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Pseudojuloides labyrinthus, a new labrid fish (Teleostei: Labridae) from the western Indian Ocean

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Abstract

The new labrid fish species, *Pseudojuloides labyrinthus* n. sp., is described from three specimens obtained via the aquarium trade from Kenya, in the western Indian Ocean. The species is similar in appearance to other Indo-Pacific *Pseudojuloides* in the *P. severnsi* complex, distinguished mainly by the markings of the terminal-phase male, which includes a maze of lines on the head and three thicker blue stripes along the rear body. Despite the similarity in appearance, the new species is 9.66% divergent in the sequence of the mtDNA barcode marker COI (minimum interspecific divergence, pairwise; 10.54% K2P distance) from its nearest relative, *P. edwardi*, also found in Kenya. A neighbor-joining tree and genetic distance matrix is presented for 12 of the 14 known species in the genus *Pseudojuloides*.

Key words: coral reef fishes, ichthyology, new species, taxonomy, systematics, Kenya, Africa, DNA barcoding.

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Introduction

The labrid genus *Pseudojuloides* Fowler was revised by Randall & Randall (1981), who recognized eight species in the genus, five of which were new. Since then, five 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* and

P. polackorum from the southwest Indian Ocean (Victor & Randall 2014, Connell *et al.* 2015); 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 large, brightly colored individuals, while smaller initial-phase (IP) fish, usually females, are reddish orange. We describe here a new species from the African coast in the western Indian Ocean, the fourth species of the genus from that location, and compare its barcode mtDNA COI sequence to 11 of the 13 described species in the genus (all except for *P. argyreogaster* and *P. erythropterus*).

Materials and Methods

Specimens have been examined from the Bernice P. Bishop Museum, Honolulu (BPBM). In addition, ethanol-preserved specimens of comparison species were collected for DNA sequencing from Bali (Indonesia), Moorea and the Marquesas Islands (French Polynesia), Cook Islands, New Caledonia, 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, Indonesia, Vanuatu, and Micronesia in the Pacific Ocean and Kenya and Mauritius in the Indian Ocean (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 µl volume including 6.25 µl of 10% trehalose, 2 µl of ultra pure water, 1.25 µl of 10× PCR buffer (10mM KCl, 10mM (NH₄)₂SO₄, 20mM Tris-HCl (pH8.8), 2mM MgSO₄, 0.1% Triton X-100), 0.625 µl of MgCl₂ (50mM), 0.125 µl of each primer (0.01mM), 0.0625 µl of each dNTP (10mM), 0.0625 µl of *Taq* DNA polymerase (New England Biolabs), and 2 µl 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 (Ratnasingham & Hebert 2007). The sequence data is 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 uncorrected p-distances and as K2P distances.

The length of specimens is given as standard length (SL), measured from the median anterior end of the upper lip to the base of the caudal fin (posterior end of the hypural plate); body depth is the greatest depth from the base of the dorsal-fin spines to the ventral edge of the abdomen (correcting for any malformation of preservation); body width is measured just posterior to the gill opening; head length from the front of the upper lip or anterior upper teeth (whichever is most anterior) to the posterior end of the opercular flap; orbit diameter is the greatest fleshy diameter of the orbital rim, and interorbital width the least bony width; snout length is measured from the median anterior point of the upper lip to the nearest fleshy rim of the orbit; caudal-peduncle depth is the least depth, and caudal-peduncle length the horizontal distance between verticals at the rear base of the anal fin and the caudal-fin base; predorsal, prepelvic and preanal lengths are angular measurements; lengths of spines and rays are measured to their extreme bases; caudal-fin and pectoral-fin lengths are the length of the longest ray; pelvic-fin length is measured from the base of the pelvic spine to the tip of the longest soft ray. Morphometric data are presented as percentages of the standard length. Proportional measurements in the text are rounded to the nearest 0.05.

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; scales above the lateral line are counted in an oblique row from the pored scales under the mid-spinous dorsal fin, the much smaller scale abutting the base of the fin is counted as 0.5 scales. The count of gill rakers is made on the first gill arch and includes all rudiments. The counts and measurements for the larger paratype (>50 mm SL) is shown in parentheses following data for the holotype (not listed if damaged). Proportional morphological measurements are presented in Table 1.



Figure 1. *Pseudojuloides labyrinthus*, BPBM 41257, TP male holotype, 65 mm SL, Kenya via aquarium trade (B.C. Victor).

***Pseudojuloides labyrinthus*, n. sp.**

Labyrinth Pencil Wrasse

urn:lsid:zoobank.org:act:A14ED652-FFF9-474D-9AA4-D4C281EDF3BC

Figures 1–6, Table 1.

Holotype. BPBM 41257, 65.0 mm SL, TP male, Mombasa region, Kenya, aquarium-trade, about April 9, 2015.

