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Review of the *Chrysiptera oxycephala* complex of damselfishes (Pomacentridae) with descriptions of three new species from the East Indian Archipelago

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Abstract

The nominal species *Chrysiptera oxycephala* has been considered a widespread species in the East Indian Archipelago, but genetic analyses and a closer examination of populations throughout the region now show it to be another example of a species complex of closely related parapatric cryptic species and genovariant populations. Three DNA lineages correlate with different color patterns and are described here as new species, including *Chrysiptera ellenae* (Raja Ampat, West Papua, Indonesia), *Chrysiptera maurineae* (Cenderawasih Bay, West Papua, Indonesia), and *Chrysiptera papuensis* (northeastern Papua New Guinea). The original *C. oxycephala* has the widest distribution, including central Indonesia, Sabah, Philippines, and Palau, as well as a local population in Sulawesi with a divergent mtDNA lineage, but no apparent phenotypic difference (Lembeh genovariant). An additional previously described species, *C. sinclairi*, is restricted to oceanic insular areas of northeastern Papua New Guinea. The five members of the species complex share most meristic and morphometric features, although some differences are evident in the modes and range of fin-ray counts and the number of scales (combined) on the preorbital and suborbital bones. Nevertheless, color patterns, especially those of small juveniles, distinguish the five species, i.e. small juveniles entirely light blue (not persisting into adulthood) in *C. ellenae*; blue with a dark streak on each scale (and pattern persisting into adulthood) in *C. sinclairi*; light blue anterodorsally and yellow posteroventrally with a blue streak on upper caudal peduncle in *C. maurineae*; and light blue anterodorsally and yellow posteroventrally but no blue streak on upper edge of caudal peduncle in *C. papuensis* and *C. oxycephala*, but the former has the bicolor pattern with a bright yellow tail persisting into adulthood. The geographic distribution corresponds directly with color-pattern differences and mitochondrial-DNA lineages. The divergence in the control-region mtDNA sequence between the five species in the complex ranges from 2.9–10.9%, with the closest relationship between the species pair of *C. maurineae* and *C. sinclairi*, who nevertheless have very different color patterns and also differ in meristics. The two mtDNA lineages within *C. oxycephala* diverge by 3%, greater than the difference between *C. maurineae* and *C. sinclairi*. These results indicate that genotypic divergence does not necessarily correlate well with phenotypic divergence within cryptic-species complexes of reef fishes.

Key words: coral reef fishes, taxonomy, systematics, Indo-Pacific Ocean, cryptic species, mitochondrial DNA sequence, genovariant.

Introduction

Damselfishes of the family Pomacentridae are among the most common inhabitants of coral reefs, with a few species also inhabiting temperate seas and fresh water. The vast majority of the nearly 400 valid species (Eschmeyer & Fricke 2015) occur in the Indo-Pacific region. Similar to other common reef fish families, damselfishes are particularly well represented in the East Indian Archipelago, where at least 187 species are known (Allen & Erdmann 2012). Despite this impressive total, the discovery of additional new species is commonplace. Some members of the family tend to develop complexes of cryptic species that are only minimally different in appearance, but show significant divergence in DNA sequence from related species (Victor 2015). The development of cryptic speciation, especially geographic complexes of parapatric lineages, appears to be correlated with reduced dispersal, either by benthic eggs in conjunction with a short larval stage or extreme distances between populations (Victor 2015). Damselfishes are one of the few reef fish families that brood benthic eggs and they also tend to have relatively short pelagic larval durations: for example, a range of 14–24 days in samples of seven species of the genus *Chrysiptera,* with a mean of 21.5 days for the subject of this study, *Chrysiptera oxycephala* (Bleeker 1877) from Palau (Wellington & Victor 1989).

With the increasingly common application of mitochondrial DNA sequencing as part of routine taxonomic procedure, new cryptic species have now been documented in a variety of pomacentrid genera. Typically, a pomacentrid species that was formerly considered to be widely distributed, either broadly across the Indo-Pacific region or in a more localized region, such as the East Indian Archipelago, is found to consist of two or more closely related species as a result of genetic analyses and a closer examination of morphology, meristics, or coloration (Allen *et al*. 2008, Drew *et al*. 2008, Drew & Barber 2009, Allen & Drew 2012, Liu *et al*. 2012, Liu *et al*. 2014, Allen *et al*. 2015, Victor 2015).

Allen *et al*. (2015) described a cryptic-species complex in the pomacentrid genus *Chrysiptera* Swainson 1839, dividing nominal *Chrysiptera rex* (Snyder 1909) of the western Pacific Ocean into three cryptic species. We find a similar, but more complex, scenario in a common East Indian nominal species, *Chrysiptera oxycephala*, which is divisible into five parapatric cryptic species (Fig. 1), including three species described herein as new. We also find a divergent local mtDNA lineage that has no apparent phenotypic difference from the widespread *C. oxycephala*, and we consider the lineage a genovariant population of the widespread species (*sensu* Victor 2015). The members of this complex share most meristic and morphometric features. However, color pattern, especially that of juveniles, is diagnostic for species. With the exception of the mainly blue *C. sinclairi*, the general color pattern of adults ranges from yellow to greyish green or yellowish green with numerous small bluish to whitish spots. The habitats of the various species consist of highly sheltered reefs of coastal bays and atoll lagoons at depths of about 3–20 m. These fishes generally occur in loose aggregations and are frequently associated with branching formations of live coral, usually hovering a short distance above the coral and feeding on zooplankton.

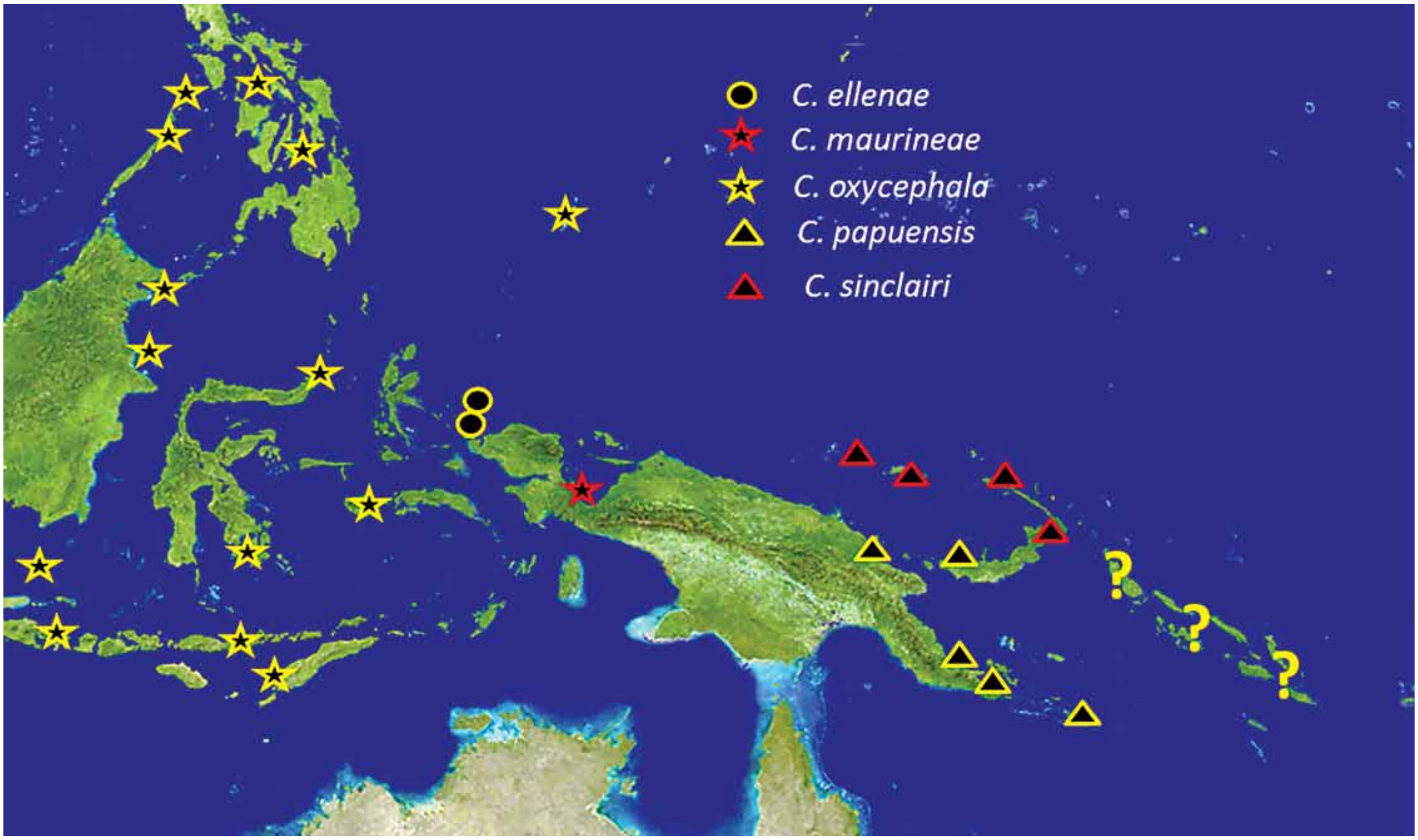

Figure 1. Map of the eastern portion of the East Indian Archipelago with distributions of the C. *oxycephala*-species complex (? = possible new species from the Solomon Islands).

Materials and Methods

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 caudal-peduncle length is the horizontal distance between verticals at the rear base of the anal fin and the caudal-fin base; lengths of fin spines and rays are measured to their extreme bases (i.e. not from the point where the ray or spine emerges from the basal scaly sheath); caudal-fin length is the horizontal length from the posterior edge of the hypural plate to a vertical at the tip of the longest ray; caudal concavity is the horizontal distance between verticals at the tips of the shortest and longest rays; pectoral-fin length is the length of the longest ray; pelvic-fin length is measured from the base of the pelvic-fin spine to the filamentous tip of the longest soft ray; pectoral-fin ray counts include the small, splint-like, uppermost rudimentary ray; only the tube-bearing anterior lateral-line scales are counted, a separate count is given for the deeply pitted scales occurring in a continuous series midlaterally on the caudal peduncle; the decimal figure ".5" appearing in the scale row count 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 (Fig. 2), these are frequently embedded and difficult to discern without probing with a dissecting needle; circumpeduncular scales were counted in a vertical "zigzag" row around the caudal peduncle, immediately anterior to the caudal fin base; 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 taxa, expressed as percentages of the standard length, are provided in Tables 1, 3 & 4. A summary of fin-ray and scale counts for the species complex is presented in Table 5.

