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Review of the Indo-Pacific *Pseudojuloides cerasinus* species complex with a description of two new species (Teleostei: Labridae)

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Abstract

The *Pseudojuloides cerasinus* species complex is a paradigm of the application of DNA taxonomy to coral-reef fish classification. Once considered a pan-Indo-Pacific species ranging from South Africa to the Hawaiian Islands, *P. cerasinus* has been divided into three different allopatric species in the Indian Ocean, based on differences in male-display color patterns and relatively deep genetic divergences. In this study, the Pacific Ocean populations are shown to represent four species: the original type population in the Hawaiian Islands; a new western Pacific species *Pseudojuloides splendens*, ranging from Japan to Australia and across most of the South Pacific; a new species *Pseudojuloides polynesica*, from French Polynesia and the Line Islands; and *Pseudojuloides pyrius* Randall & Randall, 1981, endemic to the Marquesas Islands. The mtDNA lineages of the complex diverge from 3.5–11.3% in the sequence of the mtDNA-barcode marker COI. The species illustrate some of the more interesting phenomena in the evolution of species complexes among coral reef fishes: the species differences are mainly in male-display color patterns, the degree of phenotypic divergence does not correlate with the amount of genetic divergence (the most different-appearing species is one of the least divergent), and a corollary that the various genetic lineages must be distinguished to avoid paraphyly in the taxonomic construct of the species complex. A neighbor-joining tree and genetic distance matrix are presented for the seven species of the *P. cerasinus* species complex.

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

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Introduction

The labrid genus *Pseudojuloides* Fowler was revised by Randall & Randall (1981), who recognized eight species, five of which were new. Since then, six additional new species have been described from various locations in the Indo-Pacific Ocean, including *P. kaleidos* by Kuitert & Randall (1995) from the Maldives and Indonesia; *P. severnsi* by Bellwood & Randall (2000), from the Maldives to the W. Pacific; *P. edwardi*, *P. polackorum*, and *P. labyrinthus* from the southwest Indian Ocean (Victor & Randall 2014, Connell *et al.* 2015, Victor & Edward 2016); and the deep-reef species *P. zeus* from Micronesia (Victor & Edward 2015). The genus comprises a set of small, fast-swimming wrasses, typically found on deeper slopes and in habitats dominated by rubble rather than live coral. They are distinguished morphologically by having chisel-like incisiform side teeth (unusual among the labrids) and fusiform bodies with relatively large scales. Terminal-phase (TP) males are larger, brightly colored individuals, while smaller initial-phase (IP) fish, usually females, are reddish orange.

Almost all the species in the genus have been sequenced for the mtDNA marker COI and most of the species fall into two broad species complexes: the *Pseudojuloides mesostigma* species complex with a set of five species that have TP males with quite different markings and flamboyant variations of blue stripes, and a complex containing *Pseudojuloides cerasinus* (Snyder, 1904) that exhibit similar markings, including a distinctive blue mid-lateral stripe immediately above a yellow or orange stripe and usually a prominent black posterior portion of the caudal fin. The latter species complex is wide ranging throughout the Indo-Pacific Ocean, from South Africa to Hawai‘i, and occupy mostly allopatric ranges. The color patterns of the TP males of various populations are different and there are relatively deep genetic divergences between populations. In this study, the Pacific populations are divided into four allopatric species.

Materials and Methods

Type specimens and specimens for comparisons are deposited at the Bernice P. Bishop Museum, Honolulu (BPBM) and the National Museum of Natural History, Washington, D.C. (USNM). In addition, ethanol-preserved specimens or tissues of a variety of congeners were collected by the author and various researchers for DNA sequencing from Bali (Indonesia), Philippines, Australia, Cook Islands, New Caledonia, Moorea (French Polynesia), Marquesas Islands, and Hawai‘i in the Pacific Ocean, and South Africa in the Indian Ocean, as well as obtained via the aquarium trade from the Philippines, Tonga, Vanuatu, Micronesia, and Tahiti (French Polynesia) in the Pacific Ocean and Kenya and Mauritius in the Indian Ocean (see Appendix 1).

DNA extractions were performed with the NucleoSpin96 (Machery-Nagel) kit according to manufacturer specifications under automation with a Biomek NX liquid-handling station (Beckman-Coulter) equipped with a filtration manifold. A 652-bp segment was amplified from the 5' region of the mitochondrial COI gene using a variety of primers (Ivanova *et al.* 2007). PCR amplifications were performed in 12.5 μ l volume including 6.25 μ l of 10% trehalose, 2 μ l of ultra pure water, 1.25 μ l of 10 \times PCR buffer (10 mM KCl, 10 mM (NH₄)₂SO₄, 20 mM Tris-HCl (pH8.8), 2 mM MgSO₄, 0.1% Triton X-100), 0.625 μ l of MgCl₂ (50 mM), 0.125 μ l of each primer (0.01 mM), 0.0625 μ l of each dNTP (10 mM), 0.0625 μ l of *Taq* DNA polymerase (New England Biolabs), and 2 μ l of template DNA. The PCR conditions consisted of 94°C for 2 min., 35 cycles of 94°C for 30 sec., 52°C for 40 sec., and 72°C for 1 min., with a final extension at 72°C for 10 min. Specimen information and barcode sequence data from this study were compiled using the Barcode of Life Data Systems (BOLD; Ratnasingham & Hebert 2007). The sequence data are publicly accessible on BOLD and GenBank. Sequence divergences were calculated using BOLD with the Kimura 2-parameter (K2P) model generating a mid-point rooted neighbor-joining (NJ) phenogram to provide a graphic representation of the species' sequence divergence. Genetic distances were calculated by the BOLD algorithm, both as K2P distances and uncorrected p-distances.

The length of specimens is given as standard length (SL). Other measurements follow the procedure described in Victor & Edward (2016). The upper rudimentary pectoral-fin ray is included in the count. Lateral-line scale counts include the last pored scale that overlaps the end of the hypural plate as +1. The count of gill rakers is made on the first gill arch and includes all rudiments. The range of counts and measurements for paratypes are shown in parentheses following data for the holotype.

Pseudojuloides splendens, n. sp.

Splendid Pencil Wrasse

urn:lsid:zoobank.org:act:73775C8D-9C72-4B58-A38B-864355608CCA

BOLD mtDNA barcode lineage BIN BOLD:AAG1199

Figures 1–6, 14; Table 1.

Pseudojuloides cerasinus [non Snyder] (some in part) Allen *et al.* 1977: 421 (Lord Howe Island); Ayling & Russell 1977: 172, fig. 7 (Uvea, New Caledonia & GBR, Australia); Randall & Randall 1981: 64–66 (W. Pacific); Masuda *et al.* 1984: 208, plates 202 H & I (Okinawa, Japan); Wass 1984: 22 (Samoa); Randall 1986: 226 (Enewetak, Marshall Islands); Myers 1988: 156 (Micronesia); Randall *et al.* 1990: 332, 2 figs. (GBR and Coral Sea, Australia); Francis 1993: 165 (Lord Howe Island & Australia, checklist); Ho *et al.* 1993: 9 (Taiwan); Kuitert 1993: 292 (Australia); Myers 1999: 201 (Micronesia, but figs. are *P. cerasinus* from Hawai‘i); Parenti & Randall 2000: 36 (list); Westneat 2001: 3402 (W. Pacific listing); Allen & Adrim 2003: 51 (Indonesia); Allen *et al.* 2003, 227 (W. Pacific); Myers & Donaldson 2003: 632 (Micronesia); Kuitert & Tonzuka 2004: 461, 3 figs. (W. Pacific); Lobel & Lobel 2004: 74 (Wake Island); Randall *et al.* 2004: 23 (Tonga); Randall 2005: 433, 2 figs. (S. Pacific, excluding French Polynesia); Allen *et al.* 2006: 1408 (Australia); Fricke & Kulbicki 2006: 343 (New Caledonia); Shao *et al.* 2008: 258 (Taiwan); Michael 2009: 308, fig. p. 307 (aquarium); Kuitert 2010: 333, 4 figs. (W. Pacific); Mundy *et al.* 2010: 36 (Jarvis and Palmyra, species ID?); Seeto & Baldwin 2010: 42 (Fiji); Fricke *et al.* 2011a: 402 (Vanuatu); Fricke *et al.* 2011b: 418 (New Caledonia); Allen & Erdmann 2012a: 715, 2 upper figs (East Indies); Allen & Erdmann 2012b: 55 (Bali, Indonesia); Nishiyama & Motomura 2012: 116–117, 7 figs. (Japan); Laboute & Grandperrin 2016: 463, 2 figs. (New Caledonia).

