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Chrysiptera uswanasi, a new microendemic species of damselfish (Teleostei: Pomacentridae) from West Papua Province, Indonesia

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Abstract

Chrysiptera uswanasi, n. sp., the seventh member of the Chrysiptera oxycephala species complex of Pomacentridae, is described on the basis of 10 specimens, 24.7–45.3 mm SL, collected at the Fakfak Peninsula of New Guinea (West Papua Province, Indonesia). The new taxon is a microendemic species, found only in a small area around the Fakfak Peninsula. It differs from other members of the group, C. burtjonesi (Solomon Islands), C. ellenae (Raja Ampat Islands, West Papua Province in Indonesia), C. maurineae (Cenderawasih Bay, West Papua Province), C. oxycephala (central Indonesia, Philippines, and Palau), C. papuensis (NE Papua New Guinea), and C. sinclairi (Bismarck Archipelago and islands off NE Papua New Guinea), on the basis of its distinctive color pattern and a 9.3% divergence in the sequence of the mitochondrial control region from its closest relative (C. oxycephala). Adults are mainly greenish yellow grading to pearly gray ventrally with numerous small blue or greenish spots on the head, body, and basal portion of the dorsal, anal, and caudal fins, and juveniles have a distinctive bright blue snout and forehead. The adult differs from the adults of most of the other members of the group in lacking bright yellow on the ventral body, including the pelvic and anal fins. The two other species in the complex that are also lacking bright yellow ventral bodies and fins are C. ellenae, which differs in being overall more green and having an all blue juvenile stage, and C. sinclairi, which is mostly dark blue, both as adults and juveniles.

Key words: taxonomy, systematics, ichthyology, coral reef fishes, microendemism, Indo-Pacific Ocean, FakFak Peninsula, Bird's Head Peninsula, mitochondrial DNA, cryptic species.

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Introduction

Allen et al. (2015, 2017) provided evidence for cryptic speciation in the pomacentrid genus Chrysiptera Swainson, 1839, specifically among populations of nominal Chrysiptera oxycephala (Bleeker, 1877) of the western Pacific Ocean. The complex is divisible into multiple species, including true C. oxycephala, the previously described Chrysiptera sinclairi Allen, 1987, plus 4 recently described new species by Allen et al. (2015, 2017): C. burtjonesi, C. ellenae, C. maurineae, and C. papuensis. The evolution of the C. oxycephala group appears to be strongly correlated with the zone of tectonic activity along the boundary of the Pacific and Australian plates, a highly active area of subduction with associated vulcanism and migrating island arcs (Hill & Hall 2003, Polhemus 2007). Other than true C. oxycephala, the members of the complex are endemic to portions of the dispersal corridor that Allen et al. (2015) referred to as the Solomons-North Sulawesi conduit (Fig. 1). The conduit area appears to have facilitated a wide dispersal of ancestral lineages, but subsequent localized isolation events have permitted speciation, not only in the C. oxycephala group, but in a number of other fishes. Indeed, there are at least 95 reef fish species (GRA, unpublished data) which are endemic to portions of the Solomons-North Sulawesi conduit.

The present paper describes a seventh member of the *C. oxycephala* group from the Fakfak Peninsula of West Papua (Fig. 1). This remote location includes some of the least-explored reefs of western New Guinea and is an apparent center of microendemism, as discussed by Allen *et al.* (2018). Its coral reefs are isolated from the adjacent West Papuan mainland areas by Bintuni Bay in the north and Arguni and Etna Bays in the south, each of which is characterized by considerable freshwater runoff and siltation and exceptionally large tidal fluctuations. Consequently, they are generally lacking coral reefs and likely form a barrier to planktonic dispersal of many reef organisms. At least 7 other microendemic fish species appear to be restricted to this location, including

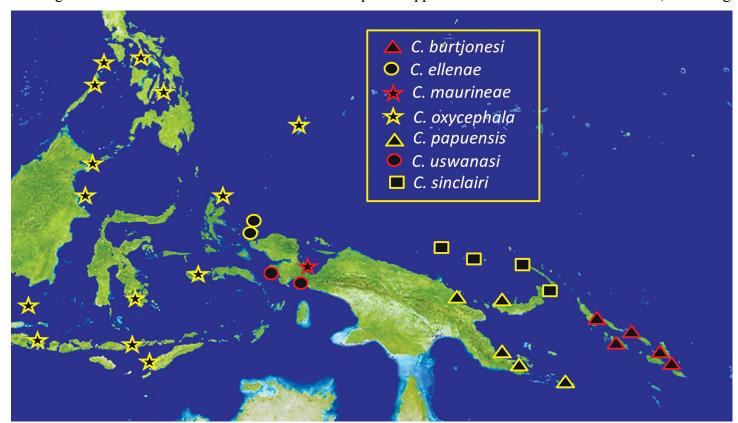


Figure 1. Map of the central western Pacific Ocean with distributions of the C. *oxycephala* species complex.

