *Paracheilinus nursalim*, nuptial-male display, approx. 55 mm SL, Triton Bay, West Papua, Indonesia (G.R. Allen).

Paracheilinus octotaenia Fourmanoir, 1955

Figures 17 & 37.

Paracheilinus octotaenia Fourmanoir in Roux-Esteve & Fourmanoir 1955: 199, fig. 1 (type locality: Abulat Island, Saudi Arabia, Red Sea); Randall & Harmelin-Vivien 1977: 331 (Gulf of Aqaba); Randall & Lubbock 1981: 21, pl. 1A (Red Sea); Randall 1983: 115 (Red Sea); Dor 1984: 206 (Red Sea); Debelius 1993: 225, 2 figs. (Red Sea); Field & Field 1998: 152 (Red Sea); Lieske & Myers 2004: 164 (Red Sea); Michael 2009: 289, 2 figs. (Red Sea); Kuiter 2010: 105, 4 figs. (Red Sea).

Material examined. Red Sea, Saudi Arabia: MNHN 52–296, (holotype), 64.0 mm SL. Red Sea, Gulf of Aqaba: BPBM 13856, 8 specimens, 25–69 mm SL; USNM 277592, 86 specimens, 33.9–90.6 mm SL.

Diagnosis. Pored lateral-line scales 13–15 + 7–9; gill rakers on first branchial arch 13–18; body depth 2.8–3.1 in SL; head length 3.3–3.6 in SL; snout length 3.4–4.1 in HL; eye diameter 4.4–4.8 in HL; interorbital width 3.4–4.7 in 1.5–2.0 in HL; dorsal fin of both sexes rounded without elongate filamentous rays; longest dorsal-fin soft ray 3.7–4.4 in SL; pelvic fin length 1.4–1.7 in HL; caudal fin of both sexes rounded; maximum size to at least 90.6 mm SL; color of TP male largely lavender bluish, grading to yellowish on head and anterior body, with eight narrow bluish stripes on the side of the body, bright red median fins, and yellowish-to-orange pelvic fins (Fig. 37).

Remarks. *Paracheilinus octotaenia* is endemic to the Red Sea where it is the only species in the genus and appears to be relatively common in clear water of outer reefs in 15–43 m depth (Randall & Harmelin-Vivien 1977). It is possibly widespread in the Red Sea, but there are no records south of about 20° N. Most specimens in museum collections are from the Gulf of Aqaba in the far north. The species is easily distinguished from all congeners by the rounded, symmetrical profile of the bright red dorsal, anal, and caudal fins, and the fully striped pattern of the body. It is also the largest species in the genus, attaining at least 90.6 mm SL. It is a member of the western-Indian-Ocean group along with *P. attenuatus*, *P. hemitaeniatus*, and *P. piscilineatus*, based on geographic and genetic affinity.

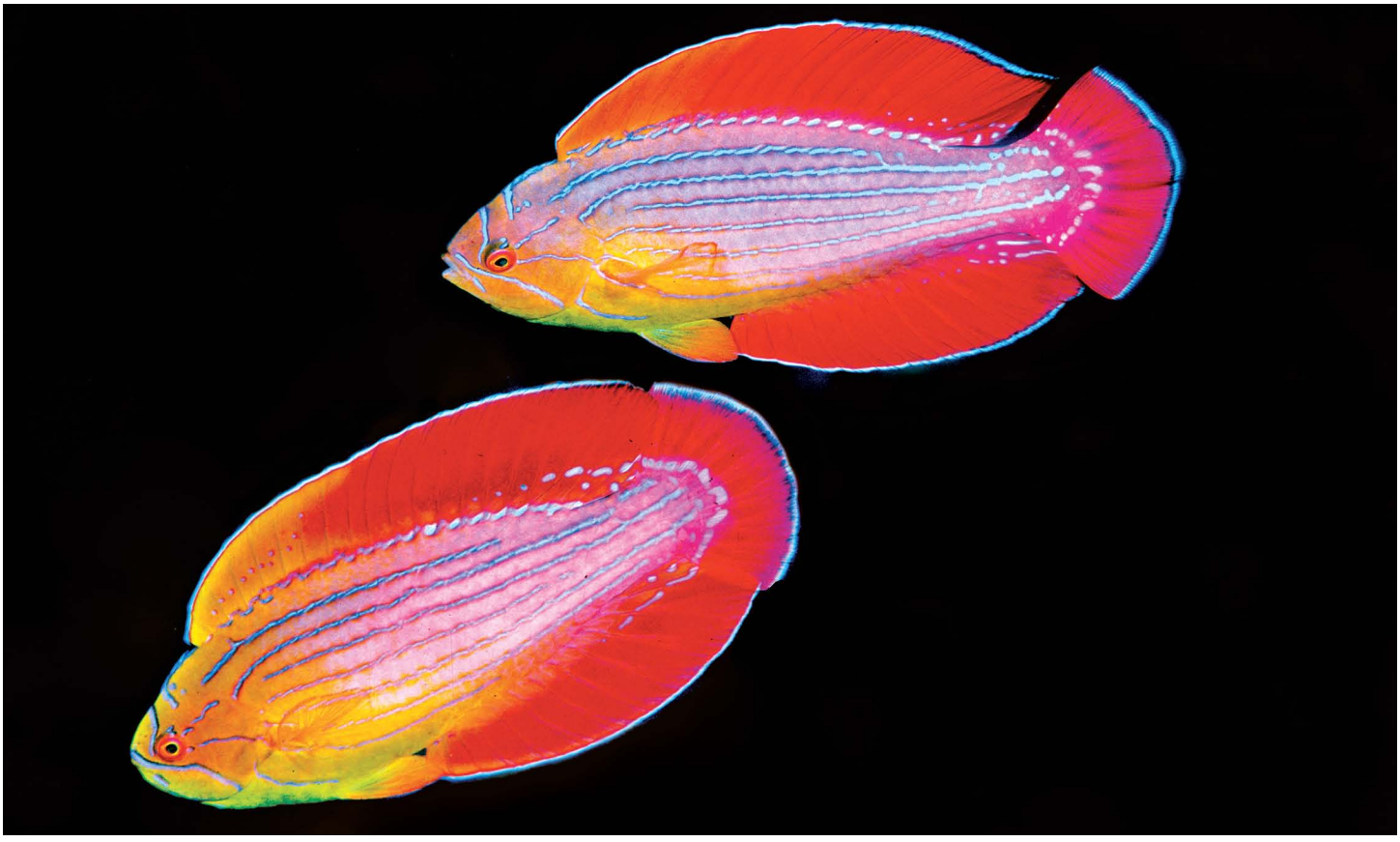


Figure 37. *Paracheilinus octotaenia*, nuptial-male display, approx. 70 mm SL, Safaga, Egypt, Red Sea (R.H. Kuiter).

Paracheilinus paineorum, n. sp.

Figures 2A, 6A, 18, 38–40; Tables 3 & 4.

Paracheilinus filamentosus [*non* Allen] Randall & Lubbock 1981: 26 (Manado, Sulawesi, Indonesia); Kuiter & Tonozuka 2004: 494, 7 figs. (Kalimantan, Bali, & Flores, Indonesia); Michael 2009; 284, 5 figs. (Sulawesi, Indonesia); Kuiter 2010: 106, figs. A & D–G (Kalimantan & Flores, Indonesia).

Holotype. MZB 22245, male, 70.0 mm SL, southwestern Flores, 08° 48.573' S, 119° 50.200' E, Lesser Sunda Islands, Indonesia, 15–20 m, spear, M.V. Erdmann, Sept. 8, 2010.

Paratypes. BPBM 41209, male, 54.2 mm SL, Malibu Point, 08° 47.833' S, 115° 35.623' E, Nusa Penida (near Bali), Lesser Sunda Islands, Indonesia, 50–65 m, spear, M.V. Erdmann, Nov. 24, 2008; USNM 432463, male, 55.7 mm SL, Nudie Falls dive site, Lembeh Strait, North Sulawesi, Indonesia, 20–25 m, clove oil, M.V. Erdmann, July 25, 2013; WAM P.30810-003, 50.1 mm SL, Pulau Putri, Seribu Islands, Indonesia, 10–15 m, spear, G.R. Allen, May 30, 1994; WAM P.33354-002, 2 specimens, males, 59.3–65.0 mm SL, collected with holotype; WAM P.33103-002, male, 50.5 mm SL, collected with BPBM paratype; WAM P.33950-001, 2 specimens, males, 43.1–47.0 mm SL, Tasik Ria, near Manado, North Sulawesi, Indonesia, clove oil, M.V. Erdmann, Sept. 4, 2013.

Diagnosis. Pored lateral-line scales 15–17 + 4–9; gill rakers on first branchial arch 12–15; body depth 2.9–3.2 in SL; head length 3.0–3.5 in SL; snout length 3.7–4.4 in HL; eye diameter 3.6–4.3 in HL; interorbital width 3.2–4.0 in HL; least depth of caudal peduncle 1.9–2.2 in HL; caudal-peduncle length 1.5–1.9 in HL; 4–7 (often 6) elongate filamentous dorsal-fin soft rays in TP male, longest dorsal-fin soft ray 1.5–1.9 in SL; pelvic fin length 1.7–1.9 in HL; deeply lunate caudal fin in TP male; maximum size to at least 70 mm SL; IP fish reddish orange dorsally grading to yellowish and white ventrally with several lavender stripes along head and body, iris bright red; color of TP male generally reddish orange to yellowish to white ventrally, with reddish-to-bluish-lavender stripes on head and body in pattern A (Fig. 39); dorsal, anal, and caudal fins orange or burgundy or maroon with sky-blue margins; nuptial-display pattern orangish yellow on head and anterior body grading to grading to red posteriorly, with thin stripes on head and body in pattern A, bluish dorsally and lavender-to-reddish ventrally; dorsal fin yellow on anterior spinous portion, bright bluish white basally on soft dorsal fin becoming bright red distally and on elongate filamentous rays; anal fin orangish to red with thin blue margin and row of blue spots along base; caudal fin with bright red elongated filamentous lobes and elaborate blue markings centrally (Fig. 40).