Type specimens are deposited at the Museum Zoologicum Bogoriense, Cibinong, Java, Indonesia (MZB); United States National Museum of Natural History, Washington, D.C. (USNM); and the Western Australian Museum, Perth (WAM). Non-types and additional comparative material are housed at the Australian Museum, Sydney (AMS); Bishop Museum, Honolulu (BPBM); British Museum (Natural History), London (BMNH); Muséum national d'Histoire naturelle, Paris (MNHN); Naturalis Biodiversity Center, Leiden, Netherlands (RMNH); and Royal Ontario Museum, Toronto (ROM).

We DNA-sequenced 47 individuals of putative *Chrysiptera oxycephala* from the following geographic regions: Indonesia (Cenderawasih Bay, Raja Ampat, Bali and North Sulawesi), Philippines (Apulit, Palawan), Palau, and Papua New Guinea (Tufi and Milne Bay). Comparison sequences were obtained from three specimens of *C. sinclairi* and four outgroup sequences were obtained from congeners, i.e. *C. rollandi*, *C. giti*, and *C. hemicyanea*. 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 CRA [5'-TTCCA CCTCT AACTC CCAAA GCTAG-3'], CRK [5'-AGCTC AGCGC CAGAG CGCCG GTCTT GTAAA-3'], and CRE [5'-CCTGA AGTAG GAACC AGATG-3'](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 $MgCl_2$ solution, 0.125 µL AmplyTaq Gold™ (Applied Biosystems), and 14.5 µL ddH_2O. The thermocycling profile included an initial denaturation of 94°C for 3 min, 35 cycles of 94° C for 30 s, 53° C for 30 s, and 72° C for 60 s, with a final extension of 72° C for 2 min. The PCR reactions were checked on 1% agarose gels stained with ethidium bromide. The PCR product was sequenced at the UC Berkeley sequencing facility. Forward and reverse sequences were proofread using MEGA5 (Tamura *et al*. 2011) and then aligned using MUSCLE with subsequent alignment by eye. Neighbor-Joining analyses were conducted in MEGA5 following the Kimura-2-Parameter model determined using 1000 bootstrap replicates to assess clade support. Analyses of polymorphic sites was conducted by DNAsp (Librado & Rozas 2009).

Figure 2. *Chrysiptera ellenae*, showing preorbital-suborbital scalation (arrows). Unlike this species, most members of the *C. oxycephala* species complex possess only a few scattered scales in this region (G.R. Allen).

Figure 3. *Chrysiptera ellenae*, preserved holotype, MZB 22771, male, 50.8 mm SL, Wayag Lagoon, Indonesia (G.R. Allen).

Chrysiptera ellenae, n. sp.

Ellen's Damselfish

Figures 2–4; Tables 1, 2 & 5.

Chrysiptera oxycephala [*non* Bleeker] Allen & Erdmann 2012: 593 (Raja Ampat Islands, West Papua, Indonesia, lower right photograph only).

Holotype. MZB 22771, male, 50.8 mm SL, Wayag Lagoon, 00° 00.058' N, 130° 01.149' E, Raja Ampat Islands, West Papua Province, Indonesia, 4–12 m, spear & clove oil, G.R. Allen & M.V. Erdmann, Oct. 15, 2014.

Paratypes. MZB 22772, 16 specimens, 42.3–53.0 mm SL, collected with holotype; USNM 432465, 6 specimens, 43.4–54.7 mm SL, collected with holotype; WAM P.33947-001, 2 specimens, 47.4–50.6 mm SL, Cape Kri Lagoon, 00° 33.328' N, 130° 41.149' E, Kri Island, Raja Ampat Islands, West Papua Province, Indonesia, 10–15 m, clove oil, M.V. Erdmann, Aug. 18, 2013; WAM P.34336-001, 13 specimens, 35.4–53.9 mm SL, near Abidon village jetty, 00° 30.107' N, 131° 07.886' E, lagoon at Ayau Besar Atoll, Raja Ampat Islands, West Papua Province, Indonesia, 4–10 m, spear, G.R. Allen, Feb. 16, 2015.

Diagnosis. A species of the pomacentrid genus *Chrysiptera* with the following combination of characters: dorsal-fin rays XIII, 10–12 (rarely 10 or 12); anal-fin rays II, 11–12 (rarely 11); pectoral-fin rays 15; gill rakers on first branchial arch 9–10 + 19–22 (usually 10 + 20–22), total gill rakers 29–32; tubed lateral-line scales 12–16 (usually 13–14); preorbital+suborbital scales 0–14 (mean 5.5, rarely 0); color of small juveniles in life mainly light blue, gradually becoming pale greenish with increased growth; adults greenish yellow and covered with small turquoise spots, extending onto head and base of median fins (Fig. 4).

Description. Dorsal-fin rays XIII, 11 (10–12); anal-fin rays II, 12 (one paratype with 11); pectoral-fin rays 15; gill rakers on first branchial arch 10 + 20 (9–10 + 19–22), total gill rakers 30 (29–32); tubed lateral-line scales 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 6 (0–14, mean 5.5).

Body depth 1.9 (1.8–2.1) in SL; maximum body width 2.6 (2.6–3.1) in depth; HL contained 3.1 (3.0–3.4) in SL; snout 4.1 (3.5–4.3), eye 2.9 (2.8–3.3), interorbital width 3.6 (3.2–3.8), least depth of caudal peduncle 1.9 (1.8–2.0), length of caudal peduncle 2.3 (1.8–2.5), all in HL.

Mouth terminal, oblique, jaws forming an angle of about 40–45° to horizontal axis of head and body; maxillary reaching to vertical through anterior edge of eye; teeth of jaws biserial, those of outer row incisiform with flattened tips, upper jaw with about 40 (36–48) teeth and lower jaw with about 40 (40–48) 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 nasal opening on each side of snout, nostril with low fleshy rim; preorbital and suborbital relatively narrow, greatest depth of suborbital about 34.0% (25.2–36.5%) eye diameter, ventral margin smooth; margin of preopercle smooth, without any denticulations; margin of opercular series smooth except for 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 embedded scales (Fig. 2), only 2 of 32 specimens with none; 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 about 60% length of pelvic-fin spine.

Tubed lateral-line scales ending below posterior spines of dorsal fin; pits or pores present on 3 (3–5) scales immediately posterior to last tubed scale; continuous series of 7 (6–9) pored or pitted scales mid-laterally on caudal peduncle to caudal-fin base.

Origin of dorsal fin at level of third tubed scale of lateral line; spines of dorsal fin gradually increasing in

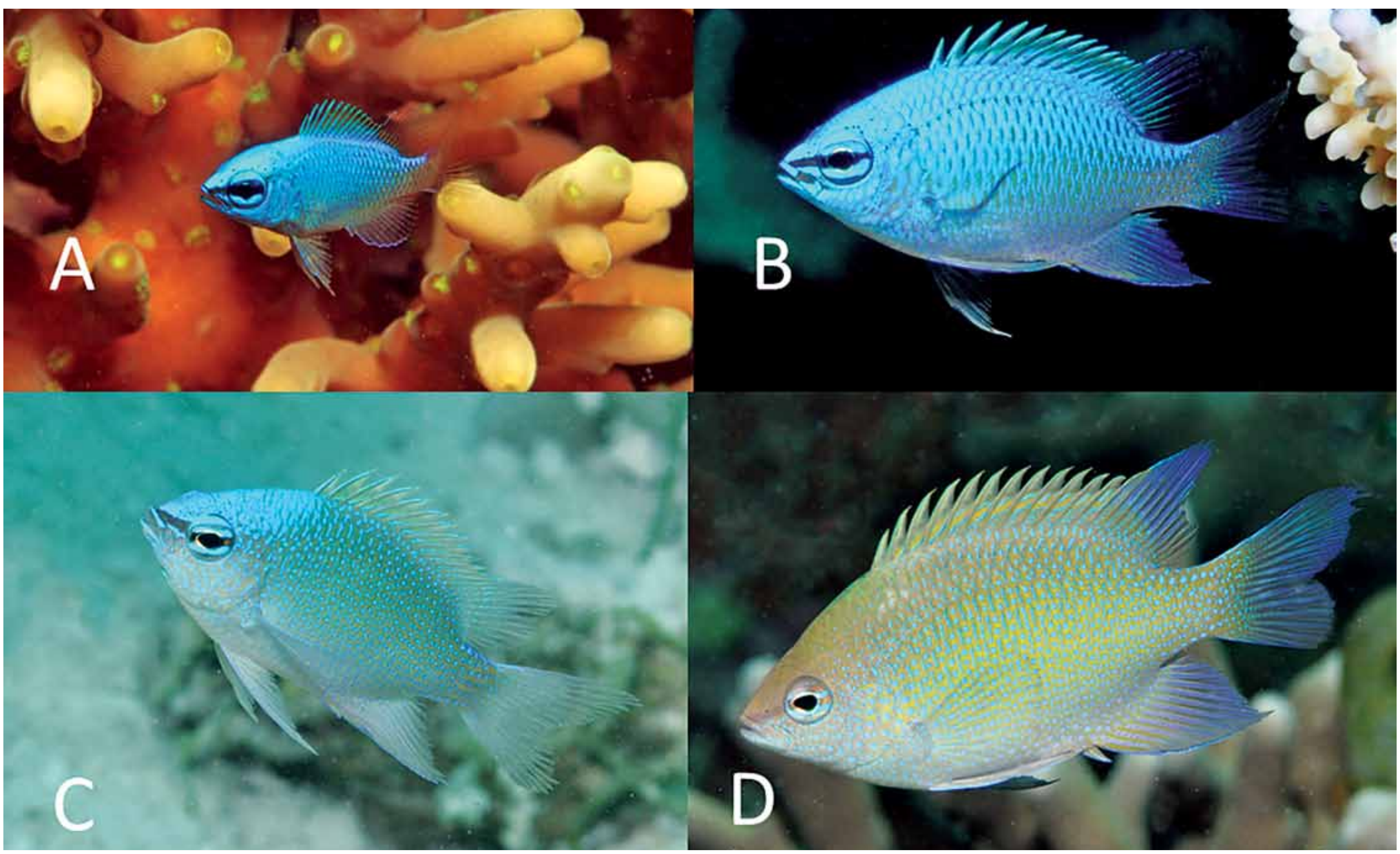

Figure 4. *Chrysiptera ellenae*, underwater photographs, Ayau Atoll, Raja Ampat Islands, West Papua Province, Indonesia: A. juvenile, approximately 15 mm SL; B. juvenile, approximately 25 mm SL; C. subadult, approximately 35 mm SL; D. adult, approximately 50 mm SL (G.R. Allen).