Holotype. BPBM 41337, 73.1 mm SL, TP male, Vanuatu, Efate, Pango, -17.778° , 168.295° , G. Norton & staff, 1 September 2013.

Paratypes. BPBM 41338, 51.8 mm SL, TP male, Vanuatu, Efate, Pango, -17.778° , 168.295° , G. Norton & staff, 1 September 2013; BPBM 26492, 89.6 mm SL, TP male, Philippines, Negros, 1.6 km south of Dumaguete City, 25 m, J.E. Randall, 4 August 1978; BPBM 41339, 7 (48.1–72.0 mm SL), New Caledonia, A. Teitelbaum, 22 January 2014; BPBM 22330, 67.1 mm SL, TP male, Japan, Ryukyu Islands, Okinawa, Sesoko Island, 2.5 m, J.E. Randall, 15 September 1977; BPBM 14614, 60.2 mm SL IP & 71.3 mm SL TP male, Fiji, Viti Levu, Mbengga Reef, 25 m, J.E. Randall, 11 March 1973; BPBM 23414, 56.6 mm SL, TP male, Taiwan, Pingtung, Nanguang, east of Houbihu harbor, 28 m, J.E. Randall, 19 July 1978.

Diagnosis. Dorsal-fin elements IX,11; anal-fin elements III,12; pectoral-fin rays 13; lateral-line scales 27 (+1 on caudal-fin base); no scales on head; gill rakers 14–17; a single pair of large, projecting, and slightly

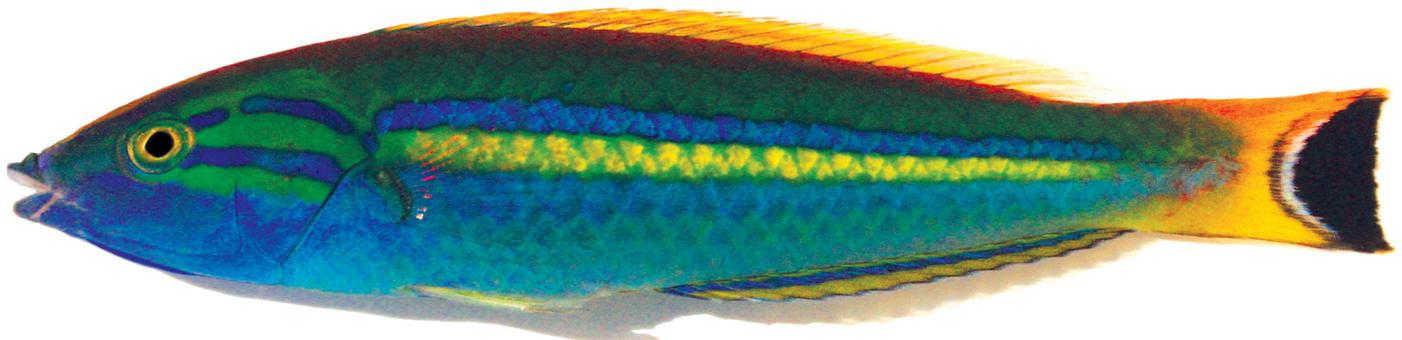


Figure 1. *Pseudojuloides splendens*, BPBM 41337, fresh holotype, TP male, 73.1 mm SL, Vanuatu (B.C. Victor).



Figure 2. *Pseudojuloides splendens*, TP male, Japan (K. Nishiyama).

recurved canine teeth anteriorly in each jaw, the upper pair slightly out-flaring, the lowers curving forward and fitting between uppers when mouth closed; a short irregular row of 3–9 chisel-like incisiform teeth on each side of upper and lower jaws, no canine posteriorly at corner of mouth; elongate body, body depth 4.0–4.3 in SL; moderately compressed, body width 1.8–2.4 in body depth; female IP orangish to reddish to pink, grading to whitish ventrally, snout yellowish and/or bluish, often with a dark spot at midline tip, no dark mark at front of dorsal fin, median fins yellowish; TP male with greenish upper body, bluish lower body, variably tan-pink along dorsal midline, distinctive mid-lateral blue stripe over yellow stripe along side of body; head green above, blue below, with two blue stripes behind eye extending across operculum, snout with a dark to tan band on anterior dorsal midline overlying a blue band and then a green band in front of eye; no dark mark at front of dorsal fin; caudal fin slightly rounded to truncate, with prominent distal black semicircle.

Description. Dorsal-fin elements IX,11; anal-fin elements III,12, all soft dorsal- and anal-fin segmented rays branched, last split to base; pectoral-fin rays 13, the first rudimentary, the second usually unbranched; pelvic-fin rays I,5; principal caudal-fin rays 14, the upper and lower unbranched; upper and lower procurrent caudal-fin rays 6; pored lateral-line scales 27 (+1 on caudal-fin base); gill rakers, including rudiments 14–17.

Body elongate (all measurements on types over 70 mm SL), the depth 4.2 (4.0–4.3) in SL, and moderately compressed, the width 1.9 (1.8–2.4) in depth; head length 3.0 (2.9–3.1) in SL; snout sharply pointed and short, its length 3.1 (3.1–3.4) in HL; orbit relatively small, diameter 5.6 (5.0–5.6) in HL; interorbital space broadly convex, the least bony width 5.4 (5.4–6.1) in HL; caudal peduncle short and narrow, the least depth 3.0 (2.9–3.2) in HL, caudal-peduncle length 3.5 (3.3–3.6) in HL.



Figure 3. *Pseudojuloides splendens*, IP female, New Caledonia (R. Bajol).



Figure 4. *Pseudojuloides splendens*, TP male, Great Barrier Reef, Australia (Sabine Penisson, AquaReefPhoto.com).

Mouth very small, terminal, corner of gape with closed jaws well anterior to anterior nostril; end of maxilla hidden, even when jaws gape. Lips moderately thick, upper lip grooved, lower lip with prominent ventral-projecting flap along side of jaw. A pair of large, moderately projecting, and slightly recurved canine teeth anteriorly in each jaw, upper pair slightly out-flaring, lowers curving forward and fitting between uppers when mouth closed; a short row of 3–9 irregularly placed chisel-like incisiform teeth along each side of upper and lower jaw; no canine tooth posteriorly on upper jaw. Upper preopercular margin free nearly to level of lower edge of orbit; lower margin free anterior to a vertical through anterior nostril. Gill rakers short, longest on first arch (at angle) about one-fifth to one-tenth length of longest gill filament. Nostrils small, in front of upper edge of orbit, anterior nostril in a short membranous tube elevated posteriorly, posterior nostril in advance of a vertical through front of orbit by a distance slightly less than internarial space. Pores on lower half of head comprise one over rear maxilla, then two anterior to orbit, followed by a curving suborbital series (counting up to rear mid-eye level) numbering 5–8 in single series; preopercular pores in a curved series after start of free edge near mandible, numbering 9–14 along free margin of preopercle up to rear mid-eye level, in a single (sometimes a shorter proximal second) series at distal tips of canals.