Description. Dorsal-fin rays IX,11 (one paratype with VIII,10); anal-fin rays III,9; pectoral-fin rays (including

Figure 38. *Paracheilinus paineorum*, preserved holotype, MZB 22245, male, 70.0 mm SL, southwestern Flores, Indonesia (G.R. Allen).

upper rudimentary ray) 14; lateral-line interrupted, pored scales 16 + 5 (15–17 + 4–9); scales above lateral line to origin of dorsal fin 2; scales below lateral line to origin of anal fin 6; median predorsal scales 5; median preventral scales 6 (one paratype with 5); transverse scale rows on cheek 2; circumpeduncular scales 15 (one paratype with 16); gill rakers 14 (12–15); pseudobranchs 12 (11–13).

Body depth 3.2 (2.9–3.2) in SL; body width 2.2 (2.1–2.3) in body depth; head length 3.3 (3.0–3.5) in SL; snout length 3.7 (4.0–4.4) in HL; eye diameter 4.2 (3.6–4.3) in HL; interorbital width 4.0 (3.2–4.0) in HL; least depth of caudal peduncle 2.2 (1.9–2.2) in HL; caudal-peduncle length 1.6 (1.5–1.9) in HL.

Mouth small, oblique, maxilla not reaching vertical at front edge of eye, its length 4.1 (3.7–4.5) in HL; three pairs of curved canine teeth anteriorly in upper jaw, progressively more laterally projecting, third (posteriormost) pair largest; single pair of canine teeth anteriorly in lower jaw, very strongly curved laterally; side of jaws with single row of small close-set conical teeth; no canine tooth at corner of mouth; no teeth on palate; fleshy flap on side of lower lip; gill rakers short, longest about one-third length of longest gill filaments on first gill arch; posterior nostril an oval opening about twice size of cephalic sensory pores, anterior to fleshy upper edge of eye and on vertical at anterior bony edge of eye; anterior nostril small with a short fleshy rim anterior and slightly ventral to posterior; internarial space about 3.4 in eye diameter; cephalic sensory system consisting of nine pores posterior and ventral along edge of eye, two supraocular pores, five occipital pores, single mid-interorbital pore, five small pores around nostril area, four mandibular pores, and six preopercular pores.

Head scaled except for interorbital space, snout, and chin; a row of pointed scales on base of dorsal and anal fins; basal half of caudal fin with large scales; axillary scale of pelvic fin slightly longer than pelvic spine; midventral scaly process of pelvic fins slightly shorter than pelvic spine.

Free ventral margin of preopercle extending to vertical at center of eye, vertical posterior margin to level of lower edge of pupil; exposed bony edge of preopercle smooth without serrations.

Origin of dorsal fin above third lateral-line scale, predorsal length 3.1 (3.0–3.3) in SL; dorsal-fin spines progressively longer, first 7.8 (6.2–9.1) in HL, and ninth 2.1 (1.7–2.3) in HL; 7 (4–7) elongate filamentous dorsal-

Figure 39. *Paracheilinus paineorum*, TP male (not nuptial display), approx. 50 mm SL, Manado, Sulawesi, Indonesia (G.R. Allen).

Figure 40. *Paracheilinus paineorum*, nuptial-male display at right, approx. 60 mm SL, IP female at left, approx. 30 mm SL, Manado, Sulawesi, Indonesia (G.R. Allen).

fin soft rays in TP male, longest (first) dorsal-fin soft ray 1.6 (1.5–1.9) in SL; origin of anal fin below base of last dorsal-fin spine, preanal length 1.9 (1.7–1.9) in SL; first anal-fin spine 3.9 (3.5–4.7) in HL; second anal-fin spine 3.5 (3.1–4.2) in HL; third anal-fin spine 2.9 (3.0–3.7) in HL; longest (penultimate) anal-fin soft ray 3.7 (3.4–4.2) in SL; caudal fin lunate, 2.1 (1.9–3.1) in SL; pectoral-fin length 1.3 (1.3–1.5) in HL; pelvic-fin length 1.8 (1.7–1.9) in HL.

Color of TP male in life. (Fig. 39) Head and body generally reddish orange to yellowish to white ventrally, with reddish-to-bluish-lavender stripes in pattern A, sometimes a few small purple or reddish spots on side of nape; dorsal fin translucent yellowish with purple to reddish rays; anal fin reddish yellow, with sky-blue outer margin and row of large sky-blue spots (often merged to form stripe) just above base of fin and along posterior margin; caudal fin translucent with purple rays; pelvic fins orange with narrow anterior bluish margin; pectoral fins translucent.

Male nuptial coloration. (Figs. 6A & 40) Orangish yellow on head and anterior body grading to red posteriorly, with thin stripes on head and body in pattern A, stripes bluish dorsally and reddish to lavender ventrally; dorsal fin yellow on anterior spinous portion over about first 6 or 7 spines, with sky-blue margin, bright bluish white basally on soft dorsal fin becoming bright red distally and on elongate filamentous rays, long blue stripe along base of entire dorsal fin extending to base of upper caudal-fin rays; anal fin orangish to red with sky-blue outer margin and row of sky-blue spots (often merged to form stripe) just above base of fin; caudal fin with bright red elongated filamentous lobes and central translucent portion with purple fin-rays and elaborate blue markings on inter-radial membranes; pelvic fins orange with narrow anterior, bluish margin; pectoral fins translucent.

Color of IP in life. (Fig. 40, left) Head and body reddish or red-orange, grading to white on the ventral aspect, with reddish to bluish stripes; iris bright red.

Color of holotype in alcohol. (Fig. 38) Overall pale grey with faint purple stripes and bands on head and body; median and pelvic fins translucent with purple rays; pectoral fins translucent. Dark stripes and bands of head and body are either barely visible or absent on most paratypes.

Distribution and habitat. The new species ranges widely in central Indonesia with collections and

TABLE 3

Proportional measurements of male type specimens of *Paracheilinus paineorum*, n. sp. as percentages of the standard length

	holotype	paratypes						
	MZB 22245	WAM P.33899	WAM P.33899	BPBM 41209	WAM P.33103	WAM P.30810	WAM P.33950	WAM P.33950
Standard length (mm)	70.0	65.0	59.3	54.2	50.5	50.1	47.0	43.1
Body depth	31.1	32.2	32.2	33.2	34.1	31.3	33.0	33.9
Body width	14.1	13.8	15.5	14.2	14.9	15.2	15.7	14.6
Head length	30.1	30.6	32.4	29.0	32.3	30.1	31.9	33.9
Snout length	8.1	7.2	8.1	7.2	8.1	7.4	7.2	8.1
Orbit diameter	7.1	7.1	7.9	7.7	8.9	8.4	7.4	8.1
Interorbital width	7.6	7.7	8.3	8.3	8.5	9.4	8.1	8.6
Upper jaw	7.3	7.4	8.8	7.9	7.1	7.8	8.1	8.1
Depth of caudal peduncle	13.9	14.6	15.3	15.1	14.5	15.0	14.7	16.5
Length of caudal peduncle	19.1	19.4	18.9	18.8	20.0	17.8	18.1	17.9
Predorsal distance	32.0	31.2	32.4	31.5	32.9	30.7	31.7	32.9
Preanal distance	53.3	54.8	51.8	55.9	54.9	56.3	54.3	58.2
Prepelvic distance	36.0	34.6	33.9	35.4	36.4	31.7	34.9	37.8
Length of dorsal-fin base	56.0	54.5	damaged	54.2	54.5	53.7	52.8	53.6
First dorsal-fin spine	3.9	4.9	4.6	4.6	4.2	4.2	4.7	3.7
Last dorsal-fin spine	14.1	13.5	17.0	16.8	15.4	15.2	16.6	16.2
Longest dorsal-fin soft ray	62.0	65.5	62.9	57.2	51.5	54.9	59.4	54.8
Length of anal-fin base	31.0	28.6	32.9	32.1	26.7	26.7	30.2	32.3
First anal-fin spine	7.7	6.8	8.6	6.6	9.1	8.0	7.9	7.2
Second anal-fin spine	8.7	8.9	10.5	8.3	9.9	9.0	8.9	8.1
Third anal-fin spine	10.4	10.2	11.0	9.2	10.3	10.2	9.6	9.3
Longest anal-fin soft ray	26.9	29.4	28.3	24.7	25.1	23.6	28.9	27.8
Caudal-fin length	46.7	53.2	46.0	44.1	32.5	45.3	50.4	46.9
Pectoral-fin length	23.1	21.7	23.3	21.4	21.8	22.4	22.1	23.2
Pelvic fin-spine length	10.1	9.4	10.5	10.3	10.5	11.2	13.0	10.4
Pelvic fin length	16.6	16.6	17.5	17.5	17.6	16.2	18.5	18.6

photographic records thus far from Flores (Maumere and southwestern tip), Komodo Islands, Bali (including nearby Nusa Penida), Java Sea (Seribu Islands), Sulawesi (Manado/Lembeh region, Togean Islands, and Banggai Islands), and northeastern Kalimantan (Fig. 18). *Paracheilinus paineorum* is generally found on sloping rubble bottoms at depths of 15–50 m in areas exposed to periodic strong currents. They occur off southwestern Flores and the Komodo Islands in large mixed aggregations with *P. flavianalis* and *P. rennyae*, sometimes forming hybrids with these species. Similarly, they co-occur with *P. togeanensis* and *P. cyaneus* in Lembeh, where a variety of hybrid nuptial males have been photographed.