TABLE 1

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

	holotype	paratypes						
	MZB 22771	WAM P P.34336	WAM P P.34336	WAM P P.34336	WAM P P.34336	MZB 22772	MZB 22772	WAM P P.34336
Standard length (mm)	50.8	53.9	51.4	49.3	47.2	46.9	45.0	43.7
Body depth	51.5	47.0	49.3	48.8	51.2	52.1	50.9	48.5
Body width	19.8	18.2	18.5	17.2	17.7	19.1	18.4	17.3
Head length	31.8	31.7	30.2	31.2	32.2	31.4	32.3	31.9
Snout length	7.8	8.6	8.1	8.4	8.9	7.6	7.4	8.8
Orbit diameter	11.1	9.7	9.8	9.8	10.4	10.4	11.2	10.3
Interorbital width	8.9	9.7	9.3	9.3	9.5	9.8	9.7	9.9
Caudal-peduncle depth	16.6	16.3	15.3	16.6	16.7	15.9	16.0	17.4
Caudal-peduncle length	14.1	15.3	14.9	14.4	17.0	16.2	15.2	13.3
Upper jaw length	10.5	10.2	10.6	10.4	11.0	9.4	10.0	10.6
Predorsal length	36.8	38.4	36.8	37.4	37.8	38.8	33.7	38.0
Preanal length	64.4	67.0	62.9	65.8	65.5	66.2	68.2	64.8
Prepelvic length	37.1	38.2	38.8	36.6	37.9	40.0	40.0	38.7
Length dorsal-fin base	62.4	61.3	62.2	60.8	63.3	60.2	60.9	60.2
Length anal-fin base	28.7	27.1	30.1	27.2	29.3	26.9	27.1	28.2
Length pectoral fin	26.9	29.6	26.7	30.2	30.7	32.1	28.6	27.3
Length pelvic fin	31.7	33.2	30.4	35.5	33.3	38.3	36.4	35.5
Length pelvic-fin spine	17.0	16.4	16.3	18.0	19.5	18.8	18.1	19.5
Length first dorsal spine	8.4	7.8	7.8	8.3	8.3	8.2	6.8	8.6
Length second dorsal spine	16.9	17.5	17.2	17.6	18.4	16.1	17.1	18.4
Length seventh dorsal spine	17.9	17.8	18.1	16.9	18.0	17.0	16.9	16.3
Length longest dorsal ray	26.1	26.8	25.7	27.2	29.0	25.5	27.9	27.8
Length first anal spine	9.0	9.2	8.9	9.0	10.9	8.7	8.3	9.4
Length second anal spine	19.3	18.6	18.5	18.7	20.2	19.6	20.1	19.5
Length longest anal ray	26.7	26.1	27.1	28.3	26.5	27.1	27.9	30.9
Length caudal fin	28.4	30.5	31.2	33.2	33.4	31.9	30.8	31.6
Caudal concavity	6.1	5.5	6.8	7.8	5.9	7.0	8.7	6.7

length to sixth or seventh spine, remaining spines slightly decreasing in length; membranes between spines deeply incised; first dorsal-fin spine 3.8 (3.4–4.7), seventh dorsal-fin spine 1.9 (1.7–2.0), last dorsal-fin spine 1.8 (1.7–1.9), longest dorsal-fin soft ray 1.2 (1.0–1.3), all in HL; length of dorsal-fin base 1.6 (1.6–1.7) in SL; first anal-fin spine 3.5 (2.9–4.0), second anal-fin spine 1.7 (1.5–1.8), longest anal-fin soft ray 1.2 (0.9–1.2), all in HL; base of anal fin 2.2 (2.1–2.3) in base of dorsal fin; caudal fin emarginate with rounded lobes, its length 3.5 (2.9–3.4) in SL; pectoral fin reaching vertical through anal opening, longest ray 3.7 (3.1–3.7) in SL; filamentous tips of pelvic fins reaching base of first or second anal-fin soft ray when undamaged (tips broken off in some specimens), longest ray 3.2 (2.6–3.3) in SL.

Color of adult in life. (Fig. 4D) Generally pale greenish to yellowish green, greyish-brown on dorsal surface of snout and interorbital region (close inspection of body scales reveal a yellow reticulum and numerous turquoise spots, giving overall pale greenish impression); turquoise spots, extending onto head (where smaller) and base of median fins; faint greyish stripe from eye to snout tip; iris yellow-orange with a pair of turquoise stripes, one on each side of pupil; spinous dorsal fin olive-grey with medial band consisting of yellow and turquoise vertical streaks; soft dorsal fin mainly translucent except olive-grey basally with turquoise spots; anal fin pale greenish with blue spots, translucent posteriorly; caudal fin mainly translucent except yellowish brown basally with turquoise spots; pelvic fins pale greenish with fine turquoise anterior margin; pectoral fins translucent.

Color of juvenile in life. (Figs. 4A–C) Smallest individuals (< about 25 mm SL) almost entirely light blue with mainly translucent fins and greyish stripe from anterior edge of eye to snout tip. Larger juveniles and subadults (to about 35–40 mm SL) gradually assume adult pattern, but blue coloration on subadults generally persists on dorsal aspect, especially on nape and head.

Color in alcohol. (Fig. 3) Generally brown, paler and slightly yellowish on ventral regions of body including thorax and abdomen; fins semi–translucent grey; urogenital papilla blackish.

Distribution. The new species is only found in the Raja Ampat Islands of West Papua, Indonesia (Fig. 1). It is common in sheltered waters around the main islands and also in the lagoon at Ayau Atoll, about 45 km northeast of the archipelago.

Etymology. The species is named in honor of Ellen Gritz of Houston, Texas, USA, in recognition of her valued friendship, illustrious career in cancer prevention research, and generous support of our East Indian reef fish investigations.

Comparisons. *Chrysiptera ellenae* is distinguished from other members of the *C. oxycephala* species complex by its almost entirely blue juvenile coloration (Table 2). Juveniles of *C. sinclairi* are also entirely blue, but the blue is darker and there are prominent dark bars on each scale. Furthermore, *C. sinclairi* differ in retaining the blue into adulthood (except for some brown on the upper head and nape). Meristics also separate *C. sinclairi*; they have one fewer modal dorsal and anal-fin rays and usually lack preorbital+suborbital scales, while *C. ellenae* rarely lack those scales (2 of 32 specimens), and most have at least five scales in this area and can have as many as 14 scales (see Fig. 2 and Table 5).

TABLE 2

Color features of the *Chrysiptera oxycephala* species complex

Species	Adult ground color	Juvenile	Special features
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 anterodorsal, bright yellow posteroventral
C. sinclairi	blue with brown forehead	entirely blue	absence of yellow in all stages, vertical bars prominent on scales

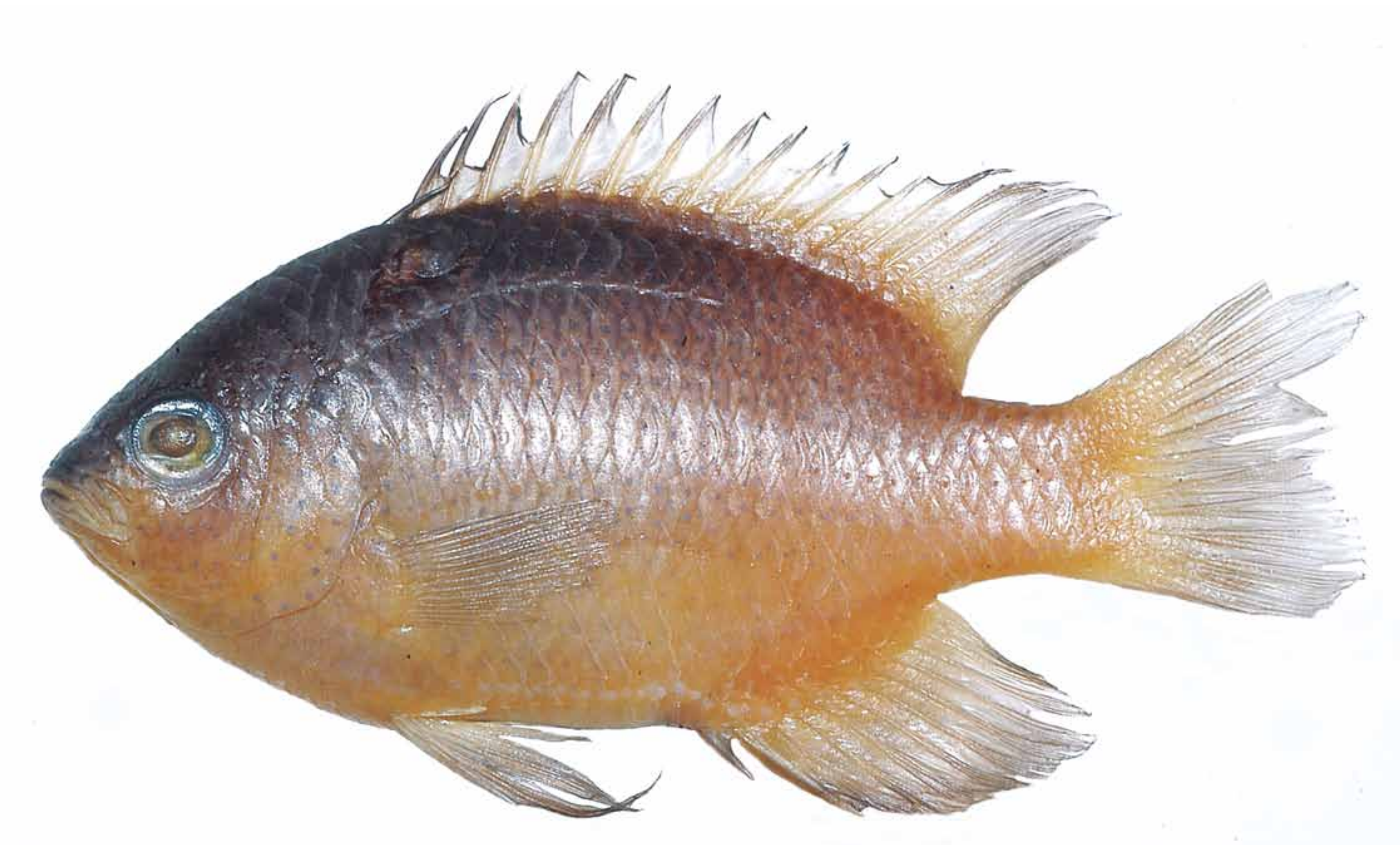

Figure 5. *Chrysiptera maurineae*, preserved holotype, MZB 22773, male, 48.8 mm SL, Cenderawasih Bay, Indonesia (G.R. Allen).