Paratypes. BPBM 41258, (2) 43.0 & 60.6 mm SL, IP females, same collection data, about May 8, 2014.

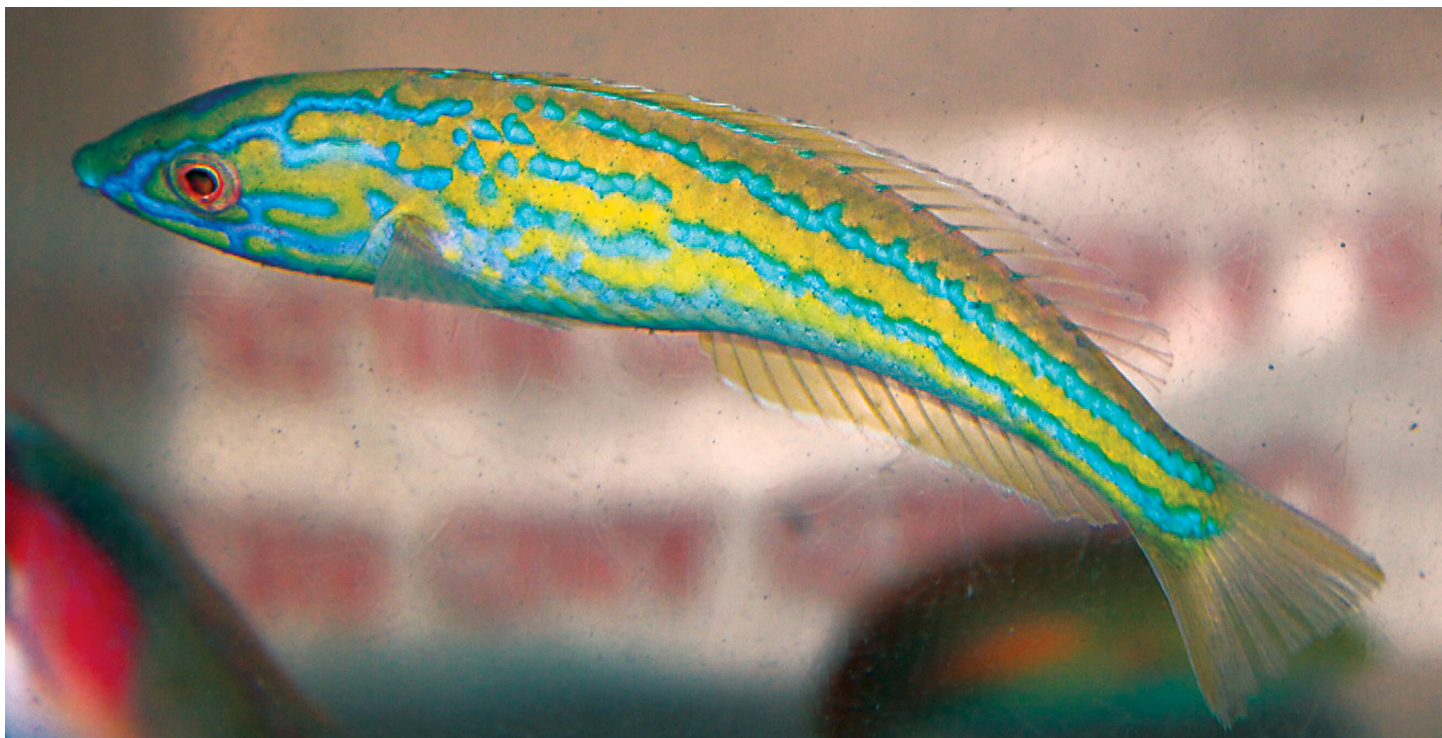


Figure 2. *Pseudojuloides labyrinthus*, BPBM 41257, TP male holotype, 65 mm SL, Kenya via aquarium trade (M. Stern).



Figure 3. *Pseudojuloides labyrinthus*, BPBM 41258, IP paratype, 43 mm SL, Kenya via aquarium trade (V. Altamirano).

Diagnosis. Dorsal-fin rays IX,11; anal-fin rays III,12; pectoral-fin rays 13; lateral-line scales 27 (+1 on caudal-fin base); no scales on head; gill rakers 14; 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 5.0–5.4 in SL; only slightly compressed, body width 1.7 in depth; caudal fin slightly rounded in initial phase, truncate in terminal-phase male; initial phase reddish orange to pink, often with more yellow tint anteriorly and grading to white ventrally on the head and abdomen, a band of bright reflective white running from tip of upper jaw back to under posterior orbit; terminal-phase male in life greenish yellow with three bright blue stripes along posterior half of body, head and anterior body often abruptly darker, with maze of lines, thinner and ranging from bright blue to reddish on head, wider (about one scale high) and bright blue on anterior body; dorsal and anal fins with broad yellow bands bordered above and below with blue stripes, upper and lower margin of caudal fin banded with yellow; iris red.