Manonichthys jamali Allen & Erdmann, 2007 (Pseudochromidae); Chrysiptera giti Allen & Erdmann, 2008; Pomacentrus bellipictus Allen, Erdmann & Hidayat, 2018; Pomacentrus fakfakensis Allen & Erdmann, 2009 (Pomacentridae); Paracheilinus nursalim Allen & Erdmann, 2008 (Labridae); an undescribed Eviota (Gobiidae); and an undescribed Ecsenius (Blenniidae).

Materials and Methods

Type specimens are deposited at the Museum Zoologicum Bogoriense, Cibinong, Java, Indonesia (MZB) and the Western Australian Museum, Perth, Australia (WAM).

Lengths of specimens are given as standard length (SL) measured from the anterior end of the upper lip to the base of the caudal fin (posterior edge of hypural plate); head length (HL) is measured from the same anterior point to the posterior edge of the opercle flap; body depth is the maximum depth taken vertically between the belly and base of the dorsal-fin spines; body width is the maximum width just posterior to the gill opening; snout length is measured from the anterior end of the upper lip to the anterior edge of the eye; orbit diameter is the horizontal fleshy diameter, and interorbital width the least fleshy width; depth of the preopercle-suborbital is the greatest depth measured at the "bulge" near the level of the posterior extent of the maxilla; upper-jaw length is taken from the front of the upper lip to the posterior end of the maxilla; caudal-peduncle depth is the least depth, and caudalpeduncle length is the horizontal distance between verticals at the rear base of the anal fin and the caudal-fin base; lengths of fin spines and rays are measured to their extreme bases (i.e. not from the point where the ray or spine emerges from the basal scaly sheath); caudal-fin length is the horizontal length from the posterior edge of the hypural plate to a vertical at the tip of the longest ray; caudal concavity is the horizontal distance between verticals at the tips of the shortest and longest rays; pectoral-fin length is the length of the longest ray; pelvic-fin length is measured from the base of the pelvic-fin spine to the filamentous tip of the longest soft ray; pectoral-fin ray counts include the small, splint-like, uppermost rudimentary ray; only the tube-bearing anterior lateral-line scales are counted, a separate count is given for the deeply pitted scales occurring in a continuous series midlaterally on the caudal peduncle; the decimal figure ".5" appearing in the scale row count above the lateral line refers to a small truncated scale at the base of the dorsal fin; preorbital+suborbital scales include all scales on the combined preorbital and suborbital bones, these are frequently embedded and difficult to discern without probing with a dissecting needle; gill-raker counts include all rudiments and are presented as separate counts for the upper and lower limbs, as well as a combined count; the last fin-ray element of the dorsal and anal fins is usually branched near the base and is counted as a single ray.

Counts and proportions appearing in parentheses apply to the paratypes when different from the holotype. Proportional measurements for the new species, expressed as percentage of the standard length, are provided in Table 1. A summary of fin-ray and lateral-line scale counts for members of the *C. oxycephala* species complex is presented in Table 2. Additional comparative data for the 6 other members of the complex are available from Allen *et al.* (2015, 2017).