Chrysiptera maurineae, n. sp.

Maurine's Damselfish

Figures 5 & 6; Tables 2, 3 & 5.

Chrysiptera oxycephala [*non* Bleeker] Allen & Erdmann 2012: 593 (Cenderawasih Bay, West Papua, Indonesia, upper right photograph only).

Holotype. MZB 22773, male, 48.8 mm SL, Pulau Nurage, 03° 01.807' S, 134° 50.058' E, Cenderawasih Bay, West Papua Province, Indonesia, 5–12 m, hand net and clove oil, G.R. Allen & M.V. Erdmann, Nov. 10, 2008.

Paratypes. MZB 22774, 5 specimens, 37.9–49.8 mm SL & WAM P.33046–009, 5 specimens, 40.2–47.8 mm SL, collected with holotype.

Diagnosis. A species of the pomacentrid genus *Chrysiptera* with the following combination of characters: dorsal-fin rays XIII, 10–12 (usually 11); anal-fin rays II, 12–13 (rarely 13); pectoral-fin rays 14–15 (rarely 14); gill rakers on first branchial arch 9–10 + 19–22, total gill rakers 30–33; tubed lateral-line scales 12–15 (usually 15); preorbital+suborbital scales 0–6 (mean 2.7); color of small juveniles in life light blue on head, anterodorsal body, and in a streak on upper edge of caudal peduncle, bright yellow on remainder of body; adults mainly bright yellow with numerous small turquoise spots on head and body (Fig. 6).

Description. Dorsal-fin rays XIII, 11 (10–12); anal-fin rays II, 12 (one paratype with 13); pectoral-fin rays 14 (15); gill rakers on first branchial arch 9 + 21 (9–10 + 20–22), total gill rakers 30 (30–33); tubed lateral-line scales 12 (all paratypes with 15, except one 14); 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 0 (0–6, mean 2.7).

Body depth 2.0 (2.0–2.1) in SL; maximum body width 2.6 (2.5–2.9) in depth; HL contained 3.1 (3.0–3.2) in SL; snout 3.3 (3.3–3.7), eye 3.4 (2.8–3.2), interorbital width 3.5 (3.3–3.6), least depth of caudal peduncle 2.0 (1.9–2.1), length of caudal peduncle 1.9 (1.9–2.6), all in HL.

Mouth terminal, oblique, jaws forming an angle of about 40–45° to horizontal axis of head and body; maxillary reaching to vertical through anterior edge of eye; teeth of jaws biserial, those of outer row incisiform with flattened tips, upper jaw with about 48 (38–50) teeth and lower jaw with about 36 (36–44) 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 nasal opening on each side of snout, nostril with low fleshy rim; preorbital and suborbital relatively narrow, greatest depth of suborbital 34.8% (26.1–36.0%) eye diameter, ventral margin smooth; margin of preopercle smooth, without any denticulations; margin of opercular series smooth except for 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 scales absent in holotype, but few scattered embedded scales usually present; 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 about 55% length of pelvic-fin spine.

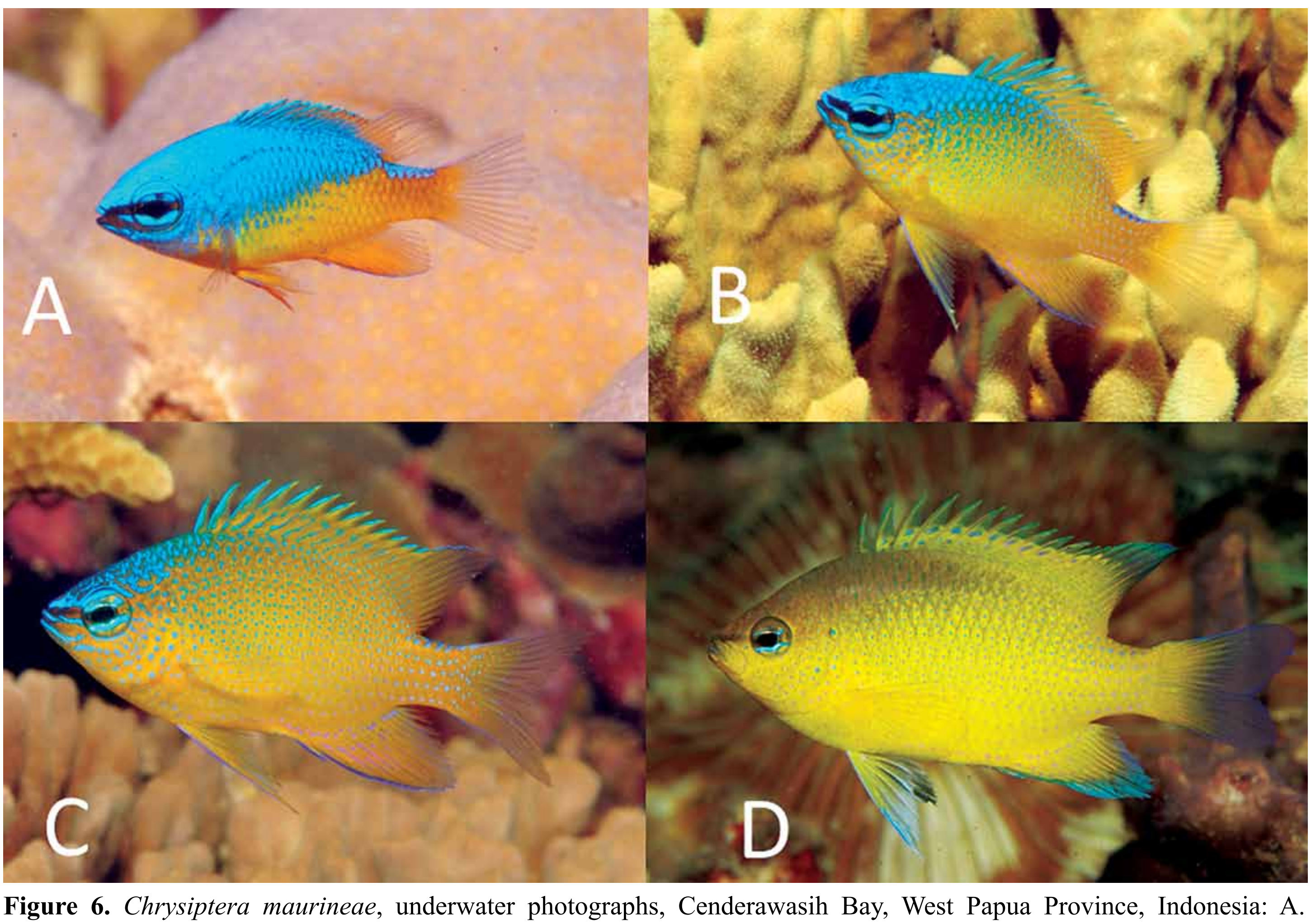

Figure 6. *Chrysiptera maurineae*, underwater photographs, Cenderawasih Bay, West Papua Province, Indonesia: A. juvenile, approximately 15 mm SL; B. juvenile, approximately 25 mm SL; C. subadult, approximately 35 mm SL; D. adult, approximately 48 mm SL (G.R. Allen).

TABLE 3

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

	holotype	paratypes						
	MZB 22773	MZB 22774	WAM P P.33046	WAM P P.33046	WAM P P.33046	MZB 22774	WAM P P.33046	MZB 22774
Standard length (mm)	48.8	49.8	47.8	45.1	44.6	43.3	40.5	37.9
Body depth	50.3	48.0	49.7	50.0	50.3	49.5	51.1	50.3
Body width	19.1	19.4	18.7	17.6	18.9	17.9	19.4	17.4
Head length	32.0	31.2	32.3	32.1	33.6	32.4	8.9	32.7
Snout length	9.8	8.8	9.7	8.6	9.5	8.9	11.3	9.9
Orbit diameter	9.4	10.0	10.1	10.0	10.8	10.8	9.7	11.5
Interorbital width	9.3	9.3	9.5	9.5	9.3	9.4	9.7	9.3
Caudal-peduncle depth	16.4	16.3	16.0	16.4	16.4	16.1	16.1	15.5
Caudal-peduncle length	17.3	16.2	13.9	15.0	14.1	14.8	16.1	15.7
Upper jaw length	10.3	10.0	10.6	10.5	11.1	10.9	10.8	11.1
Predorsal length	41.0	36.5	39.2	39.3	39.7	37.8	37.6	40.1
Preanal length	64.5	64.4	67.2	64.6	64.9	66.5	65.9	65.7
Prepelvic length	39.7	38.0	39.8	40.1	39.1	40.3	38.5	39.8
Length dorsal-fin base	57.6	61.5	59.6	61.0	62.0	60.3	60.4	60.0
Length anal-fin base	27.2	28.6	27.2	27.5	28.3	27.9	27.0	26.1
Length pectoral fin	28.1	28.8	31.2	29.2	31.1	33.5	30.0	31.7
Length pelvic fin	32.0	29.8	30.0	33.5	34.4	34.8	34.5	33.4
Length pelvic-fin spine	16.8	17.3	17.5	17.6	18.1	18.7	18.6	18.6
Length first dorsal spine	9.0	7.3	7.5	8.6	9.4	8.8	7.4	8.0
Length second dorsal spine	16.0	17.6	17.5	18.1	17.7	18.1	17.1	17.9
Length seventh dorsal spine	15.6	17.0	16.6	18.1	17.6	18.0	17.9	16.0
Length longest dorsal ray	22.9	24.3	24.7	27.2	27.4	27.4	24.5	26.5
Length first anal spine	9.0	9.1	9.9	10.3	9.3	10.7	9.2	9.6
Length second anal spine	19.1	19.1	17.8	19.9	18.8	20.7	20.7	19.8
Length longest anal ray	26.2	24.2	24.9	27.5	27.8	27.3	22.4	23.9
Length caudal fin	28.2	29.7	33.1	32.9	32.5	33.1	30.6	33.6
Caudal concavity	6.6	7.0	6.0	6.9	8.1	8.7	7.0	5.6

Tubed lateral-line scales ending below posterior spines of dorsal fin; pits or pores present on 4 (2–5) scales immediately posterior to last tubed scale; continuous series of 8 (5–8) pored or pitted scales mid-laterally on caudal peduncle to caudal-fin base.