Description. Dorsal-fin rays IX,11; anal-fin rays III,12, all soft dorsal and anal-fin segmented rays branched, last split to base; pectoral-fin rays 13, the first rudimentary, the second 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); scales above lateral line to origin of dorsal fin 4.5; scales below lateral line to origin of anal fin 8; median predorsal scales about 7–10; gill rakers 14.

Body elongate, the depth 5.0 (5.4) in SL, and only slightly compressed, the width 1.7 (1.7) in depth; head length 3.1 (3.0) in SL; dorsal profile of head nearly straight on snout, forming low angle of about 20° to horizontal axis of body, and slightly convex on nape; snout sharply pointed, its length 3.7 (3.8) in HL; orbit relatively small, diameter 5.1 (4.7) in HL; interorbital space broadly convex, the least bony width 4.2 (4.8) in HL; caudal peduncle short and narrow, the least depth 3.5 in HL, caudal-peduncle length 3.0 in HL.



Figure 4. *Pseudojuloides labyrinthus*, BPBM 41258, IP paratype, 60.6 mm SL, Kenya via aquarium trade (B.C. Victor).

TABLE 1

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

	holotype	paratypes	
	BPBM 41257 TP	BPBM 41258 IP	BPBM 41258 IP
Standard length (mm)	65.0	60.6	43.0
Body depth	19.8	18.5	19.5
Body width	11.8	11.1	11.9
Head length	32.0	33.2	33.7
Snout length	8.8	8.7	8.8
Orbit diameter	6.3	7.1	8.1
Interorbital width	7.7	6.9	7.0
Caudal-peduncle depth	9.2	-	10.0
Caudal-peduncle length	10.6	-	9.8
Predorsal length	29.4	29.9	33.0
Preanal length	56.6	58.4	58.1
Prepelvic length	35.5	36.0	35.6
Base of dorsal fin	56.0	-	55.1
First dorsal-fin spine	6.2	6.6	7.0
Ninth dorsal-fin spine	8.6	-	9.8
Longest dorsal-fin ray	11.1	-	12.8
Base of anal fin	34.0	-	31.2
First anal-fin spine	2.6	3.1	3.3
Second anal-fin spine	5.7	6.9	4.9
Third anal-fin spine	7.2	7.9	7.7
Longest anal-fin ray	9.8	-	11.6
Caudal-fin length	16.5	-	21.9
Pectoral-fin length	15.4	15.8	18.1
Pelvic-spine length	9.4	10.1	11.2
Pelvic-fin length	14.9	13.5	15.6

Mouth very small, terminal, the corner of gape with closed jaws well anterior to anterior nostril; end of maxilla buried, even when jaws gape. Lips moderately thick, the upper puffed with striations on the underside, the 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, the upper pair slightly out-flaring, the 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, the 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, the anterior in a short membranous tube elevated posteriorly, the posterior 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 9 or 10 along free margin of preopercle, plus 1 or 2 more up to rear mid-eye level, in a single 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 18th pored scale, below base of eighth dorsal soft ray, 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 5.2 (5.0) and the ninth 3.7 in HL; longest dorsal-fin soft ray 2.9 in HL; origin of anal fin below base of last dorsal-fin spine; first anal-fin spine very short, 12.2 (10.6) in HL; second anal-fin spine 5.6 (4.8) in HL; third anal-fin spine 4.4 (4.2) in HL; longest anal-fin soft ray 3.3 in HL; caudal fin with slightly extended upper and lower lobes in terminal-phase males, caudal-fin length 1.9 in HL; third pectoral-fin ray longest, 2.1 (2.1) in HL; pelvic fins short, 2.1 (2.5) in HL.

Color in life. Based on two TP male individuals (holotype and one living non-type)(Figs. 1, 2 & 5 top), head and body greenish yellow grading to white ventrally, one specimen with anterior body and head abruptly darker, sparing ventral abdomen and thorax; head with reticulated pattern of thin lines, colored bright blue to red (in same male holotype) to purplish; maze of lines on head continuing onto anterior body and partially breaking up into spots, then transitioning at mid-body to form three distinct stripes ending near base of caudal fin, body spots and stripes bright blue and wider than head stripes, about one scale wide. Dorsal and anal fins with a broad yellow band over a narrow blue stripe near base of fin, fin edged with a thin blue margin; caudal fin with thick yellow bands along the upper and lower margins also edged with a thin bluish line, central portion of fin translucent; pelvic and pectoral fins translucent. Iris reddish orange. IP individuals reddish to pinkish or orange (Figs. 3, 4 & 6), lighter ventrally, white on lower half of head and thorax; a continuous band of brighter, reflective, pearly white from tip of upper jaw back to below rear orbital margin. Fins translucent. Iris orange to bright red.