Scales thin and cycloid; scales on side of thorax less than half as high as largest scales on side of body, becoming still smaller ventroanteriorly; head naked except for small partially embedded scales on nape in irregular rows; median predorsal scales extending forward to slightly posterior to a vertical through upper free end of preopercular margin; fins naked except for several progressively smaller scales on basal region of caudal fin and mid-ventral scale projecting posteriorly from base of pelvic fins. Lateral line continuous, nearly following

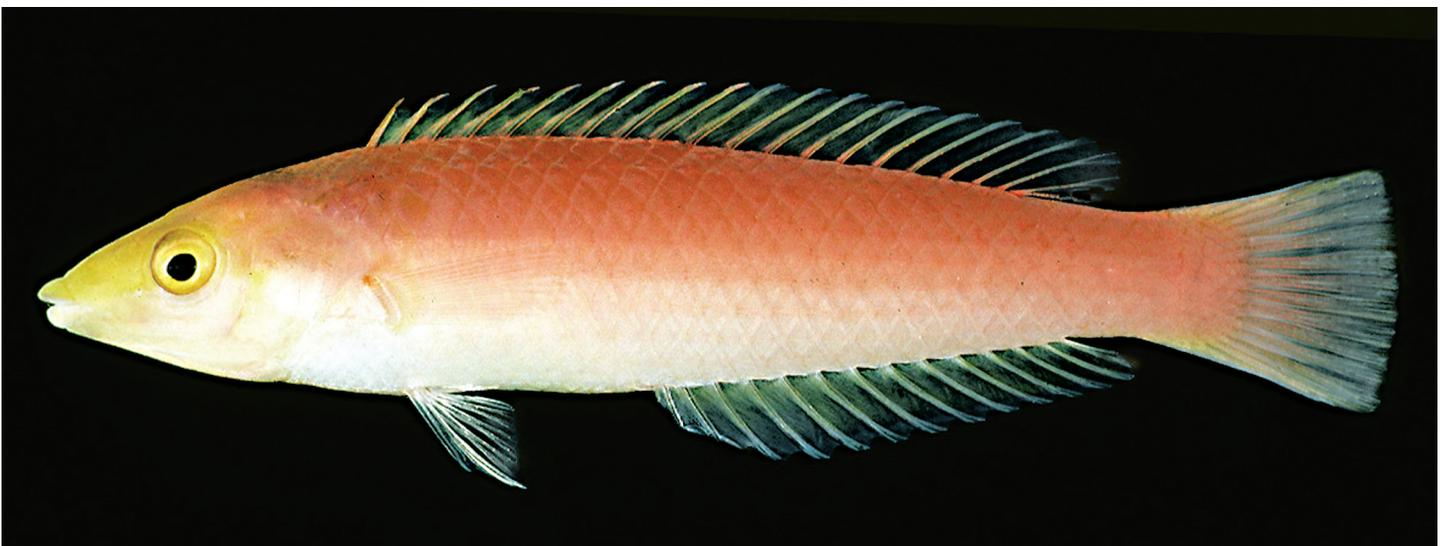


Figure 5. *Pseudojuloides splendens*, BPBM 28882, fresh IP female, 57 mm SL, Enewetak, Marshall Islands (J.E. Randall).



Figure 6. *Pseudojuloides splendens*, transitional phase (IP with TP stripes developing on head), New Caledonia (R. Bajol).

contour of back to about 18th pored scale, where deflected sharply ventrally to straight peduncular portion, single small pore per scale, last pored scale on caudal-fin base. Origin of dorsal fin above anterior edge of second lateral-line scale; dorsal-fin spines progressively longer, the first 6.4 (4.8–6.8) and the ninth 3.1 (3.0–3.7) in HL; longest dorsal-fin soft ray 2.8 (2.3–2.9) in HL; origin of anal fin below base of last dorsal-fin spine; first anal-fin spine very short, 17.3 (11.9–15.5) in HL; second anal-fin spine 5.8 (5.9–6.7) in HL; third anal-fin spine 4.6 (4.4–4.7) in HL; longest anal-fin soft ray 3.1 (2.9–3.5) in HL; caudal-fin length 1.7 (1.6–1.8) in HL; second or third pectoral-fin ray usually longest, 2.2 (2.0–2.2) in HL; pelvic fins short, 2.1 (2.0–2.2) in HL.

Color in life. (Figs. 1–6) TP males greenish above and bluish below with a mid-lateral blue stripe running from behind operculum to mid-base of caudal fin, overlying a parallel, equally wide, yellow stripe; a variable broad band of brown to orange along dorsal midline; upper head yellowish green, lower head blue, a variable dark and/or tan dorsal midline band on snout; stripes on snout in front of eye brownish dorsally, then blue and green; two blue stripes behind eye crossing operculum; dorsal and anal fins yellowish to greenish with two blue stripes, one along lower central portion and second along margin of fins, dorsal-fin-spine tips orange; caudal fin with a blue semicircular line at mid-portion outlining a black half-moon rear portion of fin, ending with a thin blue edge. Female IP orangish to reddish or pink, grading to whitish ventrally, snout yellowish, median fins yellowish, pectoral fin translucent. Juveniles uniformly reddish orange with yellowish snout and median fins.

Color in alcohol. TP male grayish brown dorsally grading to pale ventrally with some residual blue in lateral stripes. Fins are translucent. IP fish are uniform yellowish with no markings.

Etymology. Named for the splendid color pattern of the TP male, the specific epithet is a masculine singular adjective in the nominative case.

Distribution. The new species occurs widely in the tropical and sub-tropical western Pacific Ocean region, mostly associated with offshore coral-reef areas in relatively deep-water habitats over rubble bottoms. The species extends into southern Japan in the north, to New South Wales in Australia in the south, and in the W. Pacific island chains ranging from Maug Island in the Northern Mariana Islands south to Lord Howe Island, and eastward to Kwajalein Atoll in the north Pacific and to Samoa in the south Pacific (see map in Fig. 13).

Comparisons. (see Fig. 14 and Table 2) TP males of *P. splendens* differ from other species in the complex primarily by having two blue stripes on the head behind the eye. Additional differences include full-length thick blue over thick yellow stripes along the sides of the body (shared only with *P. cerasinus*), and no black spots on the first two dorsal-fin spinous membranes (shared only with *P. kaleidos*, *P. polackorum*, and some *P. cerasinus*). A photograph of a TP male from Kwajalein Atoll shows the two blue stripes on the head joined at the rear of the opercle, but rare individuals photographed in Japan and southeastern Australia also show that variation and it does not suggest a different population.

TABLE 1

Proportional measurements of type specimens of *Pseudojuloides splendens*, n. sp. and *Pseudojuloides polynesica*, n. sp. as percentages of the standard length