Origin of dorsal fin at level of fourth tubed scale of lateral line; spines of dorsal fin gradually increasing in length to sixth or seventh spine, remaining spines slightly decreasing in length; membranes between spines deeply incised; first dorsal-fin spine 3.6 (3.6–4.3), seventh dorsal-fin spine 2.0 (1.7–1.9), last dorsal-fin spine 2.0 (1.7–2.0), longest dorsal-fin soft ray 1.4 (1.2–1.4), all in HL; length of dorsal-fin base 1.7 (1.6–1.7) in SL; first anal-fin spine 3.5 (3.0–3.7), second anal-fin spine 1.7 (1.5–1.8), longest anal-fin soft ray 1.2 (1.2–1.4), all in HL; base of anal fin 2.1 (2.1–2.3) in base of dorsal fin; caudal fin emarginate with rounded lobes, its length 3.5 (3.0–3.4) in SL; pectoral fin reaching vertical through anal opening, longest ray 3.6 (3.0–3.5) in SL; filamentous tips of pelvic fins reaching to about base of first anal-fin soft ray when undamaged (tips broken off in some specimens), longest ray 3.1 (2.8–3.4) in SL.

Color of adult in life. (Fig. 6D) Generally bright yellow with 1–3 small turquoise spots on each scale of body, cheek, and opercle, except dorsal portion of head and adjacent anterodorsal body (area between lateral line and most of spinous dorsal) greyish brown; faint grey-brown stripe from eye to snout tip; iris yellow with pair of turquoise stripes, one on each side of pupil; median fins and pelvic fins yellow on basal portion, translucent bluish distally; dorsal and anal fins with 2–3 rows of turquoise spots (sometimes horizontally elongate on dorsal fin); pectoral fins translucent.

Color of juvenile in life. (Figs. 6A–C) Smallest individuals (< about 15–20 mm SL) light blue on most of head, anterodorsal portion of body (above diagonal line from upper pectoral-fin base to base of last few dorsal-fin rays), and in a streak along dorsal surface of caudal peduncle, remainder of body yellow except small blue spots present on some scales; dark grey to blackish stripe across middle of blue iris, joining dark grey stripe from front of eye to snout tip; spinous part of dorsal fin light blue, soft portion yellow to translucent; anal fin mainly yellow except translucent posteriorly; caudal fin mainly translucent except yellow at base; pelvic fins yellow; pectoral fins translucent. Larger juveniles and subadults (to about 35 mm SL) gradually assume adult pattern, but blue coloration on nape and streak on dorsal margin of caudal peduncle generally persist to some degree on subadults.

Color in alcohol. (Fig. 5) Head and body generally tan, except brownish on dorsal portion of head and adjacent anterodorsal body (darkest in area between anterior lateral line and anterior base of spinous dorsal fin); dorsal and anal fins tan basally with translucent central portion and mostly dark grey outer margin; caudal fin translucent greyish; pelvic fins tan basally and dusky grey on outer portion; pectoral fins translucent; urogenital papilla blackish.

Distribution. The new species is known only from the western portion of Cenderawasih Bay in West Papua, Indonesia (Fig. 1). This location is a hotspot for endemism among fishes and invertebrates due to its past isolation as a result of both tectonic movements and eustatic fluctuations (Wallace *et al*. 2011, Allen & Erdmann 2012; see discussion below).

Etymology. The species is named in honor of Maurine Shimlock, our dear friend of many years, who has zealously promoted marine conservation of Cenderawasih Bay and the surrounding Bird's Head region by means of her excellent journalism and photography.

Comparisons. *Chrysiptera maurineae* is distinctive in both juvenile and adult color pattern (Table 2); the juvenile shares the bicolor blue and yellow pattern with *C. oxycephala* and *C. papuensis*, however it is unique in having a streak of blue along the dorsal caudal peduncle. As an adult, *C. maurineae*, is bright yellow over much of the body vs. the predominantly greenish yellow or greenish color of the adults of *C. oxycephala* and *C. ellenae*, with bright yellow only on the thorax and abdomen, at most. In addition, there are a few slight meristic differences: *C. maurineae* has one more tubed lateral line scale on average than the other species, a mode of 15 (shared only with the Lembeh genovariant population of *C. oxycephala*). Compared to *C. ellenae*, the new species has relatively few preorbital+suborbital scales, the holotype has none and the average number of scales is less than three, vs. an average of six and rarely none in *C. ellenae*.

Chrysiptera oxycephala (Bleeker 1877)

Bluespot Damselfish

Figures 7–9; Tables 2 & 5.

Paraglyphidodon oxycephalus Bleeker 1877: 387 (Buro Island and Timor Island, Indonesia).
Abudefduf azurepunctatus Fowler & Bean 1928: 149 (Romblon Harbor, Philippines).
Chrysiptera melanomaculata Aoyagi 1941: 180 (Palau).
Chrysiptera oxycephala Allen 1991: 96, 2 figs. (Indonesia, Philippines, Palau, and New Guinea); Myers 1999: 182, pl. 100 E & F (Palau in Micronesia); Allen & Erdmann 2012: 593 (Indonesia, Philippines, New Guinea, and Solomon Islands [upper left photograph of adult from Solomon Islands; lower left photograph of juvenile from Palau]).

Material examined. BPBM 9355, 13 specimens, 32.0–46.0 mm SL, Palau Islands; USNM 89963, 2 specimens, 48.0–50.3 mm SL (cotypes of *Abudefduf azurepunctatus*), Romblon Harbour, 12° 34.807' N, 122° 15.942' E, Romblon Island, Philippines; RMNH 6506 (holotype of *Paraglyphidodon oxycephalus*), 43.9 mm SL, Buru or Timor, Indonesia; WAM P.29713-007, 13 specimens, 28.2–46.6 mm SL, Pulau Besar, 08° 29.020' S, 122° 25.077' E, Maumere Bay, Flores, Lesser Sunda Islands, Indonesia; WAM P.33766-002, 2 specimens, Teluk Banyumandi, 08° 08.215' S, 114° 33.510' E, Bali, Lesser Sunda Islands, Indonesia.

Lembeh Population: MZB 22939, 6 specimens, 39.7–51.9 mm SL, Batu Angus Lagoon, 01° 30.441' N, 125° 14.764' E, Lembeh Strait, North Sulawesi Province, Indonesia, 3–15 m, clove oil, G.R. Allen, June 23, 2015; USNM 432466, 3 specimens, 42.7–49.5 mm SL, collected with MZB 22939; WAM P.33763–001, 31.7 mm SL,

Figure 7. *Chrysiptera oxycephala*, underwater photographs: A. juvenile, approximately 20 mm SL, Bali, Indonesia; B. juvenile, approximately 30 mm SL, Bali, Indonesia; C. adult, approximately 40 mm SL, Bali, Indonesia; D. adult, approximately 50 mm SL, El Nido, Palawan, Philippines (G.R. Allen).

Batu Angus Lagoon, 01° 30.441' N, 125° 14.764' E, Lembeh Strait, North Sulawesi Province, Indonesia, 3–4 m, clove oil, G.R. Allen, Sep. 11, 2012; WAM P.34403–001, 5 specimens, 37.8–52.6 mm SL, collected with MZB 22939.

Diagnosis. A species of the pomacentrid genus *Chrysiptera* with the following combination of characters: dorsal-fin rays XIII,10–12 (usually 11); anal-fin rays II,11–13 (usually 12) ; pectoral-fin rays 13–15 (usually 15); gill rakers on first branchial arch 9–10 + 19–21, total gill rakers 29–31; tubed lateral-line scales 12–15 (usually 14); 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 0–8 (mean 2.5, n = 30). Body depth 1.9–2.1 in SL; maximum body width 2.6–3.0 in depth; HL contained 3.0–3.1 in SL; snout 3.6–3.9, eye 2.8–3.3, interorbital width 2.9–3.6, least depth of caudal peduncle 1.9–2.1, length of caudal peduncle 2.2–2.5; first dorsal-fin spine 3.4–4.2, seventh dorsal-fin spine 1.7–2.2, last dorsal-fin spine 1.9–2.4, longest dorsal-fin soft ray 1.1–1.4, length of dorsal-fin base 1.6–1.9 in SL, first anal-fin spine 3.4–4.5, second anal-fin spine 1.6–1.9, longest anal-fin soft ray 1.1–1.3, all in HL; base of anal fin 2.1–2.5 in base of dorsal fin; caudal-fin length 2.5–3.3 in SL; pectoral-fin length 3.1–3.5 in SL; pelvic-fin length 2.8–3.1 in SL; color of small juveniles in life light blue on head and anterodorsal body, yellow on posteroventral body with scattered small blue spots on scales; adults greenish yellow with numerous small turquoise spots on head and body, at most some bright yellow on thorax and abdomen of adults (Figs. 7 & 8).