The living holotype had a scattering of black pinpoint spots over the head and body; it is unclear if these are pathological or parasitic. They do not persist on the preserved specimen.

Color in alcohol. TP male uniform grey brown dorsally grading to white ventrally, except for some residual blue in stripes. Fins are translucent. IP fish are uniform yellowish with no markings.

Etymology. Named for the maze-like pattern of lines on the head and body. The specific epithet is a noun in apposition.

Distribution. The new species is described from specimens from the coast of Kenya. A record of “*P. erythrops*” from Seychelles (Randall & van Egmond 1994) is a 57-mm SL initial-phase specimen that is indistinguishable from *P. labyrinthus*: given the distance of Seychelles from the type location of *P. erythrops* in Mauritius, the record is more likely *P. labyrinthus*. Interestingly, the east African coast now has more sympatric species of *Pseudojuloides* than any other location, i.e. four species: the new species plus *P. edwardi*, *P. polackorum*, and the elusive *P. argyreogaster*.

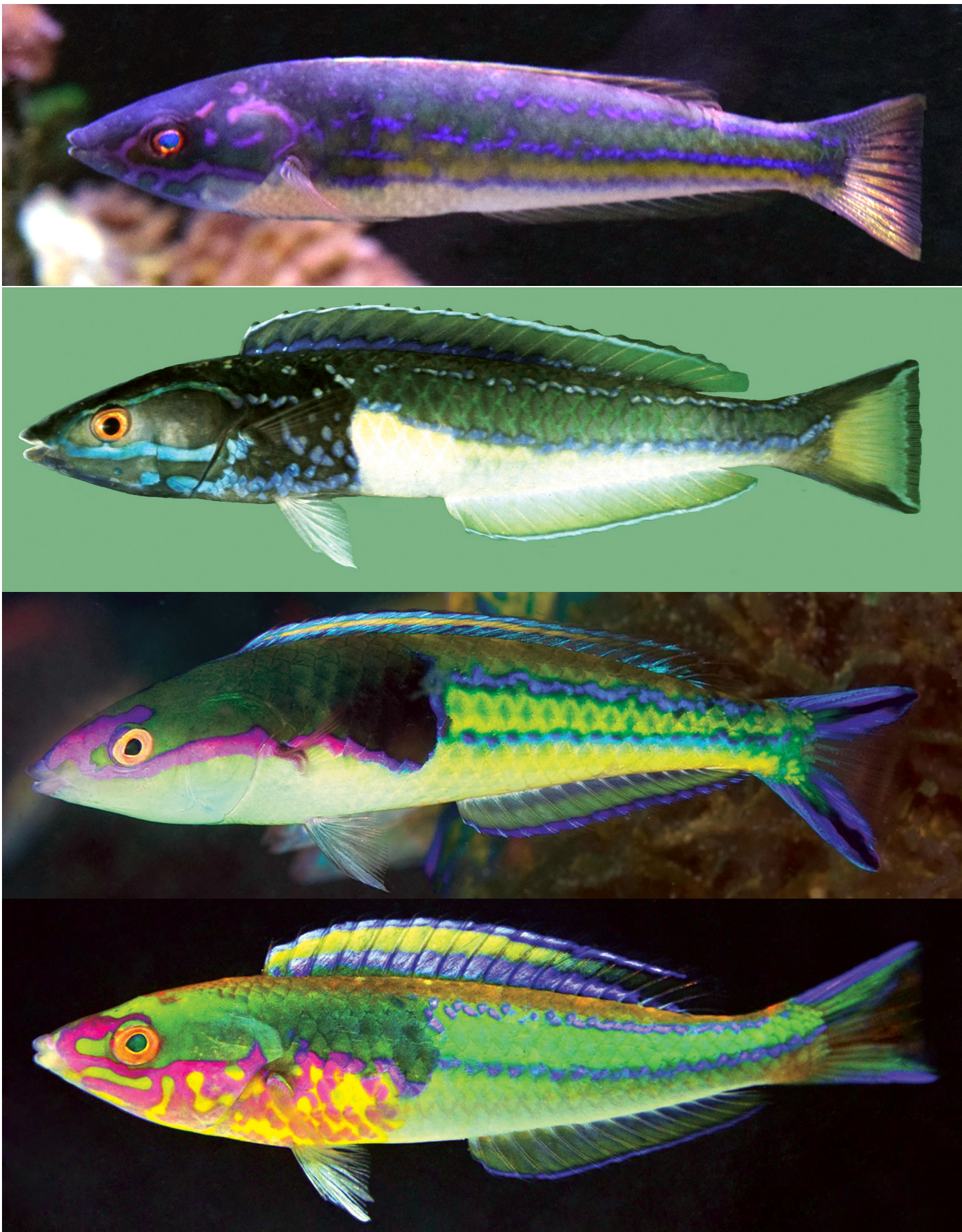


Figure 5. TP male colors in aquaria— top: *Pseudojuloides labyrinthus*, non-type, Kenya (T.J. Engels); upper middle: *P. erythroptus*, Mauritius (J.E. Randall); lower middle: *P. severnsi*, Japan (K. Nishiyama); bottom: *P. edwardi*, Kenya (V. Altamirano).