Genetic sequence data for the 6 other species in the *C. oxycephala* group, as well as for outgroup species *C. giti*, *C. rollandi*, and *C. hemicyanea* (details in Allen *et al.* [2015]), were utilized in the present study for comparison with 6 specimens of the new species. The specimens were fixed in 95% EtOH and stored at room temperature until tissues were processed for DNA extraction. Mitochondrial DNA was extracted using a 10% Chelex solution (Walsh *et al.* 1991). A portion of the control region was amplified via PCR using the primers CRE and CRK (Lee *et al.* 1995). The PCR reaction was carried out in 25 μL volumes, using 1 μL of template. Each reaction included 4 μL 10x PCR buffer (Applied Biosystems), 2.5 μL 10 mM dNTPs, 1.25 μL of each primer at 10 mM, 2 μL 25 mM MgCl₂ solution, 0.125 μL AmplyTaq GoldTM (Applied Biosystems), and 14.5 μL ddH₂O. The thermocycling profile included an initial denaturation of 94°C for 3 min, 35 cycles of 94°C for 30s, 53°C for 30s, and 72°C for 60s, with a final extension of 72° C for 2 min. The PCR reactions were checked on 1% agarose gels stained with ethidium bromide. The PCR product was sequenced at the UC Berkeley sequencing facility. Forward and reverse sequences were proofread using MEGA7 then aligned using ClustalW (Kumar *et al.* 2016). Three methods were used to generate phylogenetic reconstructions: neighbor joining and maximum likelihood using MEGA7, and Bayesian inference using MRBAYES 3.2 (Ronquist & Hulsenbeck 2003). The NJ analysis,

based on genetic distance, was conducted in MEGA7 with the Kimura 2-Parameter model using 1000 bootstrap replicates to assess clade support. Maximum likelihood analysis assessed the model of best fit for the nucleotide substitutions. The Bayesian Information Criterion (BIC) tool ranked the Tamura 3-parameter (T92) model with a discrete Gamma distribution (+G) with 5 rate categories and assuming a certain fraction of sites is evolutionarily invariable (+I) and having the best fit to the data. For the Bayesian analysis, we used a Markov Chain Monte Carlo approach with 4 chains. Analyses were run for 20,000,000 generations and the resulting phylogeny was checked for convergence using Tracer v1.5 (Rambaut & Drummond 2009).

Chrysiptera uswanasi, n. sp.

Uswanas' Damselfish

urn:lsid:zoobank.org:act:DB04CFEC-37CD-4D36-B972-60880AC28AA2

Figures 2–4; Tables 1–3.

Holotype. MZB 24616, male, 45.3 mm SL, Indonesia, West Papua Province, Fakfak Peninsula, Sebakor area, -03.6350°, 132.8325°, 10 m, , clove oil & hand net, M.V. Erdmann & R. Mambrasar, 8 September 2018.

Paratypes. MZB 24617, (5) 33.9–43.5 mm SL, collected with holotype; WAM P.34830-001, (4) 24.7–41.4 mm SL, same data as holotype, except collected 13 March 2018 by G.R. Allen & M.V. Erdmann.

Diagnosis. A species of the pomacentrid genus *Chrysiptera* characterized by a combination of dorsal-fin rays XIII,11; anal-fin rays II,11–12 (usually 11); pectoral-fin rays 14–15 (usually 15); gill rakers on first branchial arch 8–10+19–21, total gill rakers 28–31; tubed lateral-line scales 12–16 (usually 14–16); preorbital+suborbital scales



Figure 2. *Chrysiptera uswanasi*, underwater photograph, adult, approx. 45 mm SL, Fakfak Peninsula, West Papua Province, Indonesia (G.R. Allen).

2–11 (mean=7.6), color of small juveniles in life pale green with yellowish suffusion and broad zone of turquoise blue covering forehead and dorsal snout; adults mainly pale yellow grading to pale gray ventrally with numerous small blue or greenish spots on head, body, and basal portion of dorsal, anal, and caudal fins.

Description. Dorsal-fin rays XIII,11; anal-fin rays II,12 (one with 11); pectoral-fin rays 15 (one with 14 on one side); branched caudal-fin rays 13; principal caudal-fin rays 15; upper procurrent caudal-fin rays 6 (4–6); lower procurrent caudal-fin rays 5 (4–5); gill rakers on first branchial arch 10+19 (8–10+19–21), total gill rakers 29 (28–31); tubed lateral-line scales 14/15 (12–16); scales in lateral series from upper rear margin of opercle to base of caudal fin 27; scales above lateral line to base of middle dorsal-fin spines 1.5; scales below lateral line to anus 9; preorbital+suborbital scales 10 (2–11, mean 7.6).