Etymology. The new species is named in honor of the Paine family (Dexter, Susan, Mercy, Sam, and Honor), who have generously supported the authors' reef-fish taxonomic efforts since 2009 and have frequently joined us for field investigations.

Remarks. Based on the numerous elongate filamentous dorsal-fin rays and a deeply lunate caudal fin in TP males, the new species belongs to the *filamentosus* group of species (and it shares mtDNA haplotypes with other species in the complex). It is most similar in appearance to its allopatric relatives *P. filamentosus* and *P. xanthocirritus*. The nuptial-display color pattern on the dorsal fin clearly separates the three species (Fig. 6). The salient color-pattern characters for the three species are compared in Table 4. In contrast to the TP male nuptial-display pattern of *P. filamentosus*, i.e. relatively broad, electric-blue stripes on a maroon-to-violet-red background (Fig. 26), *P. paineorum* and *P. xanthocirritus* have narrower reddish stripes, becoming more bluish dorsally and posteriorly, on a bright orangish-yellow-to-red background. In addition, *P. filamentosus* differs from both in lacking a row of blue spots along the base of the anal fin. Although members of this complex are morphologically very similar, we detected some slight differences: *P. filamentosus* has a narrower interorbital measurement (7.2–7.8% of HL vs. 7.6–9.4% and mean 8.3%) and a shorter caudal peduncle (14.1–16.6% of SL vs. 16.6–20.7% and mean 18.7%). There also appears to be an apparent difference in the maximum size attained by the three species with 70.0 mm, 62.6 mm, and 49.3 mm SL recorded for *P. paineorum*, *P. filamentosus*, and *P. xanthocirritus*, respectively.

TABLE 4

Comparison of salient features of TP male nuptial-display color patterns among some members of the *filamentosus* group of East Indian *Paracheilinus* species

Color feature	***P. filamentosus***	***P. paineorum***	***P. xanthocirritus***
Background color of body	maroon to violet red	yellow orange to bright red	red to yellow or orange
Stripes on side	wide electric blue	narrow reddish to pink, blue dorsal and posterior	narrow purple or reddish, blue posterior
Spinous dorsal fin	burgundy red to yellow	mostly yellow, red posteriorly	yellow
Dorsal-fin filaments	yellow to whitish	red	yellow
Dark marking on soft dorsal fin	absent	absent	present
Primary color of anal fin	burgundy or violet red	yellow, orange, or red	yellow, orange, or burgundy
Basal blue spots on anal fin	absent	present	present on posterior 2/3
Central caudal fin	margin narrowly blue	elaborate blue markings	elaborate blue markings

Paracheilinus paineorum and at least one other member of the *filamentosus* group, *P. walton*, possess peculiar dwarf populations that appear to be associated with deeper (40–70 m depth) reefs (Fig. 41). Relatively small males, under about 40 mm SL, in these populations exhibit typical adult courtship behavior accompanied by variations of the characteristic bright nuptial-display color patterns. However, they have the truncate to slightly rounded caudal fin of initial-phase fish instead of the typical lunate shape exhibited by terminal-phase males in normal populations.

Figure 41. *Paracheilinus* dwarf males, upper: *Paracheilinus walton*, dwarf nuptial-male display, approx. 35 mm SL, 45 m depth, Cenderawasih Bay, West Papua, Indonesia (G.R. Allen); lower: *Paracheilinus paineorum* , dwarf nuptial-male display, 60 m depth, Bunaken, North Sulawesi, Indonesia (M.V. Erdmann).

Paracheilinus piscilineatus (Cornic, 1987)

Figures 17 & 42–43.

Cirrhilabrus? *piscilineatus* Cornic 1987: 141 (type locality: Mauritius).
Paracheilinus piscilineatus Randall 1999a: 31 (Mauritius); Fricke 1999: 427 (Mauritius); Kuiter 2010: 118, 4 figs. (Mauritius).

Material examined. Mauritius: BPBM 24774 (neotype), 56.5 mm SL; BPBM 17353, 47.0 mm SL; BPBM 24773, 28.5 mm SL; USNM 352066, 52.1 mm SL.

Diagnosis. Pored lateral-line scales 16–17 + 5–9; gill rakers on first branchial arch 15–16; body depth 3.6–3.8 in SL; head length 3.1–3.3 in SL; snout 3.7–3.9 in HL; eye diameter 3.8–4.2 in HL; interorbital width 3.7–4.0 in HL; least depth of caudal peduncle 2.1–2.2 in HL; caudal peduncle length 1.5–1.7 in HL; soft dorsal and anal-fin rays of both sexes generally rounded, without elongate filamentous dorsal-fin soft rays, except TP male can develop tall mid-soft-dorsal-fin rays, resulting in a pointed profile, longest dorsal-fin soft ray 3.4–5.4 in SL; pelvic fin length 1.6–1.8 in HL; caudal fin of TP male truncate to slightly emarginate; maximum size to at least 56.5 mm SL; IP fish with broad orange-brown lateral band bordered above and below with blue stripes, ventrum white, fins mostly unmarked, iris orange (Fig. 43, lower); TP male orange-red to bright yellow with prominent blue bands and stripes on head and body (Fig. 43, upper): upper stripe thin behind eye, breaking into a short wider segment on anterior body, then continuing as a wide band along back, extending onto upper margin of caudal fin; middle stripe broken into row of spots behind eye, then a thick band almost entirely circling pectoral-fin base and continuing along lower body to base of caudal fin; lower band running from snout obliquely rearward, under eye and across thorax ending above pelvic fin; dorsal fin yellowish with blue margin and reticulations and rows of spots and large red blotch posteriorly, becoming blackish and encompassing most of posterior third of fin in large TP males; anal fin pale yellow-orange to apricot with narrow blue margin; caudal fin with tapering brownish-orange band in each lobe, giving impression of forked shape, edged in blue above and below and with a wide

Figure 42. *Paracheilinus piscilineatus*, nuptial-male display, approx. 60 mm SL, aquarium fish from Mauritius (K. Kohen).

Figure 43. *Paracheilinus piscilineatus*, upper: neotype, BPBM 24774, male (not nuptial display), 57.5 mm SL, photograph in aquarium from Mauritius (G.R. Allen); lower: initial phase, same fish as photographed later in Fig. 42 (K. Kohen).

central wedge of translucent fin or blue outlining the forked orangish portion; nuptial-male display with colors intensified and neon-like appearance of blue lines and spots (Fig. 42).

Remarks. *Paracheilinus piscilineatus* is known only from the island of Mauritius in the western Indian Ocean (Fig. 17). The species was originally (and inadequately) described by Cornic (1987), who implied it was in the genus *Cirrhilabrus*. Randall (1999a) provided a detailed description and designated a neotype. The species occurs over sand/rubble bottoms to at least 35 m depth (Randall 1999a).

The species is part of the western-Indian-Ocean group, along with *P. attenuatus*, *P. hemitaeniatus*, and *P. octotaenia*, based on geographic and genetic affinity. The IP color pattern is distinctive and not similar to those of any other congeners. The TP males are distinguished by a dorsal fin with a rounded or angular profile without elongate filamentous rays, a truncate to emarginate caudal fin, and a very distinctive color pattern.

Paracheilinus rennyae Allen, Erdmann & Yusmalinda, 2013

Figures 9 & 44.

Paracheilinus rennyae Allen, Erdmann & Yusmalinda 2013: 195, figs. 1–4 (type locality: southwestern Flores, Indonesia).

Material examined. Southwestern Flores Island, Lesser Sunda Islands, Indonesia: MZB 21463 (holotype), 58.4 mm SL; WAM 33900-001 (paratypes), 2 specimens, 52.2–59.2 mm SL; USNM 410701 (paratype), 60.4 mm SL.

Diagnosis. Pored lateral-line scales 15–16 + 6–9; gill rakers on first branchial arch 12–14; body depth 2.9–3.4 in SL; head length 3.2–3.6 in SL; snout 3.7–4.0 in HL; eye diameter 3.8–4.7 in HL; interorbital width 3.7–4.0 in HL; least depth of caudal peduncle 1.9–2.1 in HL; caudal peduncle length 1.5–1.7 in HL; dorsal fin of both sexes rounded in profile without elongate filamentous dorsal-fin soft rays, longest dorsal-fin soft ray 3.6–4.7 in SL; pelvic fin length 1.6–1.8 in HL; caudal fin of both sexes rounded; maximum size to at least 60.4 mm SL; color of TP males overall orangish red grading to yellowish orange ventrally and posteriorly with numerous (more than 10) complete to broken, full length to partial, irregular (not cleanly linear), thin stripes, greyish to pinkish or more bluish dorsally and posteriorly, several blue stripes on snout and behind eye; dorsal, anal and pelvic fins overall similar reddish orange to burgundy red with thin blue edging, except contrasting yellowish orange patches at posterior basal portions of dorsal and anal fins, dorsal fin with row of blue spots along full length of base, extending onto dorsal caudal peduncle, and additional row above posteriorly, of variable length, and overlying yellowish orange patch; anal fin with variable row of blue spots along base of fin and below yellowish orange patch; caudal fin with reddish to greenish basal two-thirds with two blue bands dividing thirds, outermost third yellowish with thin reddish margin; male nuptial-display pattern showing intensified colors, especially stripes becoming bright electric blue.