Barcode DNA sequence. A 652-nucleotide sequence of the segment of the mitochondrial COI gene used for barcoding by the BOLD informatics database (Ratnasingham & Hebert 2007) was obtained for the holotype. Following the database management recommendation of the BOLD, the sequence of the holotype (GenBank accession number KT352046) is presented here as well:

CCTCTATCTAGTATTTCGGTGCCTGAGCTGGGATGGTGGGCACAGCCCTAAGCCTGCTCATTTCGGGCT
GAACTTAGCCAGCCCGGTGCTCTCCTCGGAGACGACCAAATTTATAACGTAATCGTTACGGCCCAC
GCCTTCGTAATAATCTTTTTTATAGTAATGCCAATTATGATTGGCGGGTTCGGAACTGACTAATTCC
TCTGATGATTGGGGCCCCCTGATATGGCCTTCCCTCGAATGAACAACATGAGCTTCTGACTCCCATCT
TTCCTTCTCCTCCTTGCCTCATCTGGTGTAGAAGCGGGAGCTGGAAGTGGCTGAACAGTCTACCCC
CCTCTGGCTGGCAACCTCGCCACGCAGGGGCCTCTGTAGACTTAACTATCTTCTCCCTCCACTTAG
CCGGCATCTCATCGATCCTAGGGGCAATCAACTTTATTACAACTATTGTAAATATGAAGCCCCCTGCT
ATTC TCAATACCAACACCTCTCTTTGTTTGAGCCGTCTTAATTACAGCAGTCCTACTTCTTCTCTC
ACTACCCGTGCTTGCTGCGGGCATCACAATGCTGCTAACTGATCGTAACCTCAATACCACCTTCTTT
GACCCTGCAGGGGGAGGAGATCCCATCCTTTACCAACACCTC

Comparisons. Among the *Pseudojuloides*, *P. labyrinthus* most closely resembles the *P. severnsi* species complex in basic marking patterns on the TP male, i.e. an abruptly darker head and anterior body, reticulated lines on the head, and blue stripes along the body (Fig. 5). The new species differs by having a third blue stripe along the posterior half of the body (vs. two), the third running well below the lateral midline. The TP male of *P. erythroptus* also differs from *P. labyrinthus* in having the light ventrum ending abruptly at mid-abdomen, blue spots and reticulations against a dark background on the anterior abdomen, and only a single stripe across the upper head (vs. a maze). TP males of both *P. edwardi* and *P. severnsi* are missing the maze of lines on the upper head and upper anterior body. The initial-phase specimens of the entire genus are very similar and mostly non-descript and reddish orange; however, IP *P. labyrinthus* have the prominent reflective white stripe below the eye extending in a complete wide band from the tip of the upper jaw to past the orbit, while those of the other species have the reflective white more limited to the maxilla, or maxilla and separately under the eye, not forming a continuous streak (Fig. 6; and see Victor & Edward 2015).



Figure 6. *Pseudojuloides edwardi* vs. *labyrinthus*, initial phase, (identifications by DNA barcode): *P. edwardi* at left, *P. labyrinthus* paratype, 43 mm SL, at right; Kenya via aquarium trade (J.M.B. Edward).

Morphometrics (>50 mm SL) are similar to other congeners, although the new species is more elongate than most, with body depth 18.5–19.8% SL, less than the *P. cerasinus* complex and *P. atavai* (23 to 25% SL; Randall & Randall 1981, Connell *et al.* 2015) and *P. edwardi* and *P. severnsi* (19% to 23% SL; Victor & Randall 2014); about the same as *P. erythroptus* (18.6% to 19.6% SL; Randall & Randall 1981); and slightly wider than *P. zeus* and *P. mesostigma* (less than 18% from Victor & Edward [2015]).