Body depth 2.0 (1.8–2.0) in SL; maximum body width 2.6 (2.5–2.8) in depth; HL contained 3.1 (2.8–3.2) in SL; snout 3.7 (3.4–3.8), eye 3.1 (2.7–3.2), interorbital width 3.0 (3.1–3.7), least depth of caudal peduncle 1.9 (1.9–2.2), length of caudal peduncle 2.6 (2.2–2.7), all in HL.

Mouth terminal, oblique, jaws forming an angle of about 40–45° to horizontal axis; maxillary reaching to vertical through anterior edge of eye; teeth of jaws biserial, those of outer row more or less incisiform with flattened tips, upper jaw with about 50 (46–56) teeth and lower jaw with about 40 (38–50) teeth in outer rows, largest about one-third diameter of pupil in height; secondary row of slender buttress teeth behind those of outer row in the spaces between them; single narial opening on each side of snout; naris with low fleshy rim; preorbital and suborbital relatively narrow, greatest depth of suborbital 34.1% (20.8–36.5%) of eye diameter, ventral margin smooth; margin of preopercle smooth, without any denticulations; margin of opercular series smooth except blunt flattened spine on upper portion near angle. Scales of head and body finely ctenoid; snout tip, lips, chin, and isthmus naked; pair of primary transverse scale rows on cheek with row of smaller scales along lower margin; preorbital and suborbital usually with scattered, partially embedded scales; dorsal and anal fins with a basal scaly sheath; basal half of caudal fin covered by scales; pectoral fins covered by scales only at base; axillary scale cluster between base of pelvic fins 55.3% (47.3–59.6%) length of pelvic-fin spine. Tubed lateral-line scales ending below posterior spines of dorsal fin; 3 (2–4) pits or pores present on 4 (3 or 4) scales immediately posterior to last tubed scale; continuous series of 8 (7 or 8) pored or pitted scales mid-laterally on caudal peduncle to caudal-fin base.



Figure 3. *Chrysiptera uswanasi*, underwater photograph, juvenile, approx. 20 mm SL, Fakfak Peninsula, West Papua Province, Indonesia (M.V. Erdmann).

Origin of dorsal fin at level of third tubed scale of lateral line; spines of dorsal fin gradually increasing in length to sixth or seventh spine, remaining spines about equal or slightly decreasing in length; membrane between spines deeply incised; first dorsal-fin spine 3.6 (3.4–4.8), seventh dorsal-fin spine 1.8 (1.8–2.0), last dorsal-fin spine 1.8 (1.6–2.0), longest soft dorsal-fin ray 1.2 (1.1–1.3), all in HL; length of dorsal-fin base 1.7 (1.6–1.7) in SL; first anal-fin spine 3.4 (3.4–4.1), second anal-fin spine 1.6 (1.5–1.8), longest soft anal-fin ray 1.3 (1.1–1.3), all in HL; base of anal fin 2.2 (2.0–2.3) in base of dorsal fin; caudal fin emarginate with rounded lobes, its length 3.2 (2.7–3.2) in SL; pectoral-fin reaching level of anus, length 3.2 (2.8–3.4) in SL; filamentous tips of pelvic fins reaching base of second or third anal-fin ray, longest ray 2.8 (2.5–3.0) in SL.

Color of adult in life. (Fig. 2) Greenish brown dorsally on head, grading to greenish yellow, becoming pearly gray or whitish ventrally on head and body; 1–3 small pale-green to bluish spots on each scale of cheek, opercle, and body, sparing dorsal portion of head and nape; small dark brown spot near upper limit of rear edge of operculum; faint dusky stripe from eye to snout tip; iris yellow-orange with a pair of green stripes across iris at upper and lower edges of pupil; spinous dorsal fin yellowish basally with numerous green-to-blue spots and elongate narrow bands of same color, protruding spine tips greenish, soft portion of fin yellowish basally and translucent grayish on outer portion; anal fin pale gray basally with small blue spots and translucent grayish on outer portion; caudal fin translucent grayish with small blue or green spots on basal portion; pelvic fins pale grayish with narrow blue anterior margin; pectoral fins translucent.