Remarks. This recently described species is known only from the Lesser Sunda Islands of Indonesia at the southwestern end of Flores and the nearby Komodo Islands (Fig. 9), at depths of 15–40 m (Allen, Erdmann & Yusmalinda 2013).

Paracheilinus rennyae belongs in the *angulatus* group, based primarily on the absence of elongate filamentous rays, the absence of a strongly lunate caudal fin (in this case rounded), and close genetic affinity. Notably however, *P. angulatus* is easily distinguished by sharply pointed dorsal-fin and anal-fin outlines and a moderately lunate caudal-fin shape (and is allopatric, from northern Indonesia and Philippines). Two other Indonesian species: *P. alfiani* and *P. togeanensis* are closest in appearance (placement of the latter is uncertain without any genetic sequences). The three species share a rounded dorsal-fin profile without elongate filamentous rays (note that several western Indian Ocean species share this character but are distant geographically and genetically and have very different color patterns). *Paracheilinus togeanensis* is easily distinguished by its lunate caudal fin and color pattern. *Paracheilinus rennyae* mostly shares body and fin shape with its close relative *P. alfiani*, however the color patterns of TP males of the two species are considerably different: in particular, the numerous thin broken stripes on the side of *P. rennyae* vs. the relatively few stripes of *P. alfiani* and the patch of yellow-orange on the anterior dorsal fin of *P. rennyae* occupies only the first two spinous membranes, compared to over six membranes on *P. alfiani*.

The uniform red-orange color over the body and fins and the visible confluence of the outlines of the dorsal, caudal, and anal fins in the nuptial display of *P. rennyae* superficially resembles the color pattern seen in *Paracheilinus octotaenia* from the Red Sea. In this case, the stripes of *P. rennyae* are less well-defined and tend to break up into spots and reticulations (vs. well-defined) and the caudal fin has a broad yellow posterior band (vs. only a thin blue edge), and they have contrasting yellowish patches at the posterior ends of the dorsal and anal fins (vs. uniform).

Figure 44. *Paracheilinus rennyae*, TP male, approx. 60 mm SL (upper) and nuptial-male display, approx. 55 mm SL (lower), southwestern Flores, Indonesia (G.R. Allen).

Paracheilinus rubricaudalis Randall & Allen, 2003

Figures 18 & 45–48.

Paracheilinus rubricaudalis Randall & Allen 2003: 106, figs. 2–4 (type locality: Beqa Island, Fiji); Michael 2009; 287, 2 figs. (Fiji & Vanuatu); Kuiter 2010: 117, 4 figs. (Fiji, Vanuatu, to Manus, Papua New Guinea); Allen & Erdmann 2012: 709, 3 figs. (eastern Papua New Guinea, northern Coral Sea, Fiji, & Vanuatu).

Paracheilinus carpenteri [*non* Randall & Lubbock] Randall *et al*. 2003: 22 (Tonga, species list)(most likely identification is *P. rubricaudalis*).

Material examined. Fiji: BPBM 30658 (holotype), 56.0 mm SL; USNM.372850 (paratype), 47.8 mm SL. Harrier Reef (15° 8.133' S, 145° 41.653' E), Great Barrier Reef, Australia: WAM P.33973-001, 2 specimens, 37.7–43.3 mm SL. Manus Island, Papua New Guinea: WAM P.33979-001, 3 specimens, 40.7–53.4 mm SL.

Diagnosis. Pored lateral-line scales 15 or 16 + 5–7; gill rakers on first branchial arch 12–15; body depth 3.1–3.6 in SL; head length 2.9–3.1 in SL; snout 3.5–4.0 in HL; eye diameter 3.5–5.4 in HL; interorbital width 3.7–4.6 in HL; least depth of caudal peduncle 2.1–2.4 in HL; caudal peduncle length 1.6–2.0 in HL; soft dorsal fin with a single filamentous extension, containing an elongate first and, to a lesser degree, second, and sometimes third soft ray, longest dorsal-fin soft ray 1.5–2.8 in SL; pelvic fin length 1.8–2.6 in HL; caudal fin rounded in both sexes; maximum size to at least 56.0 mm SL; TP male orangish red to yellowish orange with reddish-to-blue stripes on head and body in pattern B (Figs. 45 & 46); dorsal fin straw yellow to orange to pale brown on spinous anterior portion of fin, dark red on most of soft dorsal fin except narrow basal band, filamentous extension can be yellowish to orange to red depending on location and individual; anal fin broadly red to orange without blue markings except a narrow blue margin; caudal fin reddish, usually with only a narrow blue posterior margin but sometimes a blue band or rows of blue spots across basal portion; pelvic fins reddish with narrow anterior blue margin; male nuptial-display pattern showing intensified yellow body with blue stripes and bright red median fins (Fig. 48).

Remarks. *Paracheilinus rubricaudalis* inhabits the southwestern Pacific Ocean (Fig. 18), including Fiji, Vanuatu, northern Great Barrier Reef (Ribbon Reefs near Lizard Island), Coral Sea (Holmes Reef and Osprey Reef), and eastern Papua New Guinea (Manus and Bismarck Archipelago), in depths of 15–46 m (Allen & Erdmann 2012). The listing of "*P. carpenteri*" from Tonga by Randall *et al*. (2003) likely refers to this species, but needs to be documented; no other species of *Paracheilinus* are known from the islands of the South Pacific.

One of three allopatric species in the *mccoskeri* group in the western Pacific Ocean, the other two being *P.*

Figure 45. *Paracheilinus rubricaudalis*, TP male (not nuptial display), approx. 50 mm SL, Fiji (G.R. Allen).

Figure 46. *Paracheilinus rubricaudalis*, developing male, approx. 35 mm SL, Manus Island, Papua New Guinea (G.R. Allen).

carpenteri and *P. flavianalis*. The group is united by by a rounded caudal fin and (usually) a single filamentous extension of the soft dorsal fin in TP males and genetic affinity. TP males of *P. rubricaudalis* differ from the other members in having its namesake all red caudal fin, a mostly red soft dorsal fin and an orangish anal fin not interrupted by blue spotting. In addition, *P. carpenteri* males have two short mid-anterior stripes vs. one in *P. rubricaudalis*. Three specimens from Manus Island, Papua New Guinea have slightly lower gill-raker counts compared to specimens from other locations (12 versus 13–15). Live TP males from the Coral Sea and Great Barrier Reef differ in having prominent blue markings on the posterior dorsal fin, resembling *P. mccoskeri,* and a clear caudal fin (Fig. 47).

Figure 47. *Paracheilinus rubricaudalis*, TP male, approx. 55 mm SL, Great Barrier Reef, Australia (K. Endoh).

Figure 48. *Paracheilinus rubricaudalis*, nuptial-male display, upper: approx. 55 mm SL, Manus Island, Papua New Guinea (G.R. Allen); lower: approx. 50 mm SL, aquarium photo, originally from Vanuatu (F. Walsh).

Paracheilinus togeanensis Kuiter & Allen, 1999

Figures 18 & 49–50.

Paracheilinus togeanensis Kuiter & Allen 1999: 127, fig. 8 (type locality: Batudaka Island, Togean Islands, Sulawesi, Indonesia); Michael 2009: 280, 1 fig. (Sulawesi); Kuiter 2010: 112, 5 figs. (Sulawesi); Allen & Erdmann 2012: 709, 2 figs. (Sulawesi).

Material examined. Togean Islands, Sulawesi, Indonesia: NCIP 6168 (holotype), 47.8 mm SL.

Diagnosis. Pored lateral-line scales 15 + 4–6; gill rakers on first branchial arch 13; body depth 3.6 in SL; head length 3.0 in SL; snout 4.2 in HL; eye diameter 4.0 in HL; interorbital width 4.4 in HL; least depth of caudal peduncle 2.5 in HL; caudal peduncle length 1.7 in HL; dorsal fin of both sexes rounded in profile without elongate filamentous soft rays, soft dorsal fin high in TP males, can be slightly incised between soft rays, longest dorsal-fin soft ray 3.6 in SL; pelvic fin length 1.7 in HL; caudal fin of IP fish slightly emarginate, of TP male deeply lunate; maximum size to at least 47.8 mm SL; IP fish photographed in Kuiter (2010) orangish grading to white ventrally, with bluish stripes dorsally and reddish stripes ventrally; dorsal fin broadly reddish with orange anterior portion; anal fin yellowish with rows of blue spots along base and blue margin; color of TP male overall pinkish to orangish red with thin bluish-to-reddish stripes in pattern A; dorsal fin broadly pinkish; male nuptial-display pattern showing bright red head and body with reddish-to-bluish stripes (Figs. 49 & 50), forehead yellowish to bluish green with red or orangish-pink vermiculations; bright red dorsal fin with broad bluish-white anterior portion, sometimes bluish-white band or row of spots or double row along fin base, and a few bluish spots on posteriormost end; anal fin bright yellow or orange to red with narrow sky-blue margin and 1–2 rows of purplish-to-blue spots along base of fin; caudal fin bright red on base and along upper and lower margins out along filamentous extensions of the lobes, central portion with elaborate blue markings; pelvic fins yellow to orange with narrow bue anterior margin.