DNA Comparisons. The neighbor-joining phenetic tree based on the COI mtDNA sequences of 12 of the 14 known *Pseudojuloides* species, following the Kimura two-parameter model (K2P) generated by BOLD (Barcode of Life Database), shows deep divergences between species and relatively small differences within species, except for the *P. edwardi* and *P. severnsi* sequences, which are very close (Fig. 7). As a broad generality, among most reef

TABLE 2

K2P distances for mtDNA COI sequences of 12 species of *Pseudojuloides*

Minimum Interspecific and Maximum Intraspecific Distances (%)												
	<i>ata</i>	<i>cer</i>	<i>edw</i>	<i>elo</i>	<i>kal</i>	<i>lab</i>	<i>mes</i>	<i>pol</i>	<i>pyr</i>	<i>sev</i>	<i>xan</i>	<i>zeu</i>
<i>P. atavai</i>	0											
<i>P. cerasinus</i>	19.32	0.18										
<i>P. edwardi</i>	17.97	16.06	0.31									
<i>P. elongatus</i>	17.78	18.8	15.81	0.62								
<i>P. kaleidos</i>	16.61	10.4	15.9	19.6	NA							
<i>P. labyrinthus</i>	20.19	16.63	10.54	17.54	15.9	0.31						
<i>P. mesostigma</i>	6.89	17.64	9.07	17.5	16.49	11.78	0.93					
<i>P. polackorum</i>	14.83	9.47	14.58	18.69	8.42	16.37	14.83	0.31				
<i>P. pyrius</i>	18.57	3.5	15.27	20.38	10.71	16.89	16.76	9.47	NA			
<i>P. severnsi</i>	17.76	16.34	0.46	16.14	15.83	10.75	9.3	14.34	15.61	0.93		
<i>P. xanthomos</i>	16.22	11.34	15.51	19.16	4.48	16.52	15.08	7.5	11.23	15.45	NA	
<i>P. zeus</i>	18.2	17.49	9.29	17.94	17.51	12.0	5.31	17.09	17.23	8.61	16.28	NA

P-distances (uncorrected pairwise) for mtDNA COI sequences of 12 species of *Pseudojuloides*

Minimum Interspecific and Maximum Intraspecific Distances (%)												
	<i>ata</i>	<i>cer</i>	<i>edw</i>	<i>elo</i>	<i>kal</i>	<i>lab</i>	<i>mes</i>	<i>pol</i>	<i>pyr</i>	<i>sev</i>	<i>xan</i>	<i>zeu</i>
<i>P. atavai</i>	0											
<i>P. cerasinus</i>	16.5	0.18										
<i>P. edwardi</i>	15.67	14.12	0.31									
<i>P. elongatus</i>	15.67	16.41	14.17	0.61								
<i>P. kaleidos</i>	14.59	9.55	14.02	17.05	NA							
<i>P. labyrinthus</i>	17.36	14.68	9.66	15.51	14.13							
<i>P. mesostigma</i>	14.9	15.37	8.41	15.51	14.44	10.75	0.92					
<i>P. polackorum</i>	13.21	8.74	12.93	16.28	7.83	14.44	13.21	0.31				
<i>P. pyrius</i>	15.98	3.4	13.55	17.51	9.83	14.9	14.75	8.76	NA			
<i>P. severnsi</i>	15.51	14.34	0.46	14.44	13.98	9.83	8.6	12.75	13.82	0.92		
<i>P. xanthomos</i>	14.29	10.36	13.71	16.74	4.3	14.59	13.36	7.07	10.29	13.67	NA	
<i>P. zeus</i>	15.82	15.2	8.57	15.82	15.21	10.91	5.07	14.9	15.05	7.99	14.29	NA