	<i>Pseudojuloides splendens</i>						<i>Pseudojuloides polynesica</i>					
	holotype	paratypes					holotype	paratypes				
		BPBM					USNM	BPBM				
	41337	26492	41339	41339	14614	22330	424051	11583	11614	11614	41340	41340
	TP	TP	TP	TP	TP	TP	TP	TP	TP	TP	TP	IP
Standard length (mm)	73.1	89.6	72.0	70.0	71.3	67.1	79.0	61.2	63.6	64.4	77.5	69.3
Body depth	23.9	24.9	24.6	23.0	23.8	23.8	23.2	24.7	23.0	24.1	23.1	21.4
Body width	12.4	10.6	12.2	12.6	10.7	9.8	11.9	9.6	10.8	12.3	-	12.1
Head length	33.1	33.1	33.5	33.9	32.7	34.4	32.3	30.6	31.1	31.7	31.6	30.6
Snout length	10.5	10.9	9.7	10.6	10.5	10.0	10.8	9.2	10.7	10.2	10.6	9.8
Orbit diameter	5.9	5.9	6.7	6.4	6.0	6.7	5.3	6.2	6.0	6.1	6.1	6.5
Interorbital width	6.2	6.1	6.1	5.9	5.8	5.7	5.8	6.0	6.3	6.5	5.4	5.5
Caudal-peduncle depth	11.2	11.0	11.0	11.0	11.4	10.7	11.5	11.9	11.9	11.6	11.2	11.0
Caudal-peduncle length	9.4	9.3	10.3	9.7	9.1	10.0	10.6	8.5	8.3	8.2	8.1	9.2
Predorsal length	32.0	32.3	32.2	32.9	30.6	32.0	32.3	31.4	31.9	31.5	31.5	30.6
Preanal length	56.4	57.0	57.2	57.6	58.8	58.3	55.6	54.2	54.2	53.4	56.4	55.6
Prepelvic length	36.5	34.6	36.7	38.0	34.1	37.6	33.3	33.7	35.2	33.4	37.3	35.4
Base of dorsal fin	57.2	59.2	54.9	56.9	55.8	57.5	56.1	57.4	58.3	59.2	58.2	56.0
First dorsal-fin spine	5.2	6.9	5.6	6.7	5.0	5.1	5.8	5.7	6.3	6.2	5.9	6.5
Ninth dorsal-fin spine	10.7	10.6	9.3	10.1	10.8	9.4	8.5	9.3	9.4	9.5	9.5	9.7
Longest dorsal-fin ray	11.8	12.4	12.1	12.1	14.0	12.1	11.8	12.1	12.3	12.0	12.9	11.3
Base of anal fin	36.8	35.5	36.8	36.3	35.2	31.7	34.9	37.9	37.7	38.0	36.8	35.9
First anal-fin spine	1.9	2.8	2.2	2.6	2.1	2.2	1.8	2.0	2.8	2.0	2.2	2.6
Second anal-fin spine	5.7	5.2	5.7	5.4	4.9	5.7	4.2	4.9	5.3	5.0	5.3	5.1
Third anal-fin spine	7.3	7.5	7.4	7.3	7.3	7.3	6.5	7.7	8.3	7.5	8.1	7.4
Longest anal-fin ray	10.7	12.4	9.7	10.1	11.1	9.8	10.1	10.1	11.9	10.6	10.7	10.1
Caudal-fin length	19.6	19.9	19.4	20.6	18.8	19.5	19.6	21.4	22.5	20.7	19.7	19.3
Pectoral-fin length	15.3	15.3	14.9	17.3	16.0	16.4	15.8	16.5	17.6	16.5	-	15.0
Pelvic-fin-spine length	10.8	10.6	9.4	10.1	11.1	9.8	12.3	10.8	10.8	10.1	10.3	11.3
Pelvic-fin length	16.1	16.7	16.4	16.6	16.3	15.4	17.8	17.5	16.0	16.1	15.6	16.6

Pseudojuloides polynesica, n. sp.

Polynesian Pencil Wrasse

urn:lsid:zoobank.org:act:6CD6C244-04B6-4F5B-81FA-B98EE251C2B9

BOLD mtDNA barcode lineage BIN BOLD:ABY7201

Figures 7–12, 14; Table 1.

Leptojulius cerasinus [non Snyder] Randall 1973: 197 (checklist, Society Islands).

Pseudojuloides cerasinus [non Snyder] (some in part) Randall & Randall 1981: 64–66 (French Polynesia and Cook Islands); Randall 1985: 475 (French Polynesia); Randall 2005: 433, 2 figs. (French Polynesia); Bacchet *et al.* 2016: 409 (Society, Tuamotu, and Austral Islands); Siu *et al.* 2017: 269 (Moorea, other Society, Tuamotu, and Austral Islands).

Holotype. USNM 424051, 79.0 mm SL, TP male, French Polynesia, Austral Islands, Rimatara, outer reef slope, -22.6406° , -152.822° , AUST-2013-17, field number AUST-449, J.T. Williams, E. Delrieu-Trottin & P. Sasal, 18 April 2013.

Paratypes. BPBM 11583, 47.6 mm SL IP & 61.2 mm SL TP male, French Polynesia, Society Islands, Tahiti, Popote Bay, Papara, about 40 m, J.E. Randall *et al.*, 31 March 1971; BPBM 11614, 63.6 & 64.4 mm SL, TP males, French Polynesia, Society Islands, Huahine, Fare Bay, Teffaa Point, about 30 m, J.E. Randall, 19 March 1971; BPBM 14973, 50.8 mm SL, IP, French Polynesia, Society Islands, Tetiaroa, Rimatu'u Islet, about 70 m, J.E. Randall & R. McNair, 19 April 1973; BPBM 41340, 69.3 mm SL IP & 77.5 mm SL TP male, aquarium trade (via J.M.B. Edward), French Polynesia, Society Islands, Tahiti, 9 April 2015.

Non-type Material. BPBM 13918, 65.8 mm SL, IP, Cook Islands, Rarotonga, northwest side, Black Rock, about 35 m, J.E. Randall, 10 March 1971; BPBM 40307, 66.3 mm SL IP & 85.1 mm SL TP male, Line Islands, Kiritimati Atoll, east of north tip, about 20 m, B.D. Greene, 26 July 2005; BPBM 37553, 76.9 mm SL TP male, Line Islands, Kiritimati Atoll, north of Bay of Wrecks, about 30 m, D.R. Robertson, 1 September 1996.

Diagnosis. Dorsal-fin elements IX,11; anal-fin elements III,12; pectoral-fin rays 13; lateral-line scales 27 (+1 on caudal-fin base); no scales on head; gill rakers 14–17; a single pair of large, projecting, and slightly recurved canine teeth anteriorly in each jaw, the upper pair slightly out-flaring, the lowers curving forward and fitting between uppers when mouth closed; a short irregular row of 3–7 chisel-like incisiform teeth on each side of upper and lower jaws, no canine posteriorly at corner of mouth; elongate body, body depth 4.1–4.7 in SL; moderately compressed, body width 1.8–2.6 in body depth; female IP orangish to reddish to pink, grading to whitish ventrally, snout yellowish, first two dorsal-fin spinous membranes black, edged distally with yellow-orange margin, median



Figure 7. *Pseudojuloides polynesica*, BPBM 41340, paratype, TP male, 77.5 mm SL, aquarium trade, Tahiti (V. Altimirano).



Figure 8. *Pseudojuloides polynesica*, upper: fresh holotype, USNM 424051, TP male, 79.0 mm SL, Austral Islands, French Polynesia (J.T. Williams); lower: fresh paratype, BPBM 41340, IP, 69.3 mm SL, aquarium trade, Tahiti (B.C. Victor).

fins yellowish; TP male with greenish upper body, bluish lower body, distinctive mid-lateral blue stripe over green stripe along side of body; head yellowish above, blue below, with one blue stripe behind eye extending across operculum and usually dipping down to meet upper pectoral-fin base, upper snout yellowish with no stripes in front of eye; first two dorsal-fin spinous membranes black; caudal fin slightly rounded to truncate, with prominent medial blue bar followed by a greenish or black area and a blue margin.

Description. Dorsal-fin elements IX,11; anal-fin elements III,12, all soft dorsal- and anal-fin segmented rays branched, last split to base; pectoral-fin rays 13, the first rudimentary, the second usually unbranched; pelvic-fin rays I,5; principal caudal-fin rays 14, the upper and lower unbranched; upper and lower procurent caudal-fin rays 6; pored lateral-line scales 27 (+1 on caudal-fin base); gill rakers, including rudiments 14–17.

Body elongate (all measurements on types over 70 mm SL), the depth 4.3 (4.1–4.7) in SL, and moderately compressed, the width 1.9 (1.8–2.6) in depth; head length 3.1 (3.2–3.3) in SL; snout sharply pointed and short, its length 3.0 (2.9–3.3) in HL; orbit relatively small, diameter 6.1 (4.7–5.2) in HL; interorbital space broadly convex, the least bony width 5.5 (4.9–5.8) in HL; caudal peduncle short and narrow, the least depth 2.8 (2.6–2.8) in HL, caudal-peduncle length 3.0 (3.3–3.9) in HL.