The Lembeh population has essentially the same meristics and morphometrics, but they are listed here separately for comparison: dorsal-fin rays XIII, 11–12 (rarely 12); anal-fin rays II, 12; pectoral-fin rays 14–15 (usually 15); gill rakers on first branchial arch 9–10 + 19–21, total gill rakers 28–31; tubed lateral-line scales 14–16 (usually 15); 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 2–10 (mean 5.5, n = 15). Body depth 1.8–2.1 in SL; maximum body width 2.6–3.1 in depth; HL contained 2.9–3.3

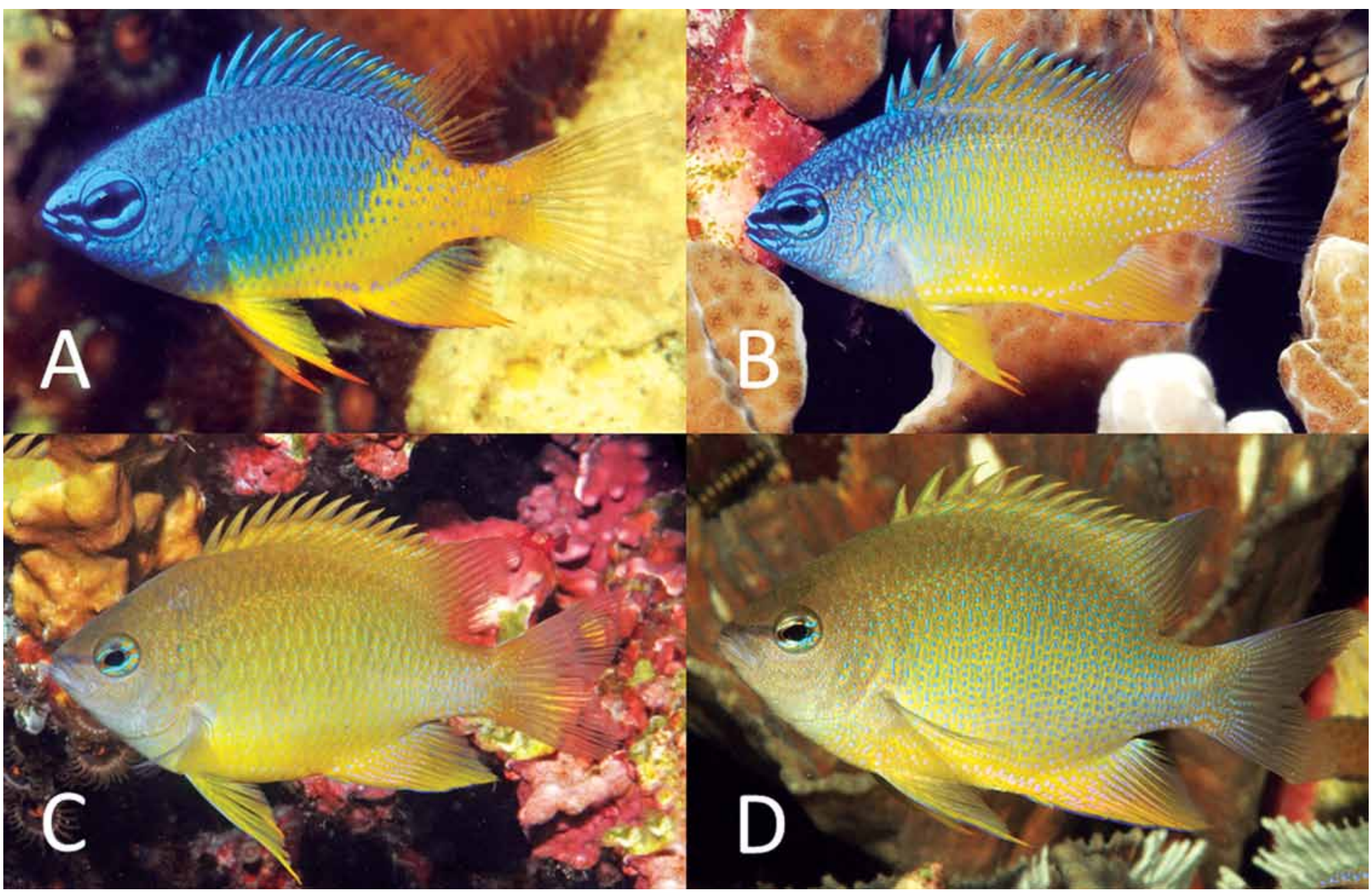

Figure 8. *Chrysiptera oxycephala* (Lembeh), underwater photographs, Lembeh Strait, North Sulawesi, Indonesia: A. juvenile, approximately 15 mm SL; B. juvenile, approximately 25 mm SL; C. adult, approximately 45 mm SL; D. adult, approximately 50 mm SL (G.R. Allen).

in SL; snout 2.9–3.9, eye 2.7–3.5, interorbital width 2.8–3.3, least depth of caudal peduncle 1.8–2.1, length of caudal peduncle 2.0–2.5; first dorsal-fin spine 3.4–5.4, seventh dorsal-fin spine 1.7–2.0, last dorsal-fin spine 1.8–2.1, longest dorsal-fin soft ray 1.1–1.2, length of dorsal-fin base 1.6–1.8 in SL, first anal-fin spine 2.7–4.4, second anal-fin spine 1.5–1.8, longest anal-fin soft ray 1.0–1.3, all in HL; base of anal fin 1.9–2.3 in base of dorsal fin; caudal-fin length 2.4–3.6 in SL; pectoral-fin length 3.1–3.6 in SL; pelvic-fin length 2.5–3.4 in SL.

Color of adult in life. (Figs. 7 & 8, C & D both) Generally greenish-yellow, brown to greenish grey on upper half of head (including forehead and side of nape); most scales of cheek, opercle, and body with 1–3 small, vertically aligned turquoise spots; thorax, abdomen, and base of anal fin usually bright yellow, scales of these areas usually with small turquoise to whitish spots; frequently with faint grey "ear" spot (about one-fourth pupil size or smaller) on upper opercle, just below level of lateral-line origin; grey stripe from eye to snout tip; iris dusky orange to grey with pair of turquoise stripes, one on each side of pupil; spinous dorsal fin greenish yellow, protruding spine tips turquoise and soft portion of fin mainly translucent bluish; anterior half and base of anal fin yellow with small turquoise or whitish spots, posterior half of fin mainly translucent bluish; caudal fin greenish yellow basally with small turquoise to whitish spots and translucent bluish outer portion; pelvic fins yellow with narrow blue anterior margin; pectoral fins translucent.

Color of juvenile in life. (Figs. 7 & 8, A & B both) Smallest individuals (about 15–20 mm SL) light blue on most of head, anterodorsal portion of body (above diagonal line from upper pectoral-fin base to base of first few soft dorsal-fin rays), remainder of body and adjacent fins pale yellow; blackish stripe across middle of blue iris, joining black stripe from front of eye to snout tip; lips charcoal grey; spinous part of dorsal fin bluish with bright blue spine tips, soft portion of fin translucent pale yellow; anal and pelvic fins yellow with narrow blue anterior margin; caudal fin pale yellow basally, remainder of fin translucent; pectoral fins translucent.

Color in alcohol. Generally brown to yellowish tan, frequently darker on head, nape, and back, grading to light tan on ventral parts of body; faint grey "ear" spot (about one-fourth pupil size or smaller) sometimes present on upper opercle, just below level of lateral-line origin; urogenital papilla blackish.

Distribution. The species is found in a wide area of the East Indies, i.e. central Indonesia including the Java Sea (Karimunjawa), Bali, Komodo, Flores, Timor, Molucca Islands (Buru), Sulawesi (Kabaena and Tobea Islands, and a distinct population in the Lembeh Straits), and northeastern Kalimantan (Berau region), ranging north to Sabah (Semporna region), as well as the Philippines (Palawan and Visayas Group), and Palau (Fig. 1).

The population of *Chrysiptera oxycephala* reported from the Solomon Islands by Allen & Erdmann (2012) most likely represents an undescribed species based on the unique juvenile and adult color patterns (see Fig. 9). Unfortunately we were unable to obtain tissue samples for DNA analysis and have examined only a single juvenile specimen (WAM P.25136–001, 28.8 mm SL) from this location. Future collecting efforts in the Solomon Islands should determine if this population represents an additional species in the *C. oxycephala* complex.

Etymology. The name *oxycephala* was derived from Greek and means "pointed head".

Comparisons. *Chrysiptera oxycephala* is distinguished by the combination of juvenile and adult coloration (Table 2). Juveniles have the bicolor blue and yellow color pattern shared only with *C. papuensis* and *C. maurineae*; notably juveniles of the latter are separated by having a blue streak on the upper caudal peduncle. Adults of *C. papuensis* differ by having a brown anterodorsal area and a bright yellow posteroventral area extending over the tail vs. the greenish yellow body of *C. oxycephala*. The other two species in the complex, *C. ellenae* and *C. sinclairi*, have entirely blue juveniles.

The Lembeh population of *C. oxycephala* shows no consistent differences in color patterns or morphometrics, and only a slight meristic difference of one additional lateral-line scale on average (Table 5). These differences are not sufficient to justify a species or subspecies-level designation. The population does diverge in mtDNA sequence (discussed below).

Remarks. Bleeker's (1877) original description of this species mentions a total of four specimens from the Indonesian islands of Buro (now Buru) and Timor. However, five specimens were present in the jar at RMNH containing the types, of which only the smallest, 43.9 mm SL, was identified as *C. oxycephala* and it agrees well with the illustrated type in the Bleeker Atlas. The other four specimens were identified as *Hemiglyphidodon plagiometopon* (and subsequently assigned a new number, RMNH 38315). Therefore the single specimen, RMNH 6506, is considered the holotype, but the precise geographic origin (Buru or Timor) remains uncertain.