Color of juvenile in life. (Fig. 3) Generally pale greenish yellow, grading to whitish ventrally and broad zone of turquoise blue covering dorsal snout and forehead; cheek, operculum, and body with numerous, inconspicuous, small blue-to-green spots; broad charcoal-gray stripe across middle of turquoise-blue to greenish iris, joining charcoal-gray stripe from front of eye to snout tip, narrower grayish stripes across upper and lower iris; lips charcoal-gray with turquoise-blue streaks; first few dorsal-fin spines and outer margin of remaining spinous dorsal fin turquoise blue, basal portion of fin pale greenish, grading to translucent on rear part of fin; anal fin pale green on basal half and translucent bluish on outer portion, with narrow blue anterior margin; scales on dorsal surface of caudal peduncle mainly turquoise blue, with color extending narrowly along dorsal edge of caudal fin; caudal fin translucent grayish with turquoise-blue longitudinal streaks on membranes; pelvic fins pale greenish with narrow blue anterior margin; pectoral fins translucent.

Color in alcohol. (Fig. 4) Generally brown, darker on head, nape, and back, grading to light tan on ventral



Figure 4. *Chrysiptera uswanasi*, preserved holotype, MZB 24616, 45.3 mm SL, Fakfak Peninsula, West Papua Province, Indonesia (G.R. Allen).

TABLE 1

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

	holotype		paratypes									
	MZB 24616	MZB 24617	MZB 24617	MZB 24617	MZB 24617	WAM P.34830	WAM P.34830	WAM P.34830	MZB 24617			
Standard length (mm)	45.3	43.5	43.5	45.3	42.3	41.4	40.7	39.9	33.9			
Body depth	50.6	53.3	51.6	51.9	55.2	49.2	51.5	50.4	51.0			
Body width	19.3	20.1	20.0	17.7	20.7	18.1	19.4	20.3	19.0			
Head length	32.2	35.2	33.4	31.2	32.8	31.5	31.8	32.8	34.3			
Snout length	8.7	10.3	9.4	9.2	8.9	8.2	8.5	9.3	9.2			
Orbit diameter	10.3	11.0	10.7	10.5	11.1	11.1	9.9	11.5	12.6			
Interorbital width	10.8	9.4	9.8	9.9	10.0	9.7	10.2	10.5	10.5			
Caudal-peduncle depth	16.7	17.8	15.6	15.7	17.1	15.8	16.0	16.1	16.2			
Caudal-peduncle length	12.5	12.8	13.2	14.7	12.2	13.3	13.1	14.3	15.7			
Upper-jaw length	11.0	11.3	10.1	10.7	10.7	10.2	10.5	10.5	11.4			
Predorsal length	38.3	42.2	39.2	40.3	40.8	37.8	37.3	39.2	42.0			
Preanal length	65.1	65.4	66.7	63.3	68.1	66.4	69.0	66.5	65.0			
Prepelvic length	39.0	42.3	39.5	39.3	41.9	40.6	41.1	40.8	41.5			
Length dorsal-fin base	59.8	64.4	58.5	60.7	61.9	60.3	60.3	60.0	58.0			
Length anal-fin base	27.2	30.4	26.3	27.1	27.2	27.3	27.2	27.9	29.4			
Length pectoral fin	31.7	34.2	30.6	32.6	35.9	29.7	29.9	31.5	32.7			
Length pelvic fin	35.6	36.1	37.0	35.9	38.9	34.9	40.0	37.4	39.5			
Length pelvic-fin spine	16.6	21.2	17.2	19.0	19.1	16.9	17.4	17.7	19.7			
Length first dorsal spine	9.0	10.2	6.9	8.4	9.7	6.7	7.3	damaged	7.4			
Length second dorsal spine	17.6	18.0	16.4	18.3	18.3	17.7	17.6	17.6	19.4			
Length seventh dorsal spine	17.5	17.7	17.2	18.2	19.2	17.7	17.3	16.8	18.3			
Length longest dorsal ray	26.1	29.7	26.1	27.4	29.9	28.6	27.4	28.9	27.6			
Length first anal spine	9.5	9.6	8.6	8.7	9.2	7.8	9.5	26.4	10.2			
Length second anal spine	20.3	21.8	20.2	20.9	20.2	19.6	18.0	21.3	22.7			
Length longest anal ray	24.8	29.2	26.3	28.8	31.0	28.5	27.9	26.4	30.7			
Length caudal fin	31.0	31.2	32.8	30.0	31.8	33.4	36.8	31.9	32.9			
Caudal concavity	5.8	5.9	7.8	7.6	9.9	8.5	9.3	6.9	4.2			

parts of body; most scales of cheek, opercle, and side of body with 1–3 small dark brown or greenish spots; fins semi-translucent, median fins brown to tan basally and outer edge of spinous dorsal fin dusky grayish; urogenital papilla blackish.