Figure 49. *Paracheilinus togeanensis*, nuptial-male display, approx. 50 mm SL, Lembeh Strait, Sulawesi, Indonesia (N. DeLoach).

Remarks. *Paracheilinus togeanensis* has a very restricted range, known only from northern Sulawesi at the Togean Islands and Lembeh Strait, at the extreme northern tip of the island (Fig. 18). It is probably more widespread along the shores of the Gulf of Tomini, the large embayment separating the northern and central peninsulas of northeastern Sulawesi. Only a single specimen has been collected to date, but it is occasionally observed by divers, particularly at Lembeh Strait. The known depth range is 16–40 m along outer reef slopes (Allen & Erdmann 2012).

The species does not fit well into any of the species groups, since it has the unique combination within the genus of no elongate filamentous rays in the dorsal fin and a deeply lunate caudal fin in the TP male. Furthermore, no genetic material is presently available. It is tentatively considered a member of the *filamentosus* group, but differing from the TP males of other members of the group by the absence of the namesake filamentous dorsal-fin rays, along with the unusual tall dorsal fin and the very distinctive nuptial-display color pattern.

Figure 50. *Paracheilinus togeanensis*, nuptial-male display, approx. 50 mm SL, Lembeh Strait, Sulawesi, Indonesia (upper, G.R. Allen; lower, N. DeLoach).

Paracheilinus walton Allen & Erdmann, 2006

Figures 3, 4C, 18, 41 upper, & 51–52.

Paracheilinus walton Allen & Erdmann 2006: 14 (type locality: Yapen Island, West Papua, Indonesia); Allen & Erdmann 2012: 710, 3 figs. (Cenderawasih Bay, West Papua, Indonesia).
Paracheilinus waltoni Allen (misspelled) Kuiter 2010: 108, 4 figs. (Raja Ampat, West Papua, Indonesia).

Material examined. Cenderawasih Bay, West Papua, Indonesia: NCIP 6311 (holotype), 40.7 mm SL; AMS I.43840-001 (paratype), 34.8 mm SL; BPBM 40413 (paratype), 38.3 mm SL; NCIP 6312 (paratype), 38.9 mm SL, WAM P.32771-001 (paratypes), 2 specimens, 27.7–40.7 mm SL; WAM P.33551-001, 2 specimens, 51.0–55.3 mm SL; WAM P.33890-002, 34.6 mm SL. Ayau Atoll (0° 20.792' N, 131° 01.495' E), Raja Ampat Islands, West Papua, Indonesia: WAM P.34338-003, 3 specimens, 35.9–38.8 mm SL.

Diagnosis. Pored lateral-line scales 15 + 5; gill rakers on first branchial arch 13–14; body depth 3.0–3.4 in SL; head length 2.9–3.0 in SL; snout length 3.8–4.2 in HL; eye diameter 3.2–4.0 in HL; interorbital width 4.2–4.5 in HL; least depth of caudal peduncle 2.2–2.3 in HL; caudal peduncle length 1.6–2.2 in HL; 3–5 (frequently 4) elongate filamentous dorsal-fin rays in TP males, longest dorsal-fin soft ray 2.0–2.2 in SL; pelvic fin 1.7–1.9 in HL; caudal fin of TP male moderately lunate; maximum size to at least 54.0 mm SL; color of TP male yellowish orange grading to white ventrally with numerous thin reddish-to bluish stripes in a pattern A variation (Fig. 51), fins mostly pale orange, caudal fin with elaborate blue markings; male nuptial-display pattern (Fig. 52 and Allen & Erdmann 2012, p. 710) showing a bright orangish or yellow head and body with blue stripes in pattern A variation; dorsal fin becoming bluish-white, contrasting with an adjacent zone of intense red on the rear upper

Figure 51. *Paracheilinus walton*, TP male (not nuptial display), approx. 50 mm SL, Cenderawasih Bay, West Papua, Indonesia (G.R. Allen).

body (blackish when viewed underwater in ambient light); anal fin mainly orangish to yellow with a narrow sky-blue margin; caudal fin with narrow dark-red upper and lower edges and filamentous extensions of lobes, and broad central area with elaborate sky-blue markings.

Remarks. *Paracheilinus walton* is known mainly from Cenderawasih Bay, West Papua, Indonesia (Fig. 18), at depths of 18–50 m. The only other record is from Ayau Atoll in the Raja Ampat Islands, which lies about 420 km northwest of Cenderawasih Bay. The first two authors recently collected and photographed specimens on the outer reef of Ayau Atoll at depths of 29–38 m. The species is apparently common on the isolated oceanic reefs of Ayau, as large numbers were sighted at two widely separated dive sites. Nonetheless, we feel confident the species is not present elsewhere in the main Raja Ampat Archipelago, as it has not been recorded by the authors in their extensive survey work, comprising thousands of dives over 15 years in the region.

Based on the numerous elongate filamentous dorsal-fin rays and a deeply lunate caudal fin in TP males (and genetic affinity), the species belongs to the *filamentosus* group, and is most similar in appearance to its nearby allopatric relative *P. nursalim* from farther south in West Papua. *Paracheilinus walton* is hypothesized to have recently evolved from the same ancestral stock of *Paracheilinus*, possibly as a result of the collision of the Bird's Head Peninsula with the New Guinea mainland and consequent isolation of Cenderawasih Bay from southern New Guinea (Allen & Erdmann 2006). Indeed, the two species still share mitochondrial DNA haplotypes. Both *P. nursalim* and *P. cyaneus* also have the stripe pattern A variation characterized by irregular rows of small dark spots on the side of the body in the spaces between the main stripes. The distinctive TP male nuptial displays are the most reliable means of separating the three species; *P. nursalim* shares the bright white dorsal-fin filaments and yellow body (although *P. walton* tends to be more orange), but the prominent rectangular black patches on the back and lower caudal peduncle are specific to *P. nursalim*. Instead, *P. walton* has a bright red band under the soft dorsal fin and also has a more yellow-to-orange anal fin (vs. bright red). *P. cyaneus* is easily distinguished by a blue and red body in the TP male nuptial display.

Males usually reach at least 54 mm SL, but the population at the far western end of Yapen Island (about 1° 36.192' S, 135° 24.632' E) has dwarf males reaching only about 41 mm SL (Fig. 41, upper). This smaller size is perhaps related to the generally deeper habitat in which this population is found (40–60 m).

Figure 52. *Paracheilinus walton*, nuptial-male display, approx. 50 mm SL, Cenderawasih Bay, West Papua, Indonesia (G.R. Allen).

Paracheilinus xanthocirritus, n. sp.

Figures 6B, 18, 53–57; Tables 4 & 5.

Holotype. MZB 22246, male, 49.1 mm SL, Selai Island, 03° 10.865’ N, 106° 29.615’ E, Anambas Islands, Indonesia, 15–16 m, clove oil and spear, M.V. Erdmann, May 29, 2012.

Paratypes. BPBM 41210, female, 33.9 mm SL, and 2 males, 43.2–46.9 mm SL, collected with holotype; MZB 22247, female, 25.5 mm SL, and 2 males, 40.9–47.0 mm SL, collected with holotype; USNM 432464, male 48.7 mm SL, collected with holotype; WAM 33128-006, 2 male specimens, 43.9–46.4 mm SL, Columbo Shoals, 05° 12.259’ N, 114° 44.393’ E, Brunei, 20–25 m, rotenone and spear, G. Allen & M. Erdmann, May 22, 2009; WAM 33736-001, 2 male specimens, 42.8–49.3 mm SL, collected with holotype.

Diagnosis. Pored lateral-line scales 15–16 + 5–7; gill rakers on first branchial arch 13–14; body depth 3.1–3.5 in SL; head length 2.9–3.2 in SL; snout length 3.9–5.0 in HL; eye diameter 3.5–4.9 in HL; interorbital width 3.8–4.1 in HL; least depth of caudal peduncle 2.0–2.4 in HL; caudal-peduncle length 1.6–2.0 in HL; 4–7 (usually 5–6) elongate filamentous dorsal-fin soft rays in TP male, longest dorsal-fin soft ray 1.7–5.0 in SL; pelvic fin length 1.6–2.2 in HL; deeply lunate caudal fin in TP male; TP males overall orangish red, grading to white ventrally with reddish to pink stripes in pattern A (Fig. 56); fins yellowish, posterior dorsal fin dark and anal fin with a row of blue spots across mid-fin; male nuptial-display pattern with head and body bright yellow to yellowish orange grading to red near caudal fin (Figs. 54 & 57), with bluish-to-reddish stripes in pattern A; most of dorsal fin, including elongate filamentous rays, yellow to yellow-orange, posterior section of fin with variable dark red blotch above band of blue running full-length of base of fin; anal fin yellow to orange, sometimes shading to red or crimson posteriorly, with sky-blue outer margin and row of blue spots near rear base; caudal fin with red to dark burgundy upper and lower margins and adjacent filamentous lobes, central portion of fin with elaborate blue markings; pelvic fins yellow to yellow-orange with narrow anterior bluish margin.

Description. Dorsal-fin rays IX,11; anal-fin rays III,9 (one paratype with III,8); pectoral-fin rays (including upper rudimentary ray) 14 (one paratype with 15 on one side); lateral-line interrupted, pored scales 15 + 6 (15–16 + 5–7); scales above lateral line to origin of dorsal fin 2; scales below lateral line to origin of anal fin 6; median predorsal scales 5; median preventral scales 6; transverse scale rows on cheek 2; circumpeduncular scales 16 (15–16); gill rakers 13 (2 paratypes with 13 and 4 with 14); pseudobranchs 12 (11–12).