Mouth very small, terminal, corner of gape with closed jaws well anterior to anterior nostril; end of maxilla hidden, even when jaws gape. Lips moderately thick, upper lip grooved, lower lip with prominent ventral-projecting flap along side of jaw. A pair of large, moderately projecting, and slightly recurved canine teeth anteriorly in each jaw, upper pair slightly out-flaring, lowers curving forward and fitting between uppers when mouth closed; a short row of 3–7 irregularly placed chisel-like incisiform teeth along each side of upper and lower jaw; no canine tooth posteriorly on upper jaw. Upper preopercular margin free nearly to level of lower edge of orbit; lower margin free anterior to a vertical through anterior nostril. Gill rakers short, longest on first arch (at angle) about one-fifth to one-tenth length of longest gill filament. Nostrils small, in front of upper edge of orbit, anterior nostril in a short membranous tube elevated posteriorly, posterior nostril in advance of a vertical through front of orbit by a distance slightly less than internarial space. Pores on lower half of head comprise one over rear maxilla, then two anterior to orbit, followed by a curving suborbital series (counting up to rear mid-eye level) numbering 5–7 in single series; preopercular pores in a curved series after start of free edge near mandible, numbering 11–13 along free margin of preopercle up to rear mid-eye level, in a single (sometimes a shorter proximal second) series at distal tips of canals.

Scales thin and cycloid; scales on side of thorax less than half as high as largest scales on side of body, becoming still smaller ventroanteriorly; head naked except for small partially embedded scales on nape in

irregular rows; median predorsal scales extending forward to slightly posterior to a vertical through upper free end of preopercular margin; fins naked except for several progressively smaller scales on basal region of caudal fin and mid-ventral scale projecting posteriorly from base of pelvic fins. Lateral line continuous, nearly following contour of back to about 18th pored scale, where deflected sharply ventrally to straight peduncular portion, single small pore per scale, last pored scale on caudal-fin base. Origin of dorsal fin above anterior edge of second lateral-line scale; dorsal-fin spines progressively longer, the first 5.5 (4.7–5.3) and the ninth 3.8 (3.2–3.3) in HL; longest dorsal-fin soft ray 2.7 (2.5–2.7) in HL; origin of anal fin below base of last dorsal-fin spine; first anal-fin spine very short, 18.2 (11.0–15.7) in HL; second anal-fin spine 7.7 (5.8–6.4) in HL; third anal-fin spine 5.0 (3.7–4.3) in HL; longest anal-fin soft ray 3.2 (2.6–3.0) in HL; caudal-fin length 1.6 (1.4–1.6) in HL; second or third pectoral-fin ray usually longest, 2.0 (1.8–2.0) in HL; pelvic fins short, 1.8 (1.8–2.0) in HL.

Color in life. (Figs. 7–12) TP males greenish above and bluish below with a mid-lateral blue stripe running from behind operculum to mid-base of caudal fin, overlying an equally wide greenish stripe that is inconspicuous; head yellowish green above and bluish below, with a thick blue stripe behind mideye, usually curving down to meet upper pectoral-fin base; no stripes on snout forward of eye; dorsal fin with prominent black basal area on first two spinous membranes, remainder of fin and anal fin greenish to yellowish with blue stripes along lower central portion and margin of fins, dorsal-fin-spine tips orange; caudal fin with medial blue bar followed by a darker area that is yellowish green, dusky, or black in some live individuals (see Fig. 9). Some TP males in captivity develop a blanced color pattern of yellow and purple, where upper body is pale bluish

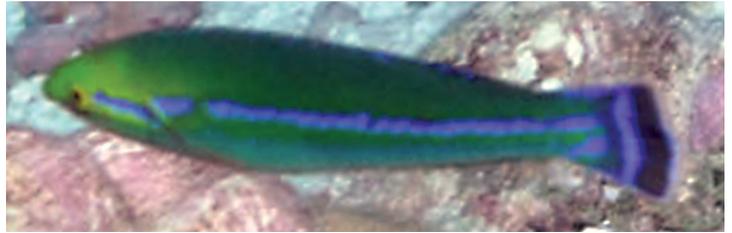


Figure 9. *Pseudojuloides polynesica*, TP male underwater, with a black caudal fin, Rangiroa, French Polynesia (K. Muramatsu).



Figure 10. *Pseudojuloides polynesica*, fresh paratypes, upper: BPBM 11583, TP male, 63 mm SL, Papara, Tahiti, French Polynesia (J.E. Randall); lower: BPBM 11583, IP female, 50 mm SL, Papara, Tahiti, French Polynesia (J.E. Randall).



Figure 11. *Pseudojuloides polynesica*, aquarium-trade specimens, TP male above, IP female below (aqualovers2011.com).

yellow and ventral body is yellowish to pale and mid-lateral stripe is purple (Fig. 11). Female IP orangish to reddish or pink, grading to whitish ventrally, snout yellowish, first two dorsal-fin spinous membranes mostly black with a distal yellow-orange margin, remaining median fins yellowish, pectoral fin translucent. Juveniles uniformly reddish orange with yellowish snout tip and median fins (Fig. 12).

Color in alcohol. TP male grayish brown dorsally grading to pale ventrally, with two black spots on first two dorsal-fin spinous membranes; there is some residual blue in lateral stripes. Fins are translucent. IP fish are uniform yellowish with two black spots on first two dorsal-fin spinous membranes; juvenile uniform yellowish.

Etymology. Named for the type origin in French Polynesia. The specific epithet is a noun in apposition.

Distribution. The new species occurs in French Polynesia (but not Marquesas Islands), at Tahiti, Moorea, and Rangiroa in the Tuamotu Archipelago, as well as ranging south to the Austral Islands, west to the Cook Islands (where Randall & Randall [1981] report an IP fish with the diagnostic two dorsal-fin black spots), and north to the



Figure 12. *Pseudojuloides polynesica*, USNM 395610, fresh juvenile, 24.4 mm SL, Moorea, French Polynesia (J.T. Williams).

Line Islands, at Kiritimati Atoll. The Kiritimati records comprise TP males collected twice (BPBM 37553 in 1996 and BPBM 40307 in 2005), both showing the diagnostic single stripe behind the eye, two black spots at the front of the dorsal fin, and no, or an indistinct, black rear portion on the caudal fin. In addition, an IP female from the latter collection also has the diagnostic two black spots at the front of the dorsal fin. The Kiritimati specimens are not considered type specimens due to the long distance from the type location and the absence of DNA sequences for comparison. The Cook Islands specimen is not considered a type specimen due to the lack of a TP male from the location and the absence of DNA sequences for comparison.

Comparisons. (Fig. 14 and Table 2) TP males of *P. polynesica* differ from other species in the complex primarily by having a uniform yellowish snout in front of the eye. Additional differences include a single blue stripe on the head behind the eye (shared only with *P. cerasinus*), two black spots on the first two dorsal-fin spinous membranes (shared only with *P. pyrius*), no yellow or orange mid-lateral stripe (shared only with *P. kaleidos*), and often no black rear portion of the caudal fin (shared only with *P. kaleidos* and *P. pyrius*). IP females are distinctive in also having the two black spots at the front of the dorsal fin, a feature not exhibited by the IP phase of any other species in the complex.

The *Pseudojuloides cerasinus* species complex

Biogeography. The species of the *P. cerasinus* complex extend throughout the Indo-Pacific region, from South Africa to the Hawaiian Islands, occupying almost all areas with coral reefs, except the northwestern Indian Ocean (Red Sea, Oman, Persian Gulf, and Seychelles), western Australia, and Easter Island in the far SE Pacific Ocean (Fig. 13). They do not extend into the eastern Pacific Ocean, with anecdotal reports of *P. cerasinus* (as IP phase) in the region almost certainly representing an unrelated labrid, *Sagittalarva inornatus* (Gilbert, 1890), recently redescribed (Victor *et al.* 2013). The species' distributions are allopatric, except for potential overlap of *P. kaleidos* and *P. splendens* in Indonesia (Allen 2002, Allen & Erdmann 2012a), with sightings of *P. kaleidos* in Halmahera and West Papua and, in particular, documented from Bali (Allen *et al.* 2012b); interestingly, Bali is known as a focus of overlap of Indian Ocean and W. Pacific sibling species for a number of other labrid species (Kuitert 2010, Victor 2015).