Etymology. This species is named *uswanasi* in honor of Bupati Mohammad Uswanas, the Regent of Fakfak in West Papua, who has shown tremendous foresight and leadership in creating large marine protected areas along the Fakfak coastline in order to protect its extraordinary marine biodiversity (including this species) and its fish stocks for the well-being of his constituent coastal communities.

Distribution and habitat. On the basis of specimens and underwater photographs, *C. uswanasi* appears to be a microendemic species, mostly restricted to the Fakfak Peninsula (historically known as the Bomberai Peninsula) (Fig. 5), although scattered individuals have also been seen to the southeast, just east of Triton Bay (-3.909°, 134.1613°). Most sightings are from a relatively small area, mainly in Sebakor and Selassi Bays in the Karas District of Fakfak Regency, West Papua Province. Given our extensive collections and observations in the surrounding regions of West Papua and the Maluku Province, we are confident it is confined to this area. It was found in typical habitat for the species complex, consisting of sheltered lagoonal reefs associated with large open branching acroporid coral colonies in depths from 3–15 m.

Comparisons. The members of the *C. oxycephala* species complex are mainly separated on the basis of color pattern (Figs. 6 & 7), in addition to their genetic differences (see results below and Fig. 8). *Chrysiptera uswanasi* can be distinguished from the adults of most of the other members of the group in lacking bright yellow on the ventral body and on the pelvic and anal fins. The two other species that also lack bright yellow ventral bodies and fins are *C. ellenae*, which differs in being overall more green and having a distinctive bright-blue juvenile

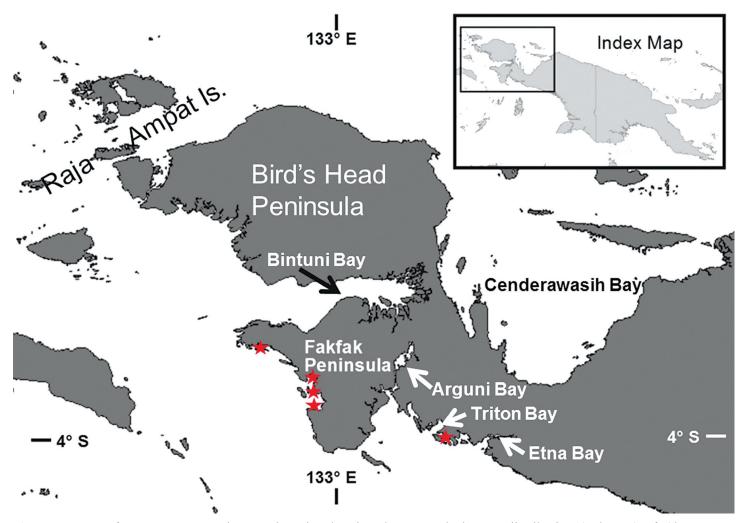


Figure 5. Map of West Papua Province, Indonesia, showing the presently known distribution (red stars) of *Chrysiptera uswanasi*.

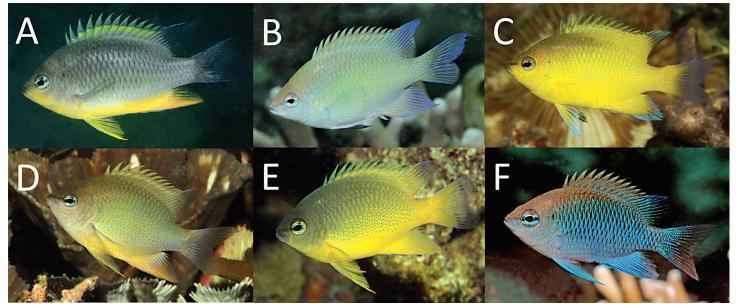


Figure 6. Comparison of adult color patterns of the *C. oxycephala* species complex, approx. 45–50 mm SL: A) *C. burtjonesi*, Solomon Islands, B) *C. ellenae*, Raja Ampat Islands, Indonesia, C) *C. maurineae*, Cenderawasih Bay, Indonesia, D) *C. oxycephala*, North Sulawesi, Indonesia, E) *C. papuensis*, Milne Bay, Papua New Guinea, F) *C. sinclairi*, Hermit Islands, Papua New Guinea (G.R. Allen).

stage, and C. *sinclairi*, which is mostly dark blue, both as adults and juveniles (Figs. 6 & 7). The juvenile of *C. uswanasi* can be distinguished from all other juveniles in the species complex by its bright blue patch limited to the dorsal shout and forehead (Figs. 3 vs. 7). The members of the complex exhibit similar fin-ray and lateral-line scale counts, however the new species tends to have more scales on the preorbital/suborbital bones than the other species, although the range broadly overlaps that of *C. ellenae*, *C. oxycephala*, and *C. papuensis*.