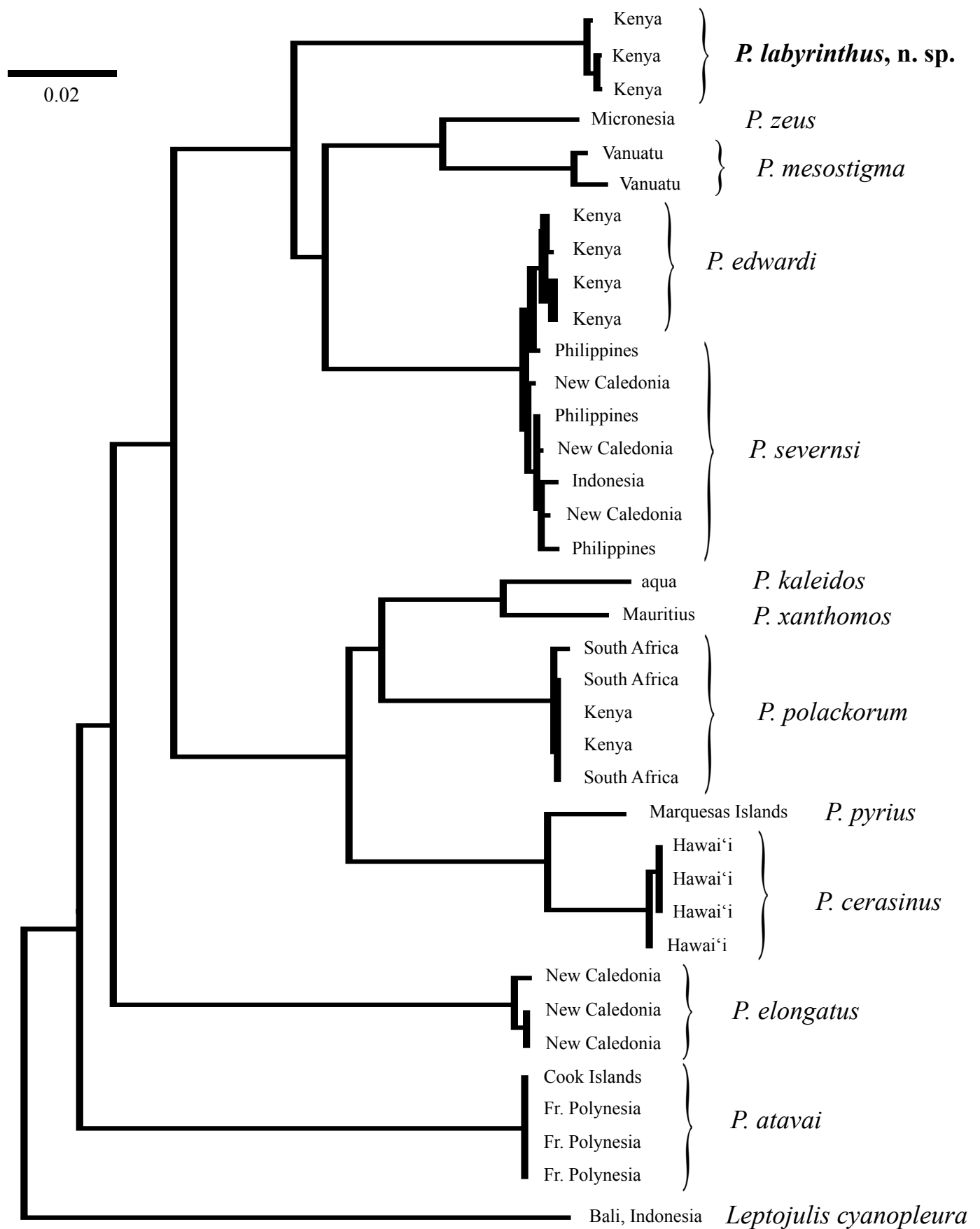


Figure 7. The neighbor-joining phenetic tree of *Pseudojuloides* following the Kimura two-parameter model (K2P) generated by BOLD (Barcode of Life Database). The scale bar at left represents a 2% sequence difference. Collection locations for specimens are indicated, and *Leptojuilis cyanopleura* is used 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.

fishes the minimum interspecific distance between close congeners is often up to an order of magnitude greater than the maximum intraspecific distance, which is precisely what makes the barcode database particularly useful. It appears that the majority of reef fish species (with many exceptions) differ by more than 2% from their nearest relatives (Steinke *et al.* 2009, Ward *et al.* 2009, Victor 2015). Our genetic results show that *P. labyrinthus* falls in a broad clade made up of *P. severnsi/edwardi* and *P. zeus* and *P. mesostigma*. The nearest-neighbor sequence to *P. labyrinthus* is *P. edwardi*, which differs by 9.66% in COI sequence (uncorrected pairwise distance; 10.54% by K2P). The divergence is on a similar scale to that from the remaining species in the complex, i.e. *P. severnsi*, *P. zeus*, and *P. mesostigma*. It is somewhat unexpected that *P. labyrinthus* is more distant from *P. severnsi* than are *P. zeus* and *P. mesostigma*, since the TP males of *P. labyrinthus* share the basic marking patterns of *P. severnsi* and *P. edwardi* and appear quite different from *P. zeus* and *P. mesostigma*. Interestingly, in this case, the initial-phase marking differences (although slight) may be more reflective of the genetic relationship than the TP male pattern.

Genetic divergences within the genus *Pseudojuloides* vary widely (Table 2). For all but one pair, minimum interspecific distances range from 3.4% to 17.51% (uncorrected pairwise; 3.5% to 20.38% by K2P). The maximum intraspecific distances range from 0 to 0.92% (uncorrected pairwise; 0 to 0.93% by K2P), showing a clear “barcode gap” between species. The exception is the species pair of *P. edwardi* and *P. severnsi*, which diverge by only 0.46% (three nucleotides of the 652-bp barcode segment), and may be an example of phenotypic differences outpacing the rate of neutral substitutions in the mitochondrial COI DNA sequence early in the process of speciation (Victor & Randall 2014, Allen *et al.* 2015).

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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. 7, following the order in the tree. Holotype in bold.