Comparisons. Within the complex, species differ primarily in color patterns on the TP male (Figs. 14 & 15; Table 2), with only *P. polynesica* showing a difference in the markings on females, i.e. the black marks edged with orange on the first two dorsal-fin spine membranes (which persist on TP males). The predominance of TP-male color-pattern variations is a typical finding among closely related species-complexes among Indo-Pacific reef fishes, particularly the brightly colored labrids that have elaborate male courtship displays, e.g. *Cirrhilabrus* (Allen & Hammer 2016, Tea *et al.* 2016, Victor 2016, Walsh *et al.* 2017), *Paracheilinus* (Allen *et al.* 2016), and

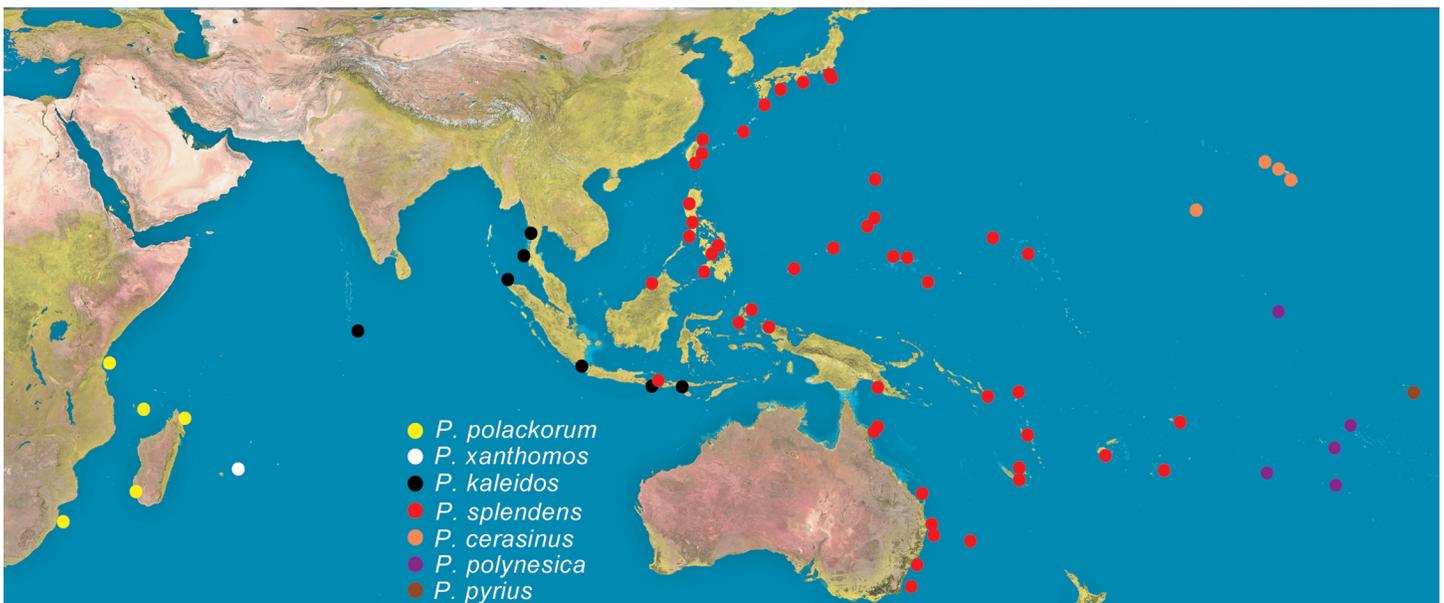


Figure 13. Indo-Pacific distribution of members of the *Pseudojuloides cerasinus* species complex.

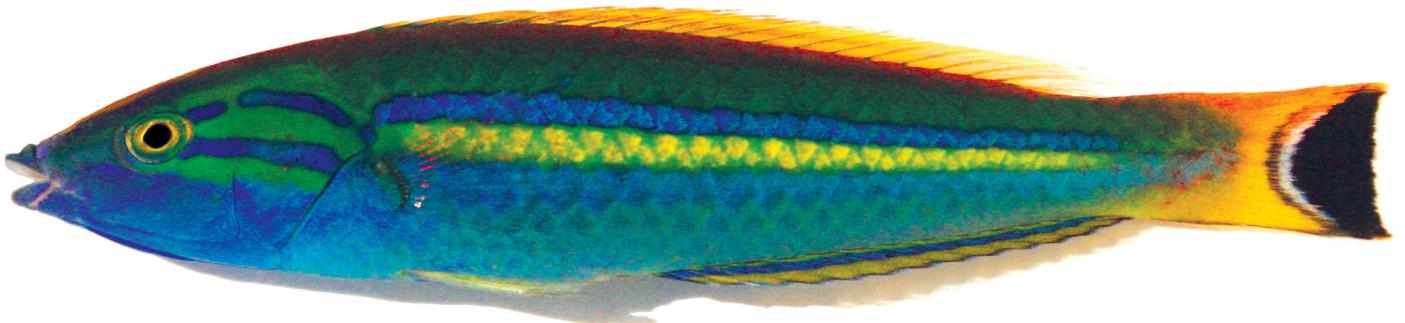


Figure 14. *Pseudojuloides cerasinus* species complex in the Pacific Ocean, TP males, top to bottom: *P. cerasinus*, Hawai'i (B. Pardau); *P. splendens*, Vanuatu (B.C. Victor); *P. polynesica*, Tahiti (J.T. Williams); *P. pyrius*, Marquesas Islands (J.E. Randall).



Figure 15. *Pseudojuloides cerasinus* species complex in the Indian Ocean, TP males, top to bottom: *P. xanthomos*, Mauritius via aquarium (Y.K. Tea); *P. polackorum*, Kenya via aquarium (B.C. Victor); *P. kaleidos*, Indian Ocean via aquarium (S. Pennison).

TABLE 2

Color-pattern features of the *Pseudojuloides cerasinus* species complex

Species	upper snout stripe series	operculum stripes	blue body stripe	yellow body stripe	dorsal mid-line stripe	anterior dorsal fin spots	black caudal-fin
<i>P. cerasinus</i>	tan-blue-green	1 blue	thick	thick	tan	–/1	+
<i>P. splendens</i>	tan-blue-green	2 blue	thick	thick	tan	–	+
<i>P. polynesica</i>	none	1 blue	blue/purple	indistinct	–	2	+/-
<i>P. pyrius</i>	none	none	none	none	–	2	–
<i>P. xanthomos</i>	(dark)-blue-yellow	1 yellow	short	short	–	1	+
<i>P. polackorum</i>	none	line only	thin	wide (orange)	–	–	+
<i>P. kaleidos</i>	dark-blue-green	line only	thick	(green)	lavender	–	–

Pseudocoris (Randall *et al.* 2015). The first characters expected to diverge in isolation would be in aspects of mate choice, and colorful displays would be most amenable to changes due to sexual selection.

The color pattern on TP males in the complex vary mostly in the arrangement of stripes on the head, notably in the blue stripes behind the eye (either two, one, or none); stripes vs. no stripes on the upper snout in front of the eye; the thickness of the blue lateral stripe and the intensity and shade of the yellow or orange lateral stripe (and the length of the stripes, i.e. shortened in *P. xanthomos*); the color, if any, of a dorsal midline stripe; the presence or absence of black spots on the first and/or second dorsal-fin spine membranes; and the presence or absence of the rear semicircular black portion of the caudal fin (Table 2). The Marquesan species *P. pyrius* is a marked exception, with the TP male being bright orange and missing most of the markings shared by all the other members of the complex. The TP color of *P. pyrius* is more similar to the female color for the complex, but with an added highly contrasted black-and-white edge to the dorsal, anal, and caudal fins, differentiating the male from the females.