Genetic analysis. We resolved relationships within the *C. oxycephala* species complex using a 384-base-pair segment of the mtDNA control region. The tree from the NJ topology (Fig. 8) shows the species in the complex form a set of related monophyletic lineages corresponding to the allopatric species. Pairwise genetic distances (Table 4) between *C. uswanasi* and other species in the *C. oxycephala* complex were in the range of 0.093–0.135,

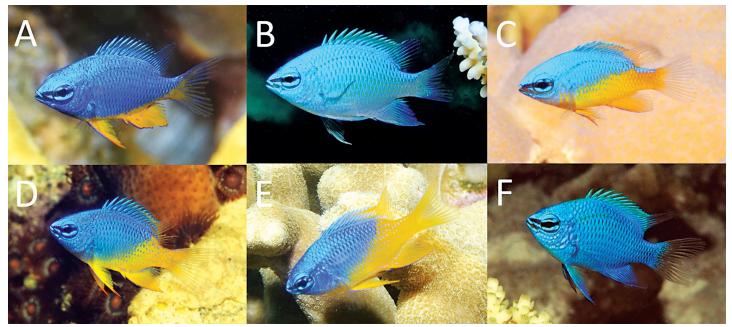


Figure 7. Comparison of juvenile color patterns of the *C. oxycephala* species complex, approx. 10–20 mm SL: A) *C. burtjonesi*, Solomon Islands, B) *C. ellenae*, Raja Ampat Islands, Indonesia, C) *C. maurineae*, Cenderawasih Bay, Indonesia, D) *C. oxycephala*, North Sulawesi, Indonesia, E) *C. papuensis*, Milne Bay, Papua New Guinea, F) *C. sinclairi*, Manus Island, Papua New Guinea (G.R. Allen).

TABLE 2
Color features of the *Chrysiptera oxycephala* species complex

Species	Adult ground color	Juvenile	Special features
C. burtjonesi	gray-brown or greenish	mostly blue	mainly blue to brownish, yellow ventrally
C. ellenae	pale greenish-yellow	entirely light blue	juvenile entirely light blue
C. maurineae	bright yellow	blue and yellow	juvenile: blue streak on dorsal caudal peduncle
C. oxycephala	greenish yellow	blue and yellow	adult: bright yellow only thorax & abdomen
C. papuensis	brown and bright yellow	blue and yellow	adult: brown anterodorsally, bright yellow posteroventrally
C. sinclairi	blue with brown forehead	entirely blue	absence of yellow in all stages, vertical bars prominent on scales
C. uswanasi	greenish yellow dorsum, pearly gray ventrum	greenish and blue	juvenile: blue confined to dorsal head

TABLE 3

Frequency distribution of soft dorsal-fin, anal-fin, and pectoral-fin-ray counts and selected scale counts for members of the *Chrysiptera oxycephala* species complex

Species	pecies Soft dorsal-fin rays			Soft anal-fin rays					Preorbital+suborbital scales				
	10	11	12		11 12 13				range	range mean			
C. burtjonesi	1	22	1			22	2		0–3	0.4	24		
C. ellenae	2	28	2		1	31			0–14	5.5	32		
C. maurineae	2	8	1			10	1		0–6	2.7	11		
C. oxycephala	1	40	4		1	28	1		2-10	4.0	45		
C. papuensis	5	28				32	1		0–10	4.1	33		
C. sinclairi	11	9			13	7			0–1	0.2	24		
C. uswanasi		9			1 8				2–11	7.6	9		