Genus	species	Collection site	Voucher	GenBank #	Collector/Source
<i>Pseudojuloides</i>	<i>labyrinthus</i> , n. sp.	Mombasa, Kenya	BPBM 41258 (43.0)	KP975975	J. Edward/aq. trade
<i>Pseudojuloides</i>	<i>labyrinthus</i>, n. sp.	Mombasa, Kenya	BPBM 41257	KT352046	J. Edward/aq. trade
<i>Pseudojuloides</i>	<i>labyrinthus</i> , n. sp.	Mombasa, Kenya	BPBM 41258 (60.6)	KT352050	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 60.6	KP975989	J. Edward/aq. trade
<i>Pseudojuloides</i>	<i>mesostigma</i>	Vanuatu	BPBM 41216 60.9	KP975968	J. Edward/aq. trade
<i>Pseudojuloides</i>	<i>edwardi</i>	Mombasa, Kenya	BPBM 41172	KJ591643	J. Edward/aq. trade
<i>Pseudojuloides</i>	<i>edwardi</i>	Mombasa, Kenya	je14pe1	KP975964	J. Edward/aq. trade
<i>Pseudojuloides</i>	<i>edwardi</i>	Mombasa, Kenya	BPBM 41173 63.4	KJ591642	A. DeJong/aq. trade
<i>Pseudojuloides</i>	<i>edwardi</i>	Mombasa, Kenya	BPBM 41173 70.6	KJ591644	J. Edward/aq. trade
<i>Pseudojuloides</i>	<i>severnsi</i>	Philippines	BPBM 41174 72.3	KJ591652	J. Edward/aq. trade
<i>Pseudojuloides</i>	<i>severnsi</i>	New Caledonia	BPBM 41175 55.4	KJ591651	A. Teitelbaum
<i>Pseudojuloides</i>	<i>severnsi</i>	Philippines	M1496	JQ839573	D. Bellwood, JCU
<i>Pseudojuloides</i>	<i>severnsi</i>	New Caledonia	BPBM 41175 70.1	KJ591655	A. Teitelbaum
<i>Pseudojuloides</i>	<i>severnsi</i>	Indonesia	je13ps	KJ591653	J. Edward/aq. trade
<i>Pseudojuloides</i>	<i>severnsi</i>	New Caledonia	qm14ps2	KJ591654	A. Teitelbaum
<i>Pseudojuloides</i>	<i>severnsi</i>	Philippines	BPBM 41174 79.8	JQ839574	J. Edward/aq. trade
<i>Pseudojuloides</i>	<i>kaleidos</i>	aquarium trade	je14pk610	KP975974	J. Edward/aq. trade
<i>Pseudojuloides</i>	<i>xanthomos</i>	Mauritius	dej13px360	KJ591657	A. DeJong/aq. trade
<i>Pseudojuloides</i>	<i>polackorum</i>	South Africa	DSFSG592-11	KF489719	A. Connell/ SAIAB
<i>Pseudojuloides</i>	<i>polackorum</i>	South Africa	DSFSG925-13	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>	South Africa	ac13pc	KP975978	A. Connell/ SAIAB
<i>Pseudojuloides</i>	<i>pyrius</i>	Marquesas Islands	MARQ-424	KJ591650	J. Williams/S. Planes
<i>Pseudojuloides</i>	<i>cerasinus</i>	Hawai'i	FLHI398-09	KJ591646	D. Carlon/A. Faucci
<i>Pseudojuloides</i>	<i>cerasinus</i>	Hawai'i	h83pc370	JQ839570	B. Victor
<i>Pseudojuloides</i>	<i>cerasinus</i>	Hawai'i	FLHI318-09	KJ591645	D. Carlon/A. Faucci
<i>Pseudojuloides</i>	<i>cerasinus</i>	Hawai'i	h83pc260	JQ839571	B. Victor
<i>Pseudojuloides</i>	<i>elongatus</i>	New Caledonia	jr14pe3	KJ591647	A. Teitelbaum
<i>Pseudojuloides</i>	<i>elongatus</i>	New Caledonia	jr14pe2	KJ591649	A. Teitelbaum
<i>Pseudojuloides</i>	<i>elongatus</i>	New Caledonia	jr14pe1	KJ591648	A. Teitelbaum
<i>Pseudojuloides</i>	<i>atavai</i>	Rarotonga, Cook Islands	ck98425pa210	JQ839568	B. Victor
<i>Pseudojuloides</i>	<i>atavai</i>	Moorea, French Polynesia	MBIO1549	JF435150	S. Planes/J. Williams
<i>Pseudojuloides</i>	<i>atavai</i>	Moorea, French Polynesia	M106	JQ839569	D. Bellwood, JCU
<i>Pseudojuloides</i>	<i>atavai</i>	Moorea, French Polynesia	MBIO1289	JF435151	S. Planes/J. Williams
<i>Leptojulius</i>	<i>cyanopleura</i>	Bali, Indonesia	bal11700px124	JQ839546	B. Victor