Meristic differences are not significant in the species complex, although Randall & Randall (1981) report that *P. pyrius* have one or two fewer modal gill-raker totals, however sample sizes are small. Morphometric differences, if any, are more difficult to detect, especially with small samples, varying sizes of some species (allometric variation), and observer differences in measuring protocols. Nevertheless, Randall & Randall (1981) document that the pelvic fins of *P. pyrius* TP males (reaching past the anus) are relatively longer than those of TP males of relatives (see Fig. 14).

DNA Comparisons. The neighbor-joining phenetic tree based on the COI mtDNA sequences of all 7 species in the *P. cerasinus* complex, following the Kimura two-parameter model (K2P) generated by BOLD (the Barcode of Life Database), shows relatively deep divergences between species and relatively small differences within species, except for a high maximum intraspecific divergence of *P. splendens* of 1.74%, driven by a single variant sequence (Fig. 16 and Table 3). The 7 species' mtDNA lineages diverge from 2.08% to 11.34% (K2P; 2.04% to

TABLE 3
**Variation in mtDNA COI sequences of the 7 species
in the *Pseudojuloides cerasinus* species complex**
Minimum Interspecific and Maximum Intraspecific Distances (%)

	K2P distances						
	<i>cer</i>	<i>kal</i>	<i>pola</i>	<i>poly</i>	<i>pyr</i>	<i>splen</i>	<i>xan</i>
<i>P. cerasinus</i>	0.18						
<i>P. kaleidos</i>	10.40	NA					
<i>P. polackorum</i>	9.48	8.42	0.31				
<i>P. polynesica</i> , n. sp.	2.08	10.00	9.86	0.38			
<i>P. pyrius</i>	3.50	10.71	9.47	3.81	NA		
<i>P. splendens</i> , n. sp.	5.63	11.11	8.41	5.48	5.30	1.74	
<i>P. xanthomos</i>	11.34	4.48	7.50	11.07	11.23	9.96	NA

	P-distances (uncorrected pairwise)						
	<i>cer</i>	<i>kal</i>	<i>pola</i>	<i>poly</i>	<i>pyr</i>	<i>splen</i>	<i>xan</i>
<i>P. cerasinus</i>	0.18						
<i>P. kaleidos</i>	9.55	NA					
<i>P. polackorum</i>	8.74	7.83	0.31				
<i>P. polynesica</i> , n. sp.	2.04	9.22	9.06	0.38			
<i>P. pyrius</i>	3.40	9.83	8.76	3.69	NA		
<i>P. splendens</i> , n. sp.	5.35	10.14	7.83	5.22	5.07	1.72	
<i>P. xanthomos</i>	10.36	4.30	7.07	10.14	10.29	9.22	NA

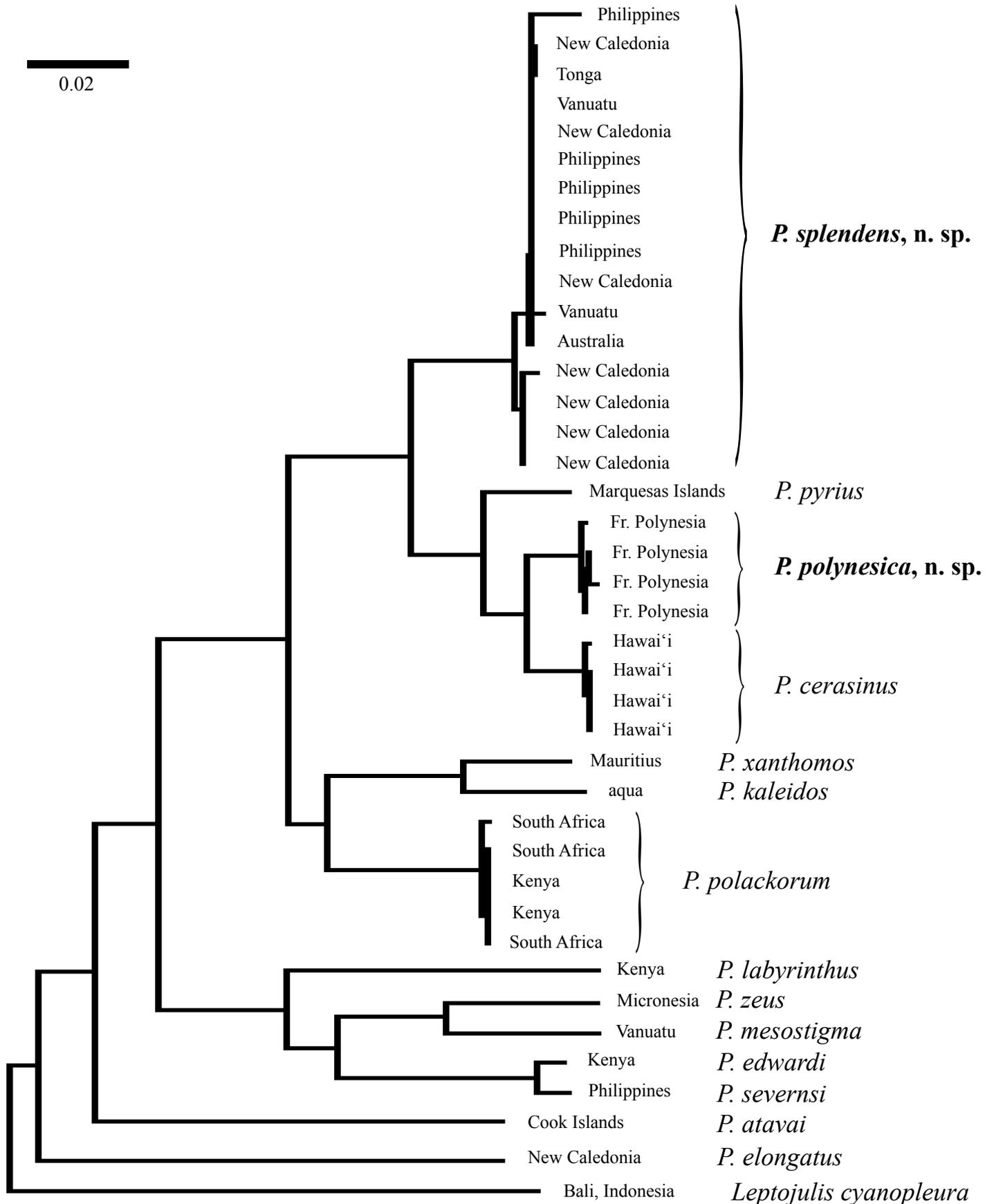


Figure 16. The neighbor-joining phenetic tree of *Pseudojuloides* following the Kimura two-parameter model (K2P) generated by BOLD (Barcode of Life Database). The scale bar at left represents a 2% sequence difference. Collection locations for specimens are indicated, and *Leptojuulis cyanopleura* is used as an outgroup. The “aqua” label indicates an aquarium-trade specimen of unknown provenance. GenBank accession numbers and collection data for the sequences in the tree are listed in Appendix 1.

10.36% uncorrected pairwise), a similar range of divergences to many other labrid species complexes in the Indo-Pacific Ocean.

There is some genetic similarity between neighboring species, with the closest lineages being *P. cerasinus*, *P. polynesica*, and *P. pyrius*, the three adjacent central Pacific species, all with black spots at the front of the dorsal fin (about 2–4% divergence). The Indian Ocean split from the Pacific species is the oldest, with about 10% divergence between oceans; the maximum divergence within the complex is between *P. xanthomos* from Mauritius and *P. cerasinus* from Hawai‘i.