Species	Pectoral-fin rays						Lateral-line scales						
	12	13	14	15	16		11	12	13	14	15	16	
C. burtjonesi			5	40	1				6	14	10	2	
C. ellenae				32				1	9	15	5	2	
C. maurineae			1	10				1		1	9		
C. oxycephala		2	7	36				1	4	20	5		
C. papuensis			6	27					5	21	6	1	
C. sinclairi	1	1	9	9			1	4	6	5	4		
C. uswanasi			1	17				1	1	3	7	4	

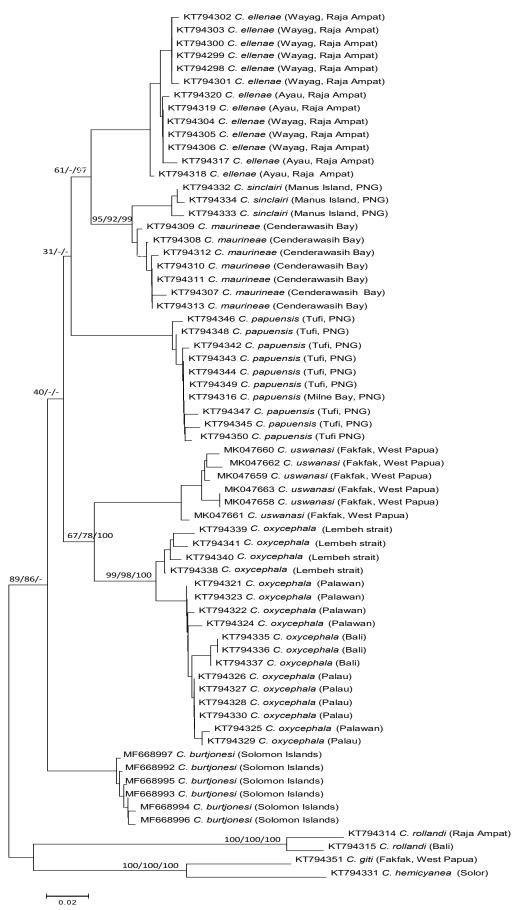


Figure 8. Neighbor Joining (NJ) topology generated from 384-bp of mtDNA control-region sequence data from *Chrysiptera* species. Numbers above the major nodes indicate bootstrap support for 1000 replicates using neighbor-joining, maximum likelihood, and Bayesian posterior probability, respectively. GenBank accession numbers and collection location are listed for each individual. Papua New Guinea is abbreviated as PNG.

TABLE 4

Average interspecific pairwise genetic distance matrix for sequences of the mtDNA control region for the *Chrysiptera oxycephala* species complex and some congeners

	Species	Location	1	2	3	4	5	6	7	8	9	10	11
1	C. burtjonesi	Solomon Is.											
2	C. uswanasi	Fakfak, West Papua	0.130										
3	C. sinclairi	Manus Island, PNG	0.090	0.118									
4	C. ellenae	Raja Ampat Is.	0.101	0.122	0.081								
5	C. maurineae	Cendrawasih Bay	0.073	0.117	0.029	0.067							
6	C. oxycephala	Bali, Palau & Philippines	0.118	0.106	0.109	0.119	0.104						
7	C. oxycephala	Lembeh Strait	0.110	0.093	0.104	0.107	0.100	0.031					
8	C. papuensis	Tufi, PNG	0.104	0.135	0.111	0.101	0.094	0.123	0.107				
9	C. rollandi	Raja Ampat	0.214	0.218	0.229	0.245	0.235	0.225	0.241	0.243			
10	C. rollandi	Bali	0.210	0.215	0.225	0.235	0.223	0.221	0.228	0.220	0.044		
11	C. giti	Fakfak	0.188	0.231	0.216	0.200	0.196	0.221	0.220	0.221	0.276	0.272	
12	C. hemicyanea	Solor	0.198	0.229	0.235	0.203	0.225	0.252	0.241	0.243	0.277	0.267	0.116

with the minimum divergence recorded between *C. uswanasi* and *C. oxycephala* from Lembeh Strait (North Sulawesi) and the largest observed between *C. uswanasi* and *C. papuensis*. Although there is a genetic distance (in the mitochondrial control region sequence) of 0.031 between the population of *C. oxycephala* from Lembeh Strait and populations from Bali, Palau, and the Philippines, the Lembeh lineage is considered as a genovariant (*sensu* Victor 2015) within *C. oxycephala*, especially in view of its lack of both color and morphological differences (Allen *et al.* 2015).

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