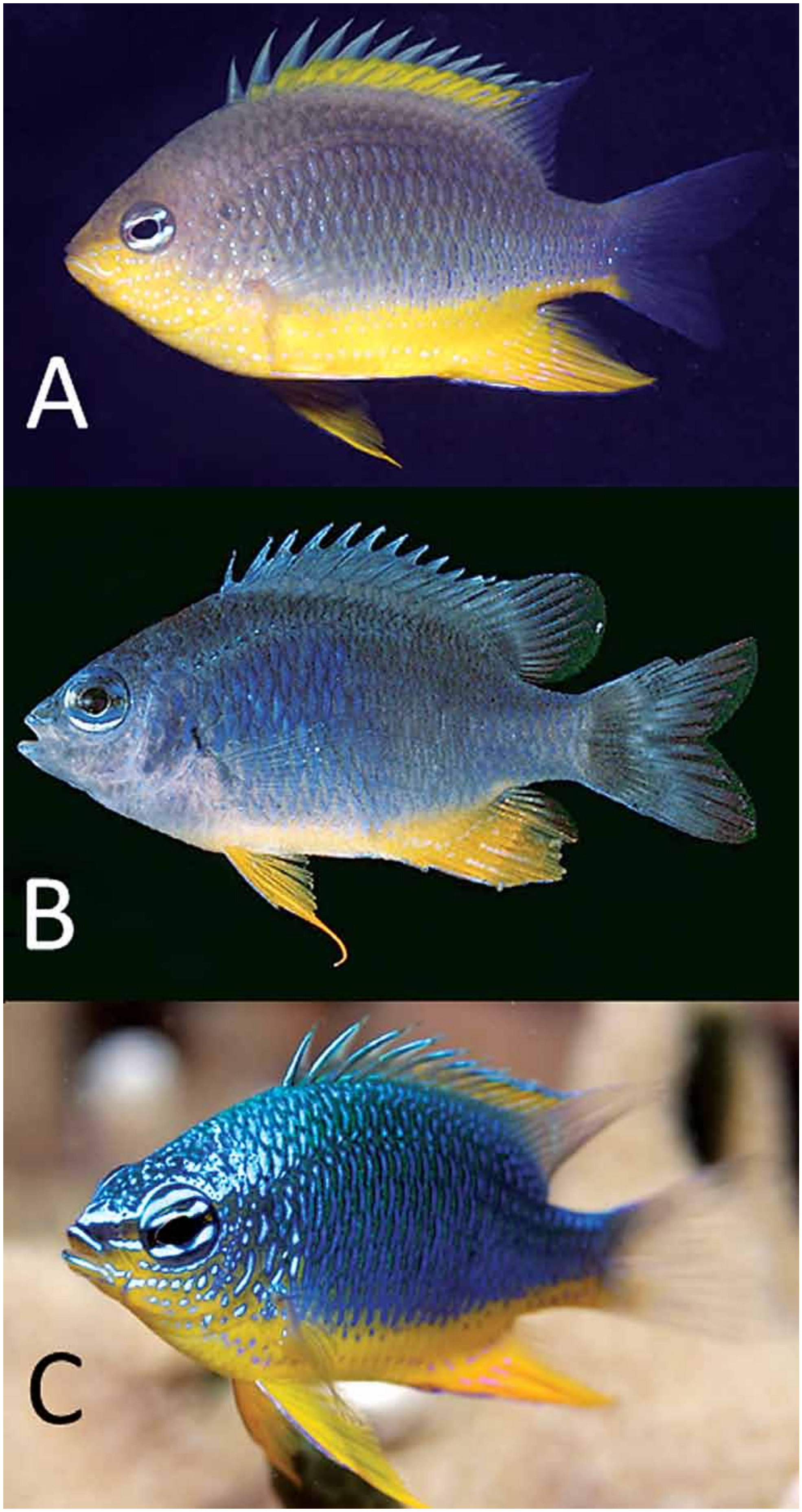

Figure 9. *Chrysiptera* cf. *oxycephala* from the Solomon Islands: A. live adult, approximately 50 mm SL; B. fresh juvenile, 28.8 mm SL (WAM P.25136–001); C. live juvenile, approximately 20 mm SL (G.R. Allen).

Figure 10. *Chrysiptera papuensis*, preserved holotype, WAM P.34426-001, male, 44.5 mm SL, Waga Waga, Papua New Guinea (G.R. Allen).

Chrysiptera papuensis, n. sp.

Papuan Damselfish

Figures 10 & 11; Tables 2, 4 & 5.

Holotype. WAM P.34426-001, male, 44.5 mm SL, deck of *Muscoota*, a World War II shipwreck, 10° 24.429' S, 150° 24.650' E, Waga Waga, Milne Bay Province, Papua New Guinea, 25–10 m, clove oil and hand net, G. R. Allen, Aug. 28, 2015.

Paratypes. USNM 432446, 4 specimens, 30.0–41.9 mm SL, collected with holotype; WAM P.34320-001, 6 specimens, 30.2–38.6 mm SL, same data as holotype except collected Dec. 14, 2014.

Non-type specimens. AMS I.16687-004, 9 specimens, 31.2–50.8 mm SL, Kranket Lagoon, 05° 11.550' S, 145° 49.440' E, Madang, Papua New Guinea, 3–10 m, spear, G.R. Allen & W. Starck, April 3, 1972; AMS I.17083-007, 17 specimens, 20.5–52.7 mm SL, Kranket Lagoon, 05° 11.550' S, 145° 49.440' E, Madang, Papua New Guinea, 3 m, rotenone, B. Collette, May 23, 1970; AMS I.17088-015, 39 specimens, 21.6–51.3 mm SL, Pig Island, 05° 10.152' S, 145° 50.410' E, Madang, Papua New Guinea, 5–14 m, explosives, B. Collette, May 29, 1970.

Diagnosis. A species of the pomacentrid genus *Chrysiptera* with the following combination of characters: dorsal-fin rays XIII, 10–11 (uncommon 10); anal-fin rays II,12–13 (rare 13); pectoral-fin rays 14–15 (usually 15); gill rakers on first branchial arch 9–10 + 19–21, total gill rakers 29–31; tubed lateral-line scales 13–16 (usually 14); preorbital+suborbital scales 0–10 (mean 4.4); color of small juveniles in life light blue on head and anterodorsal body, bright yellow on remainder of body and adjacent fins; adults greyish brown on head, nape, and anterodorsal body, bright yellow with numerous small turquoise to whitish spots on posteroventral body (Fig. 11).

Description. Dorsal-fin rays XIII, 10 (10–11, uncommon 10); anal-fin rays II, 12 (rare 13); pectoral-fin rays 15 (14–15); gill rakers on first branchial arch 9 + 21 (9–10 + 9–21), total gill rakers 30 (29–31); tubed lateral-line scales 14 (13–15, rare 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 3 (0–10, mean 4.4).

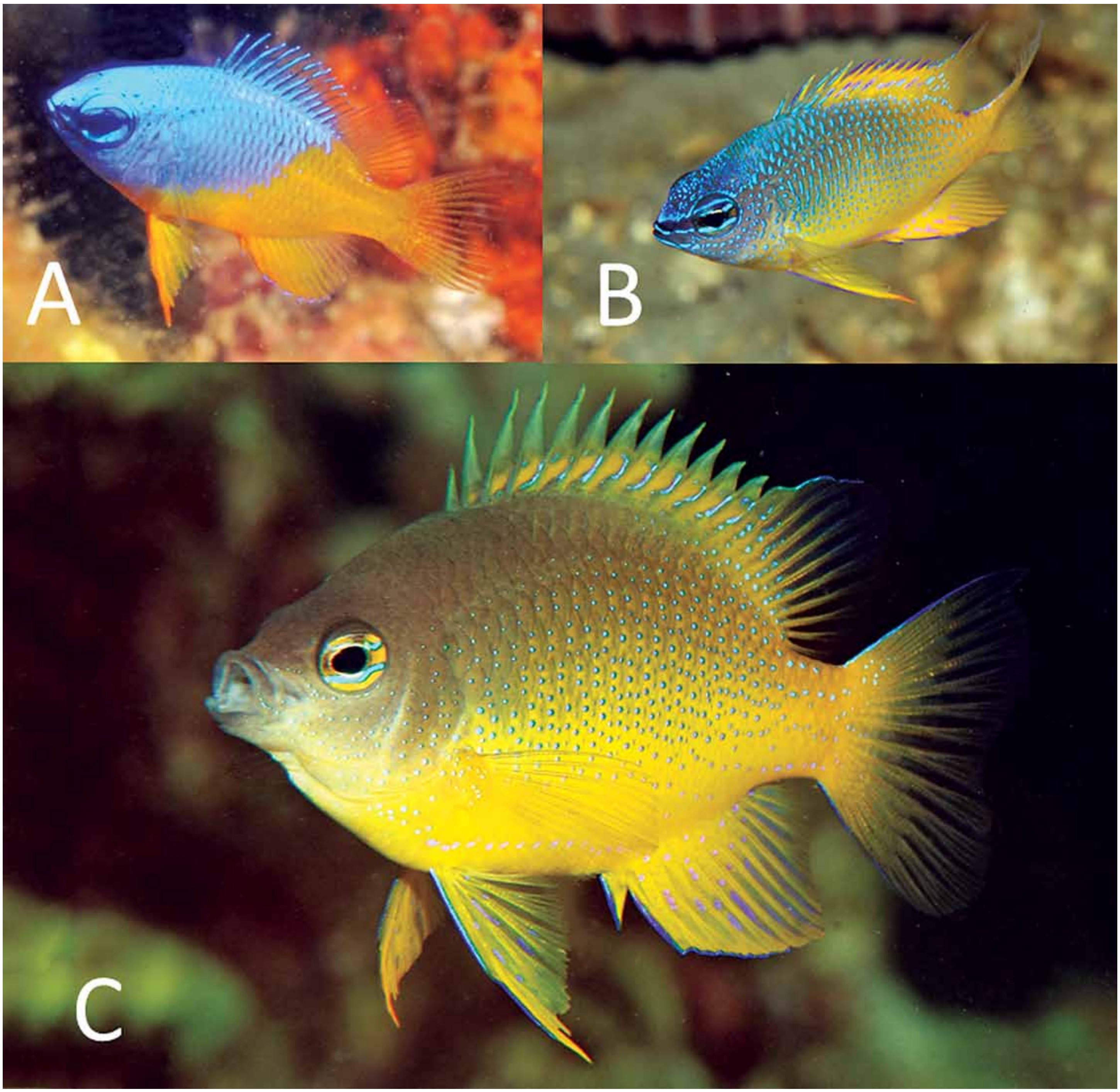

Figure 11. *Chrysiptera papuensis*, underwater photographs, Milne Bay Province, Papua New Guinea: A. juvenile, approximately 20 mm SL; B. subadult, approximately 30 mm SL; C. adult holotype, 44.5 mm SL (G.R. Allen).