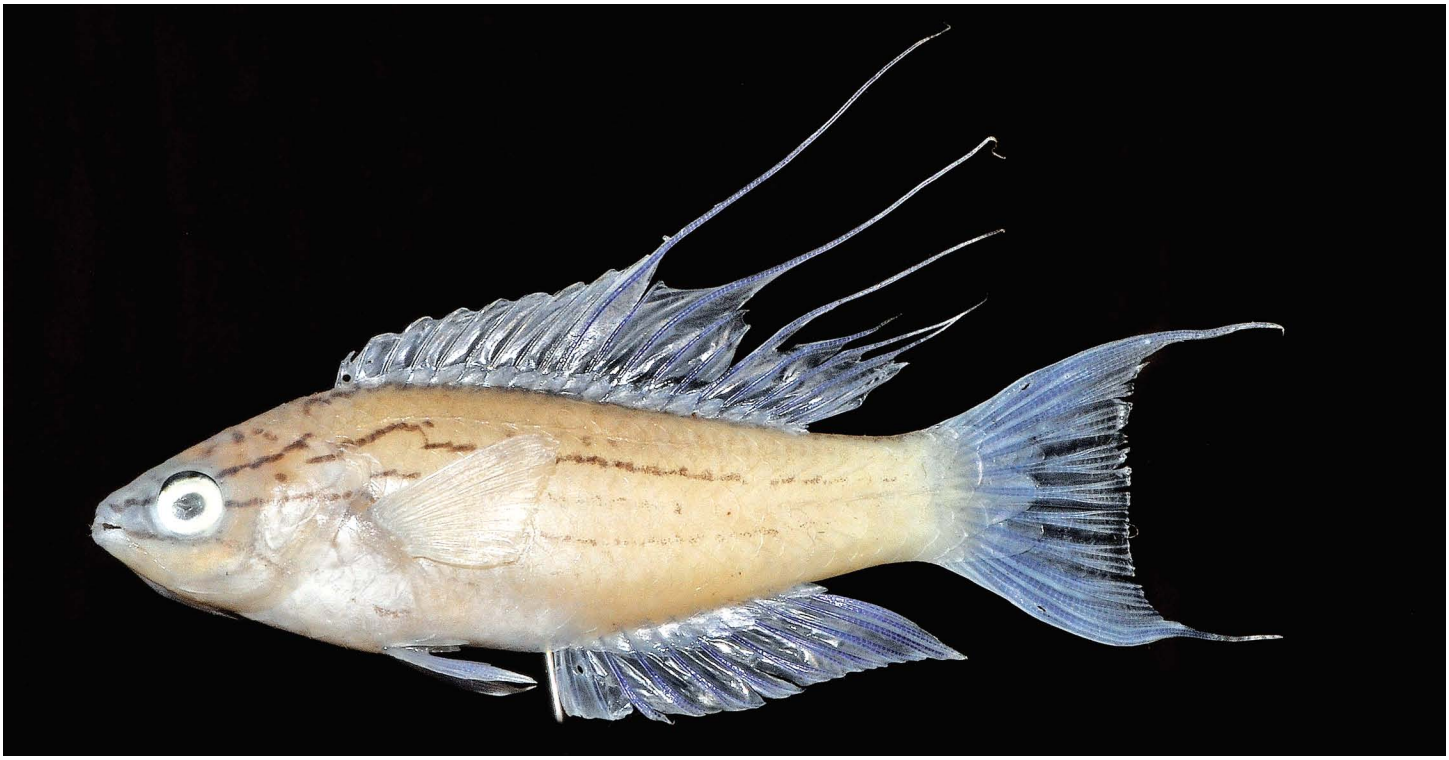


Figure 53. *Paracheilinus xanthocirritus*, preserved holotype, MZB 22246, male, 49.1 mm SL, Anambas Islands, Indonesia (G.R. Allen).

Body depth 3.3 (3.1–3.5) in SL; body width 2.1 (1.9–2.3) in body depth; head length 3.2 (2.9–3.2) in SL; snout short, length 4.1 (3.9–5.0) in HL; eye diameter 4.1 (3.5–4.9) in HL; interorbital width 3.9 (3.8–4.1) in HL; least depth of caudal peduncle 2.1 (2.0–2.4) in HL; caudal-peduncle length 1.8 (1.6–2.0) in HL.

Mouth small, oblique, the maxilla nearly reaching a vertical at front edge of eye; three pairs of curved canine teeth anteriorly in upper jaw, progressively more laterally projecting, third (posteriormost) pair well largest; a single pair of canine teeth anteriorly in lower jaw, very strongly curved laterally; side of jaws with a single row of small close-set conical teeth; no canine tooth at corner of mouth; no teeth on palate; a fleshy flap on side of lower lip; gill rakers short, the longest about one-fourth to one-third length of longest gill filaments on first gill arch; posterior nostril an oval opening about twice size of cephalic sensory pores, anterior to fleshy upper edge of eye and on vertical at anterior bony edge of eye; anterior nostril small with a short fleshy rim anterior and slightly ventral to posterior; internarial space about 3.2 in eye diameter; cephalic sensory system consisting of nine pores posterior and ventral along edge of eye, two supraocular pores, five occipital pores, three mid-interorbital pores, four small pores around nostril area, four mandibular pores, and five preopercular pores.

Head scaled except for interorbital space, snout, and chin; a row of pointed scales on base of dorsal and anal fins; basal half of caudal fin with large scales; axillary scale of pelvic fin slightly shorter than pelvic spine; midventral scaly process of pelvic fins slightly longer than pelvic spine.

Free ventral margin of preopercle extending to vertical at center of eye, vertical posterior margin to level of lower edge of pupil; exposed bony edge of preopercle smooth without serrations.

Origin of dorsal fin above third lateral-line scale, predorsal length 3.3 (3.0–3.2) in SL; dorsal-fin spines progressively longer, first 7.0 (6.4–9.2) in HL, and ninth 1.6 (1.7–2.4) in HL; 6 (4–7) soft dorsal-fin rays forming prolonged filaments; longest (first) dorsal-fin soft ray 1.4 (1.7–5.0) in SL; origin of anal fin below base of last dorsal-fin spine, preanal length 1.8 (1.7–1.9) in SL; first anal-fin spine 3.4 (3.6–5.2) in HL; second anal-fin spine 3.3 (3.0–3.8) in HL; third anal-fin spine 2.9 (2.8–3.3) in HL; longest (penultimate) anal-fin soft ray 3.9 (3.2–7.4) in SL; caudal fin rounded, 2.1 (2.1–4.3) in SL; pectoral-fin length 1.3 (1.3–1.6) in HL; pelvic-fin length 1.6 (1.6–2.2) in HL.

Figure 54. *Paracheilinus xanthocirritus*, nuptial-male display, approx. 50 mm SL, Anambas Islands, Indonesia (G.R. Allen).

TABLE 5

Proportional measurements of type specimens of *Paracheilinus xanthocirritus*, n. sp. as percentages of the standard length

	holotype	paratypes					
	MZB 22246	WAM P.33736	MZB 22247	BPBM 41210	WAM P.33128	WAM P.33128	BPBM 41210
	male	male	male	male	male	male	female
Standard length (mm)	49.1	48.7	47.0	46.9	46.4	43.9	33.9
Body depth	30.8	30.8	32.8	31.1	29.1	31.4	31.0
Body width	14.9	14.4	14.5	15.8	14.0	14.6	15.9
Head length	31.6	30.8	33.4	33.3	31.5	31.2	33.9
Snout length	7.7	7.6	8.3	7.2	8.0	8.0	6.8
Orbit diameter	7.7	8.2	8.1	8.7	6.5	8.0	9.7
Interorbital width	8.1	8.2	8.1	8.5	8.0	8.2	8.6
Upper jaw	7.9	7.0	8.1	7.0	7.1	7.1	7.7
Depth of caudal peduncle	15.1	13.6	15.5	13.6	15.5	14.6	15.6
Length of caudal peduncle	17.7	17.2	18.1	20.7	20.3	17.1	20.6
Predorsal distance	30.5	31.8	32.3	32.6	32.3	31.4	33.6
Preanal distance	55.2	57.1	57.0	55.9	53.4	51.9	57.8
Prepelvic distance	34.2	35.3	36.8	36.2	35.8	31.7	35.4
Length of dorsal-fin base	55.6	53.0	54.0	56.7	51.5	53.3	54.9
First dorsal-fin spine	4.5	4.5	4.0	3.6	3.7	5.0	5.3
Last dorsal-fin spine	19.6	17.2	19.1	17.3	15.7	15.3	13.9
Longest dorsal-fin soft ray	69.0	56.5	56.0	44.1	58.2	45.8	20.1
Length of anal-fin base	30.8	31.0	28.7	29.2	28.2	28.7	26.0
First anal-fin spine	9.4	8.6	8.9	7.9	7.8	7.1	6.5
Second anal-fin spine	9.6	9.0	11.1	9.0	8.6	9.3	8.8
Third anal-fin spine	10.8	10.9	11.9	10.2	10.8	10.9	10.3
Longest anal-fin soft ray	25.5	20.3	26.2	22.4	31.0	21.6	13.6
Caudal-fin length	48.1	36.3	48.1	44.3	40.9	28.2	23.3
Pectoral-fin length	24.6	22.2	23.4	23.9	23.7	20.3	21.2
Pelvic fin-spine length	11.6	12.1	11.5	11.1	10.8	10.5	14.2
Pelvic fin length	20.4	18.7	18.5	18.1	18.1	18.2	16.2

Figure 55. *Paracheilinus xanthocirritus*, TP male (not nuptial display), approx. 40 mm SL, Brunei (G.R. Allen).