It is notable that *P. pyrius* from the Marquesas Islands is very different phenotypically from the remaining species of the complex, having a flame-reddish TP male. However, the species is very close genetically to the adjacent species from nearby central French Polynesia (3.81% K2P; 3.69% uncorrected pairwise) and Hawai‘i (3.50% K2P; 3.40% uncorrected pairwise). This pattern of phenotypic difference not correlating with genetic divergence within species complexes has been previously noted and is frequent among coral reef fishes (Victor 2015). The Marquesas Islands have been noted to be a focus of endemism (Randall & Earle 2000, Delrieu-Trottin *et al.* 2015), where local species have adapted to high turbidity and undergone recent strong disruptive selection (Gaither *et al.* 2015).

Lastly, the set of DNA lineages representing the species complex illustrate a common problem in recent taxonomy, where the validity of species or, more commonly, genera (sometimes even families, such as Scaridae) are brought into question by the creation of paraphyly in the remaining lineages in a tree of related lineages. If taxa represent complete sets of genetic lineages that are monophyletic, a generally agreed-upon point in modern evolution-based species concepts, then a paraphyletic taxon made up of two or more lineages broken up by another named taxon between those lineages is invalid due to paraphyly, i.e. the former taxon no longer represents the complete set of lineages that are monophyletic. In the case of the *P. cerasinus* species complex, the occurrence of the very different *P. pyrius*, nested within lineages that are very similar to each other in color pattern, requires that the surrounding lineages be recognized as different species, if invalidity due to paraphyly is to be avoided. Fortunately, the color patterns of the various lineages within the species complex are sufficiently different to support species-level distinctions, but, if they were not, a paradox would develop where the morphological species concept would conflict with evolutionary species concepts and we would be in an intractable taxonomic quandary.

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Appendix 1. Specimen data and GenBank accession numbers for the mtDNA COI barcode sequences used to generate the phenogram in Fig. 16, following the order in the tree. Holotypes in bold.

Genus	species	Collection site	Voucher	GenBank #	Collector/Source
<i>Pseudojuloides</i>	<i>splendens</i> , n. sp.	Batangas, Philippines	USNM 436374	KY250422	J. Williams,USNM
<i>Pseudojuloides</i>	<i>splendens</i> , n. sp.	New Caledonia	BPBM 41339	KP975962	A. Teitelbaum
<i>Pseudojuloides</i>	<i>splendens</i> , n. sp.	Tonga	je144pc	KP976010	J. Edward/aq. trade
<i>Pseudojuloides</i>	<i>splendens</i> , n. sp.	Vanuatu	BPBM 41338	KP975985	G. Norton/aq. trade
<i>Pseudojuloides</i>	<i>splendens</i> , n. sp.	New Caledonia	BPBM 41339	KP975999	A. Teitelbaum
<i>Pseudojuloides</i>	<i>splendens</i> , n. sp.	Batangas, Philippines	USNM 431907	KY250423	J. Williams,USNM
<i>Pseudojuloides</i>	<i>splendens</i> , n. sp.	Philippines	je13pc	KP976001	J. Edward/aq. trade
<i>Pseudojuloides</i>	<i>splendens</i> , n. sp.	Batangas, Philippines	USNM 431819	KY250426	J. Williams,USNM
<i>Pseudojuloides</i>	<i>splendens</i> , n. sp.	Batangas, Philippines	USNM 436300	KY250425	J. Williams,USNM
<i>Pseudojuloides</i>	<i>splendens</i> , n. sp.	New Caledonia	BPBM 41339	MF120963	A. Teitelbaum
<i>Pseudojuloides</i>	<i>splendens</i>, n. sp.	Vanuatu	BPBM 41337	KP975986	G. Norton/aq. trade
<i>Pseudojuloides</i>	<i>splendens</i> , n. sp.	Lizard Isl., GBR, Australia	AMS I.40665-033	KY079340	J. Leis/D. Bellwood
<i>Pseudojuloides</i>	<i>splendens</i> , n. sp.	New Caledonia	BPBM 41339	MF120951	A. Teitelbaum
<i>Pseudojuloides</i>	<i>splendens</i> , n. sp.	New Caledonia	BPBM 41339	MF120952	A. Teitelbaum
<i>Pseudojuloides</i>	<i>splendens</i> , n. sp.	New Caledonia	BPBM 41339	KP976005	A. Teitelbaum
<i>Pseudojuloides</i>	<i>splendens</i> , n. sp.	New Caledonia	BPBM 41339	KP975966	A. Teitelbaum
<i>Pseudojuloides</i>	<i>pyrius</i>	Marquesas Islands	USNM 409424	KJ591650	J. Williams/S. Planes
<i>Pseudojuloides</i>	<i>polynésica</i> , n. sp.	Tahiti	BPBM 41340	KT352038	J. Edward/aq. trade
<i>Pseudojuloides</i>	<i>polynésica</i> , n. sp.	Tahiti	BPBM 41340	KT352056	J. Edward/aq. trade
<i>Pseudojuloides</i>	<i>polynésica</i> , n. sp.	Moorea, French Polynesia	Bellwood M133	JQ839572	D. Bellwood, JCU
<i>Pseudojuloides</i>	<i>polynésica</i>, n. sp.	Austral Islands, FRP	USNM 424051	KY250424	J. Williams, USNM
<i>Pseudojuloides</i>	<i>cerasinus</i>	Hawai'i	h83pc260	JQ839571	B. Victor
<i>Pseudojuloides</i>	<i>cerasinus</i>	Hawai'i	FLHI398-09	KJ591646	D. Carlon/A. Faucci
<i>Pseudojuloides</i>	<i>cerasinus</i>	Hawai'i	FLHI318-09	KJ591645	D. Carlon/A. Faucci
<i>Pseudojuloides</i>	<i>cerasinus</i>	Hawai'i	h83pc370	JQ839570	B. Victor
<i>Pseudojuloides</i>	<i>xanthomos</i>	Mauritius	dej13px360	KJ591657	DeJong Marinelife
<i>Pseudojuloides</i>	<i>kaleidos</i>	Aquarium trade	je14pk610	KP975974	J. Edward/aq. trade
<i>Pseudojuloides</i>	<i>polackorum</i>	Kwa-Zulu, South Africa	ADC11_220.51	KF489719	A. Connell/SAIAB
<i>Pseudojuloides</i>	<i>polackorum</i>	Kwa-Zulu, South Africa	ADC2013 220.51	KP975998	A. Connell/SAIAB
<i>Pseudojuloides</i>	<i>polackorum</i>	Kenya	BPBM 41207	KP975967	J. Edward/aq. trade
<i>Pseudojuloides</i>	<i>polackorum</i>	Kenya	BPBM 41208	KP975996	J. Edward/aq. trade
<i>Pseudojuloides</i>	<i>polackorum</i>	Kwa-Zulu, South Africa	ac13pc	KP975978	A. Connell/SAIAB
<i>Pseudojuloides</i>	<i>labyrinthus</i>	Kenya	BPBM 41257	KT352046	J. Edward/aq. trade
<i>Pseudojuloides</i>	<i>zeus</i>	Majuro, Marshall Islands	BPBM 41215	KJ591656	J. Edward/aq. trade
<i>Pseudojuloides</i>	<i>mesostigma</i>	Vanuatu	BPBM 41216	KP975968	J. Edward/aq. trade
<i>Pseudojuloides</i>	<i>edwardi</i>	Kenya	BPBM 41173	KP975964	J. Edward/aq. trade
<i>Pseudojuloides</i>	<i>severnisi</i>	Philippines	aqps910	JQ839574	J. Edward/aq. trade
<i>Pseudojuloides</i>	<i>atavai</i>	Rarotonga, Cook Islands	ck98425pa210	JQ839568	B. Victor
<i>Pseudojuloides</i>	<i>elongatus</i>	New Caledonia	jr14pe3	KJ591647	A. Teitelbaum
<i>Leptojuilis</i>	<i>cyanopleura</i>	Bali, Indonesia	bali18001157	KX459127	B. Victor