Color of TP male in life. (Fig. 55) Head and body generally reddish orange to white ventrally, with reddish-to-bluish-lavender stripes in pattern A; dorsal, anal, and pelvic fins yellowish with a blue row of spots along dorsal-fin base, a stripe along basal third of soft dorsal fin, and a row or two of bue spots along basal portion of anal fin; caudal fin translucent with blue and purple spots; pectoral fins translucent.

Male nuptial coloration. (Figs. 6B, 54 & 57) Bright orangish yellow on head and anterior body grading to red posteriorly, with thin stripes on head and body in pattern A, stripes bluish dorsally and reddish to lavender ventrally; dorsal fin yellow to yellowish orange over anterior two-thirds of fin including elongate filamentous rays with narrow blue edge and blue-to-purplish stripe or row of blue spots along full-length base of dorsal fin, posterior portion of soft dorsal fin with broad bluish band at base, underlying dark-red-to-blackish patch roughly in the shape of three merged triangles with the apex of each directed dorsally and forming basal portion of yellowish filamentous rays; anal fin orangish to red with sky-blue outer margin and row of sky-blue spots (about pupil-size), often merged to form a stripe, mostly on posterior portion of fin just above base; caudal fin with bright red elongate filamentous lobes and central translucent portion with purple fin-rays and blue markings on membranes; pelvic fins

Figure 56. *Paracheilinus xanthocirritus*, initial phase, approx. 25 mm SL, Anambas Islands, Indonesia (G.R. Allen).

Figure 57. *Paracheilinus xanthocirritus*, peak nuptial-male displays, all approx. 50 mm SL, , Anambas Islands, Indonesia (G.R. Allen).

orange with narrow anterior, bluish margin; pectoral fins translucent. During peak nuptial display, colors intensify and body shows more yellow and blue-to-purple stripes and bands on head, body, edge of fins, and along base of dorsal fin transform to bright sky-blue or electric blue, and caudal fin shows intense sky-blue markings on otherwise translucent middle portion of fin.

Color of IP in life. (Fig. 56) Head and body pink to red-orange, grading to yellow on side of body and white on ventral aspect, with reddish stripe on head behind middle of eye and several faint reddish stripes or rows of spots on side of body; fins translucent; narrow yellow ring around pupil and red iris with blue rim to dorsal sclera.

Color of holotype in alcohol. (Fig. 53) Overall pale grey to yellowish white with purple head and body stripes as described above, but most faintly visible; median and pelvic fins translucent with purple rays; pectoral fins translucent. Color of paratypes from Brunei similar, except overall pale tan.

Distribution and habitat. *Paracheilinus xanthocirritus* is currently known from the South China Sea at the Anambas Islands, Indonesia (about 250 km northeast of Singapore) and Brunei (Fig. 18). It probably occurs more widely in the South China Sea, but so far has escaped detection. It was not seen by the authors during extensive reef surveys at northern Palawan, Philippines, nor was it recorded at Layang Layang Atoll, Sabah (about 300 km northwest of Kota Kinabalu, Sabah). The habitat consisted of a sloping rubble bottom with low coral outcrops (Anambas Islands) or among extensive live corals (Brunei) at depths of 15–25 m. The new species was generally uncommon at both locations, although it was locally common at both collection sites.

Etymology. The new species is named *xanthocirritus* (Latin: yellow-thread), with reference to the diagnostic yellow, thread-like filaments of the dorsal fin of TP males.

Remarks. Based on the numerous elongate filamentous dorsal-fin rays and a deeply lunate caudal fin in the TP male, the new species belongs to the *filamentosus* group of species (and it shares mtDNA haplotypes with other species in the complex). It is most similar in appearance to its allopatric relatives *P. paineorum* and *P. filamentosus*. The nuptial-display color pattern on the dorsal fin clearly separates the three species (e.g. Fig. 6). The salient color-pattern characters for the three species are compared in Table 4. In contrast to the TP male nuptial-display pattern of *P. filamentosus*, i.e. relatively broad, electric-blue stripes on a maroon-to-violet-red background (Fig. 26), *P. xanthocirritus* and *P. paineorum* have narrower reddish stripes, becoming more bluish dorsally and posteriorly, on a bright orangish-yellow-to-red background. Further morphological differences are summarized under the comments for *P. paineorum*.

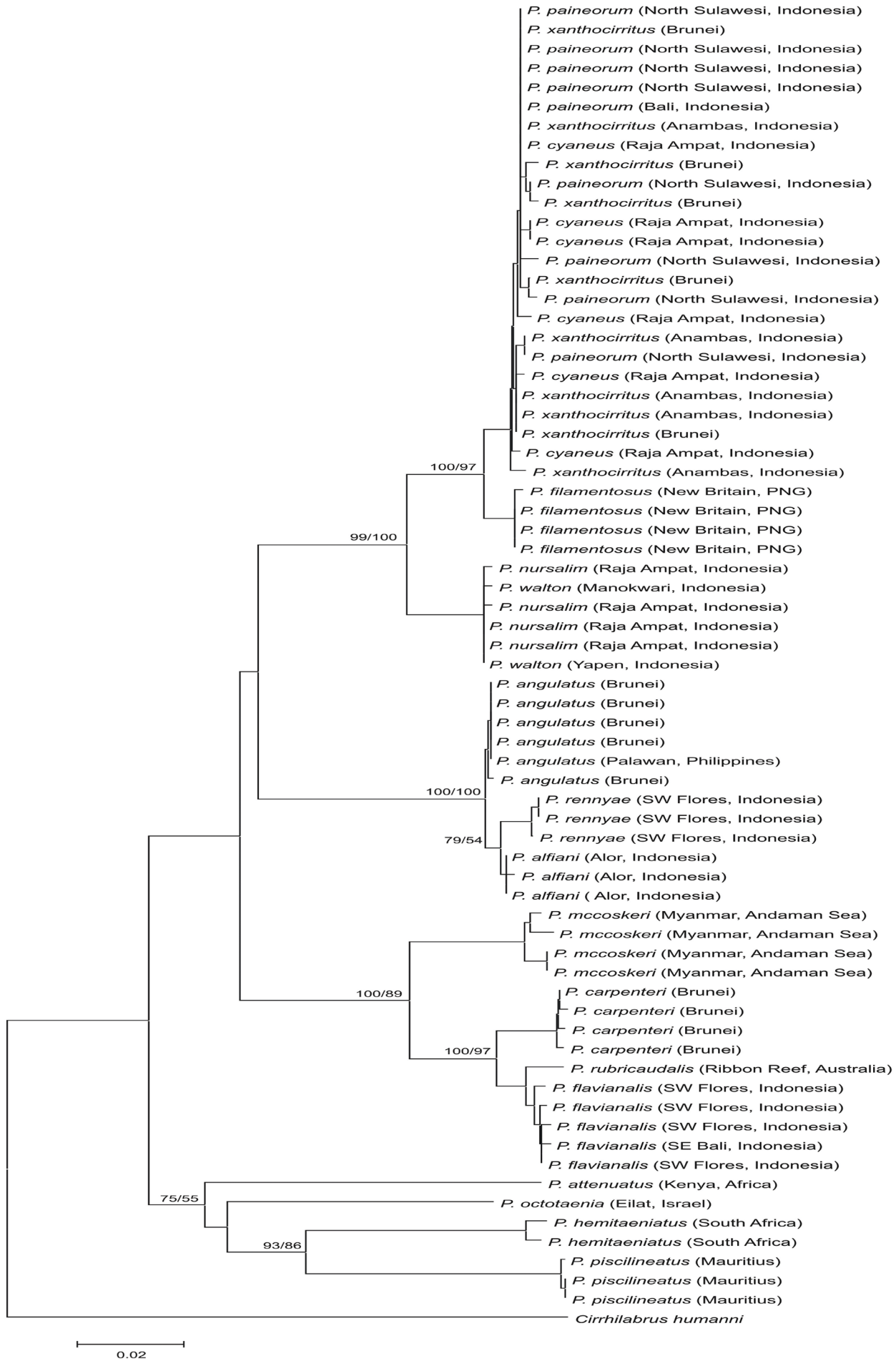
Genetic Analysis. We resolved relationships among the species of *Paracheilinus* using the mtDNA barcode sequence of the COI marker from 17 of the 20 recognized species in the genus. GenBank accession numbers and associated data are provided in Table 1. We recovered 45 unique haplotypes, plus 4 more contributed from other laboratories. The total *Paracheilinus* alignment contained 166 parsimony-informative characters with average nucleotide frequencies for the combined samples as follows: A=21.9, C=26.4, G=19.4, and T=32.2.

The neighbor-joining tree obtained comprised four major clades that match to the four species groups we proposed for the genus in the introductory redescription of the genus (Fig. 58).

The *filamentosus* species-complex is the largest grouping of *Paracheilinus* species, comprising *P. cyaneus*, *P. filamentosus*, *P. nursalim*, *P. paineorum*, *P. walton*, and *P. xanthocirritus*. This complex can be further divided into 3 sub-clades, one containing the true *P. filamentosus* from Papua New Guinea and the Solomon Islands, another with the sibling-species pair of *P. nursalim* and *P. walton* from West Papua, and a third containing three Indonesian species that span a large distribution from the South China Sea to West Papua (*P. cyaneus*, *P. paineorum*, and *P. xanthocirritus*).

The *angulatus* species-complex is a very closely related clade of three species (*P. alfiani*, *P. angulatus* and *P. rennyae*), all allopatric in the region. The *mccoskeri* species-complex contains four species (*P. carpenteri*, *P. flavianalis*, *P. mccoskeri*, and *P. rubricaudalis*) that are generally not as close to each other as in the previously listed complexes, with the Indian Ocean species *P. mccoskeri* the most outlying. Finally, the four members of the western-Indian-Ocean species-complex (*P. attenuatus*, *P. hemitaeniatus*, *P. octotaenia* and *P. piscilineatus*) form a

Figure 58 (opposite). Neighbor-joining (NJ) tree of the mtDNA COI sequences for 17 species of *Paracheilinus* with *Cirrhilabrus humanni* as an outgroup. Numbers above the major nodes indicate bootstrap support for 1000 replicates using neighbor joining and bayesian posterior probability, respectively.


P. paineorum (North Sulawesi, Indonesia)
P. xanthocirritus (Brunei)
P. paineorum (North Sulawesi, Indonesia)
P. paineorum (North Sulawesi, Indonesia)
P. paineorum (North Sulawesi, Indonesia)
P. paineorum (Bali, Indonesia)
P. xanthocirritus (Anambas, Indonesia)
P. cyaneus (Raja Ampat, Indonesia)
P. xanthocirritus (Brunei)
P. paineorum (North Sulawesi, Indonesia)
P. xanthocirritus (Brunei)
P. cyaneus (Raja Ampat, Indonesia)
P. cyaneus (Raja Ampat, Indonesia)
P. paineorum (North Sulawesi, Indonesia)
P. xanthocirritus (Brunei)
P. paineorum (North Sulawesi, Indonesia)
P. cyaneus (Raja Ampat, Indonesia)
P. xanthocirritus (Anambas, Indonesia)
P. paineorum (North Sulawesi, Indonesia)
P. cyaneus (Raja Ampat, Indonesia)
P. xanthocirritus (Anambas, Indonesia)
P. xanthocirritus (Anambas, Indonesia)
P. xanthocirritus (Brunei)
P. cyaneus (Raja Ampat, Indonesia)
P. xanthocirritus (Anambas, Indonesia)
100/97
P. filamentosus (New Britain, PNG)
P. filamentosus (New Britain, PNG)
P. filamentosus (New Britain, PNG)
P. filamentosus (New Britain, PNG)
99/100
P. nursalim (Raja Ampat, Indonesia)
P. walton (Manokwari, Indonesia)
P. nursalim (Raja Ampat, Indonesia)
P. nursalim (Raja Ampat, Indonesia)
P. nursalim (Raja Ampat, Indonesia)
P. walton (Yapen, Indonesia)
P. angulatus (Brunei)
P. angulatus (Brunei)
P. angulatus (Brunei)
P. angulatus (Brunei)
P. angulatus (Palawan, Philippines)
P. angulatus (Brunei)
100/100
P. rennyae (SW Flores, Indonesia)
P. rennyae (SW Flores, Indonesia)
79/54
P. rennyae (SW Flores, Indonesia)
P. alfiani (Alor, Indonesia)
P. alfiani (Alor, Indonesia)
P. alfiani (Alor, Indonesia)
P. mccoskeri (Myanmar, Andaman Sea)
P. mccoskeri (Myanmar, Andaman Sea)
P. mccoskeri (Myanmar, Andaman Sea)
P. mccoskeri (Myanmar, Andaman Sea)
100/89
P. carpenteri (Brunei)
P. carpenteri (Brunei)
P. carpenteri (Brunei)
100/97
P. carpenteri (Brunei)
P. rubricaudalis (Ribbon Reef, Australia)
P. flavianalis (SW Flores, Indonesia)
P. flavianalis (SW Flores, Indonesia)
P. flavianalis (SW Flores, Indonesia)
P. flavianalis (SE Bali, Indonesia)
P. flavianalis (SW Flores, Indonesia)
P. attenuatus (Kenya, Africa)
75/55
P. octotaenia (Eilat, Israel)
P. hemitaeniatus (South Africa)
93/86
P. hemitaeniatus (South Africa)
P. piscilineatus (Mauritius)
P. piscilineatus (Mauritius)
P. piscilineatus (Mauritius)
Cirrhilabrus humanni
0.02

much less cohesive monophyletic lineage (with 75% bootstrap support), with relatively deep divergences among the species in the complex.

Pairwise mean interspecific genetic distances among species ranged from 0.002–0.164 (Table 6). However, the minimum interspecific divergence was zero, i.e. shared haplotypes with other species, for almost all species in the *filamentosus* species-complex (except for *P. filamentosus*). In the other species complexes, haplotypes were not shared, but lineages were sometimes very close, with *P. angulatus* and *P. alfiani* separated by only 0.4% on average, and several other pairs by barely more.

Discussion. Most recent studies show that the majority of marine fish species are characterized by monophyletic mitochondrial lineages that are well separated (usually by more than 2%) from related species (Steinke *et al*. 2009, Ward *et al*. 2009). However, there are frequent exceptions among reef fishes that challenge the standard species definition (Victor 2015). Often the sequence differences between closely related species are minimal, fractions of a percent, or even the same, with shared mitochondrial haplotypes between species (phenovariant species *sensu* Victor 2015). In the case of *Paracheilinus*, both patterns are evident: among the species of the *filamentosus* species-complex, five of six species share haplotypes with at least one other species. In both the *angulatus* and *mccoskeri* species-complexes, many species are only slightly divergent from one another, often by less than 1%. Despite these slight or no mitochondrial sequence differences, there are clear and consistent differences in dorsal-fin morphology and color patterns of TP males, indicating that phenotypic divergence has outpaced the rate of change in mitochondrial genotype in these fishes.

This finding is not unique to this genus, indeed recent studies have shown similar findings in other labrid fishes with striking nuptial dispays among males, i.e. in *Cirrhilabrus* (Allen *et al*. 2015) and *Pseudojuloides* (Victor & Randall 2014). In these cases, the selection for reproductive-isolating mechanisms, such as colorful male displays, has clearly outpaced the rate of accumulation of neutral mutations in the mitochondrial genome. It is likely that this reflects very recent evolutionary divergence, similar to that suggested by Tornabene *et al*. (2015), who provided evidence for similar rapid evolutionary change during the Pleistocene in the gobiid genus *Eviota*.

TABLE 6

Average interspecific pairwise genetic-distance matrix for mtDNA COI sequences of *Paracheilinus*

No.	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	*walton*																
2	*xanthocirritus*	0.037															
3	*mccoskeri*	0.102	0.109														
4	*cyaneus*	0.037	0.004	0.108													
5	*carpenteri*	0.108	0.109	0.054	0.110												
6	*angulatus*	0.081	0.092	0.103	0.091	0.113											
7	*nursalim*	0.002	0.037	0.103	0.037	0.108	0.081										
8	*flavianalis*	0.107	0.108	0.048	0.108	0.021	0.105	0.107									
9	*rennyae*	0.091	0.101	0.110	0.100	0.119	0.011	0.090	0.112								
10	*filamentosus*	0.034	0.014	0.111	0.014	0.111	0.092	0.034	0.110	0.102							
11	*paineorum*	0.036	0.003	0.108	0.003	0.109	0.092	0.036	0.108	0.101	0.013						
12	*hemitaeniatus*	0.142	0.139	0.148	0.140	0.148	0.129	0.141	0.143	0.129	0.140	0.140					
13	*piscilineatus*	0.147	0.145	0.151	0.144	0.157	0.131	0.146	0.149	0.132	0.146	0.144	0.091				
14	*rubricaudalis*	0.111	0.112	0.054	0.112	0.024	0.107	0.111	0.010	0.113	0.114	0.112	0.141	0.149			
15	*alfiani*	0.085	0.096	0.107	0.095	0.117	0.004	0.084	0.109	0.008	0.096	0.095	0.130	0.133	0.111		
16	*attenuatus*	0.134	0.142	0.154	0.142	0.153	0.133	0.133	0.157	0.135	0.134	0.141	0.123	0.117	0.164	0.132	
17	*octotaenia*	0.132	0.132	0.146	0.132	0.139	0.114	0.132	0.132	0.118	0.127	0.131	0.105	0.112	0.130	0.112	0.120

A number of recent reviews and studies (Rocha & Bowen 2008, Helfman *et al*. 2009, Victor & Randall 2014, Allen *et al*. 2015) have shown that rapid evolution of sibling-species pairs and closely related complexes of reef fishes are frequently characterized by the development of different color patterns, especially among breeding males. The mating strategy of *Paracheilinus*, and many other labrid fishes, in which relatively few males compete for the attention of numerous females, strongly selects for conspicuous male secondary-sexual characters, such as bright and complex nuptial color patterns as well as exaggerated dorsal fins, which are erected during courtship, not unlike the well-documented behavior found in terrestrial birds-of-paradise (Laman & Scholes 2012). The same situation is found in the closely related genus *Cirrhilabrus*, which is also known for both spectacular male nuptial displays (Allen & Erdmann 2012) as well as sibling species that show little or no mitochondrial sequence divergence (Allen *et al*. 2015). As the cost of whole genome sequencing continues to decrease, in-depth genomic studies of phylogeographic questions (Eble *et al*. 2015) may provide valuable new insights into micro-evolutionary processes and the role of sexual selection in speciation.

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