TABLE 4

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

	holotype	paratypes						
	WAM P P.34426	USNM 432446	WAM P P.34320	WAM P P.34320	WAM P P.34320	WAM P P.34320	WAM P P.34320	WAM P P.34320
Standard length (mm)	44.5	41.9	38.6	37.9	34.8	34.7	30.2	30.5
Body depth	52.3	48.6	52.2	50.4	46.2	53.1	49.9	50.7
Body width	19.5	19.5	17.6	17.6	18.1	18.0	16.4	16.9
Head length	32.4	31.9	33.0	31.8	33.1	33.7	33.0	33.9
Snout length	8.4	8.2	7.8	8.2	8.6	7.8	8.2	10.1
Orbit diameter	11.1	11.8	11.3	12.1	12.5	11.9	12.1	12.1
Interorbital width	9.4	9.1	9.0	9.1	9.2	8.8	9.3	9.6
Caudal-peduncle depth	15.5	15.2	15.7	16.4	15.2	15.7	15.8	16.2
Caudal-peduncle length	13.2	14.2	12.7	15.5	14.0	13.9	13.5	12.0
Upper jaw length	9.9	10.6	10.2	10.2	10.5	10.1	10.2	10.7
Predorsal length	37.4	39.3	37.6	37.1	38.5	39.0	38.2	41.3
Preanal length	66.4	64.2	69.3	65.9	65.7	66.2	65.3	67.6
Prepelvic length	38.7	39.1	40.1	37.7	38.8	38.9	37.6	39.8
Length dorsal-fin base	60.4	58.2	57.6	60.8	60.1	55.1	57.9	57.0
Length anal-fin base	26.9	25.6	27.0	26.8	25.6	27.3	26.5	28.6
Length pectoral fin	30.4	28.9	33.0	30.2	29.6	31.2	32.7	31.1
Length pelvic fin	35.1	35.3	37.6	39.7	37.8	36.6	38.8	41.2
Length pelvic-fin spine	17.3	17.9	18.8	19.6	19.6	19.2	20.5	20.8
Length first dorsal spine	9.0	7.2	7.1	7.8	7.9	6.7	8.9	9.5
Length second dorsal spine	16.9	15.7	17.3	18.2	17.1	17.0	18.2	17.5
Length seventh dorsal spine	15.7	15.1	16.7	17.5	16.9	16.6	18.2	16.4
Length longest dorsal ray	24.1	23.6	21.6	31.9	23.8	26.0	26.1	31.4
Length first anal spine	8.6	7.8	8.9	10.0	9.8	8.5	9.6	8.8
Length second anal spine	18.8	18.8	20.3	18.8	20.0	21.3	21.5	20.2
Length longest anal ray	24.6	23.2	28.3	29.8	27.4	27.8	29.2	32.8
Length caudal fin	32.6	29.6	35.2	38.0	36.0	34.5	35.8	39.5
Caudal concavity	6.1	7.0	8.9	8.6	10.2	10.0	7.0	12.8

Body depth 1.9 (2.0–2.1) in SL; maximum body width 2.7 (2.5–2.9) in depth; HL contained 3.1 (3.0–3.2) in SL; snout 3.9 (3.3–4.3), eye 2.9 (2.6–2.8), interorbital width 3.4 (3.1–3.8), least depth of caudal peduncle 2.1 (1.9–2.2), length of caudal peduncle 2.5 (2.0–2.8), all in HL.

Mouth terminal, oblique, jaws forming an angle of about 40–45° to horizontal axis of head and body; maxillary reaching to vertical through anterior edge of eye; teeth of jaws biserial, those of outer row incisiform with flattened tips, upper jaw with about 44 (42–48) teeth and lower jaw with about 44 (36–46) 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 nasal opening on each side of snout, nostril with low fleshy rim; preorbital and suborbital relatively narrow, greatest depth of suborbital 29.2% (19.2–28.5%) eye diameter, ventral margin smooth; margin of preopercle smooth, without any denticulations; margin of opercular series smooth except for 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 a few scattered, 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 about 52% length of pelvic-fin spine.

Tubed lateral-line scales ending below posterior spines of dorsal fin; pits or pores present on 4 (3–5) scales immediately posterior to last tubed scale; continuous series of 8 (7–8) pored or pitted scales mid-laterally on caudal peduncle to caudal base.

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 slightly decreasing in length; membrane between spines deeply incised; first dorsal-fin spine 3.6 (3.4–5.0), seventh dorsal-fin spine 1.9 (1.7–2.0), last dorsal-fin spine 2.1 (1.8–2.1), longest dorsal-fin soft ray 1.3 (1.0–1.5), all in HL; length of dorsal-fin base 1.7 (1.6–1.8) in SL; first anal-fin spine 3.8 (3.1–4.0), second anal-fin spine 1.7 (1.5–1.7), longest anal-fin soft ray 1.3 (1.0–1.4), 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 3.1 (2.5–3.4) in SL; pectoral fin reaching vertical through anal opening, longest ray 3.3 (3.0–3.5) in SL; filamentous tips of pelvic fins reaching base of first to third anal-fin soft ray when undamaged (tips broken off in most specimens), longest ray 2.8 (2.4–2.8) in SL.

Color of adult in life. (Fig. 11C) Greyish brown over head and adjacent anterodorsal part of body (above diagonal from lower operculum to last few dorsal-fin rays), remainder of body bright yellow; 1–3 small pale blue to turquoise spots on each scale of body, cheek, and opercle, except dorsal portion of head and nape (and often area between lateral line and most of spinous dorsal-fin base); faint grey-brown stripe from eye to snout tip; iris yellow-orange with a pair of turquoise stripes, one on each side of pupil; spinous dorsal fin yellowish basally with numerous turquoise spots and elongate narrow bands of same color, protruding spine tips turquoise to yellow, soft portion of fin yellowish basally and translucent bluish on outer portion; anal fin yellow basally with small whitish to turquoise spots with bluish streaks on membranes and narrow, blue anterior margin; caudal fin yellow basally with small whitish to turquoise spots and translucent bluish outer portion; pelvic fins yellow with narrow blue anterior margin; pectoral fins translucent.

Color of juvenile in life. (Figs. 11A & B) Smallest individuals (< about 15–20 mm SL) light blue on most of head and anterodorsal portion of body (above diagonal line from upper pectoral-fin base to base of first few soft dorsal-fin rays), remainder of body and adjacent fins bright yellow; blackish stripe across middle of blue iris, joining brown stripe from front of eye to snout tip; lips charcoal grey and blue; spinous part of dorsal fin blue and pectoral fins translucent. Larger juveniles and subadults (to about 35 mm SL) gradually assume adult pattern with less blue on head and body and more small blue or turquoise spots on the yellow parts.

Color in alcohol. (Fig. 10) Generally brown, darker on head, nape, and back, grading to light tan or yellowish on ventral parts of body; most scales of cheek, opercle, and side of body with 1–3 small dark brown spots; fins semi-translucent grey, median fins brown to tan basally; urogenital papilla blackish.

Distribution. The new species is restricted to the northeastern section of Papua New Guinea (Fig. 1). We have examined specimens from the vicinity of Alotau (Milne Bay Province) and Madang (Madang Province). Underwater observations were also made throughout the Louisiade Archipelago and D'Entrecasteaux Islands (both in Milne Bay Province), Tufi in Northern Province, and Kimbe Bay in West New Britain Province. Field observations by the first author indicate *C. papuensis* is absent from the outer island groups of New Ireland and Manus provinces (e.g. New Ireland, New Hanover, Manus, Hermit Islands, and Ninigo Islands), where it is replaced by *C. sinclairi*.

Etymology. The species is named for its geographic distribution, which is confined to Papua New Guinea.

Comparisons. *Chrysiptera papuensis* is distinguished from the other members of the *C. oxycephala* species complex by a combination of juvenile and adult coloration (Table 2). Juveniles have the bicolor blue and yellow color pattern shared only with *C. oxycephala* and *C. maurineae*; note that juveniles of the latter species can be distinguished by having a blue streak on the upper caudal peduncle. Adults of *C. oxycephala* differ by having a greenish yellow body with bright yellow limited to the thorax and abdomen vs. a more brownish anterodorsal area and a more extensive bright yellow posteroventral area, including the caudal peduncle and anal and caudal-fin bases, in *C. papuensis*. The remaining two species in the complex, *C. ellenae* and *C. sinclairi*, have entirely blue juveniles and *C. sinclairi* has a blue adult as well, along with a set of meristic differences in fin-ray counts and scale characters.

TABLE 5

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	**Soft dorsal-fin rays**				**Soft anal-fin rays**				**Preorbital+suborbital scales**		
	10	**11**	**12**		**11**	**12**	**13**		**range**	**mean**	**n**
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	26	3		1	28	1		0-8	2.5	30
C. oxycephala (L)		14	1			15			2-10	5.5	15
C. papuensis	5	28				32	1		0–10	4.1	33
C. sinclairi	11	9			13	7			0–1	0.2	24

Species	**Pectoral-fin rays**					**Lateral-line scales**					
	12	**13**	**14**	**15**		**11**	**12**	**13**	**14**	**15**	**16**
C. ellenae				32			1	9	15	5	2
C. maurineae			1	10			1		1	9	
C. oxycephala		2	4	24			1	4	20	5	
C. oxycephala (Lembeh)			3	12					3	11	1
C. papuensis			6	27				5	21	6	1
C. sinclairi	1	1	9	9		1	4	6	5	4	

Chrysiptera sinclairi Allen 1987

Sinclair's Damselfish

Figure 12; Tables 2 & 5.

Chrysiptera sinclairi Allen 1987: 107 (Manus Island, Papua New Guinea); Allen 1991: 99, 1 fig. (Bismarck Archipelago, Melanesia).

Material examined. WAM P.27827-056 (holotype), 42.5 mm SL, Manus Island, 02° 03.483' S, 147° 25.643' E; all paratypes (same location as holotype): BPBM 30926, 4 specimens, 21.3–33.2 mm SL; BMNH 1986.5.7: 1–4, 4 specimens, 27.6–33.6 mm SL; MNHN 1986-40, 4 specimens, 24.5–30.3 mm SL; USNM 278055, 3 specimens, 27.2–37.4 mm SL; WAM P.27827-010, 14 specimens, 14.9–49.0 mm SL; WAM P.27825-042, 5 specimens, 15.0–31.0 mm SL; WAM P.27828-002, 5 specimens, 18.0–32.0 mm SL.

Diagnosis. A species of the pomacentrid genus *Chrysiptera* with the following combination of characters: dorsal-fin rays XIII, 10–11; anal-fin rays II, 11–12 ; pectoral-fin rays 12–15 (usually 14–15); gill rakers on first branchial arch 9–10 + 19–24, total gill rakers 31–34; tubed lateral-line scales 11–15 (usually 13–14); 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 scale series usually absent, occasionally with a single scale.

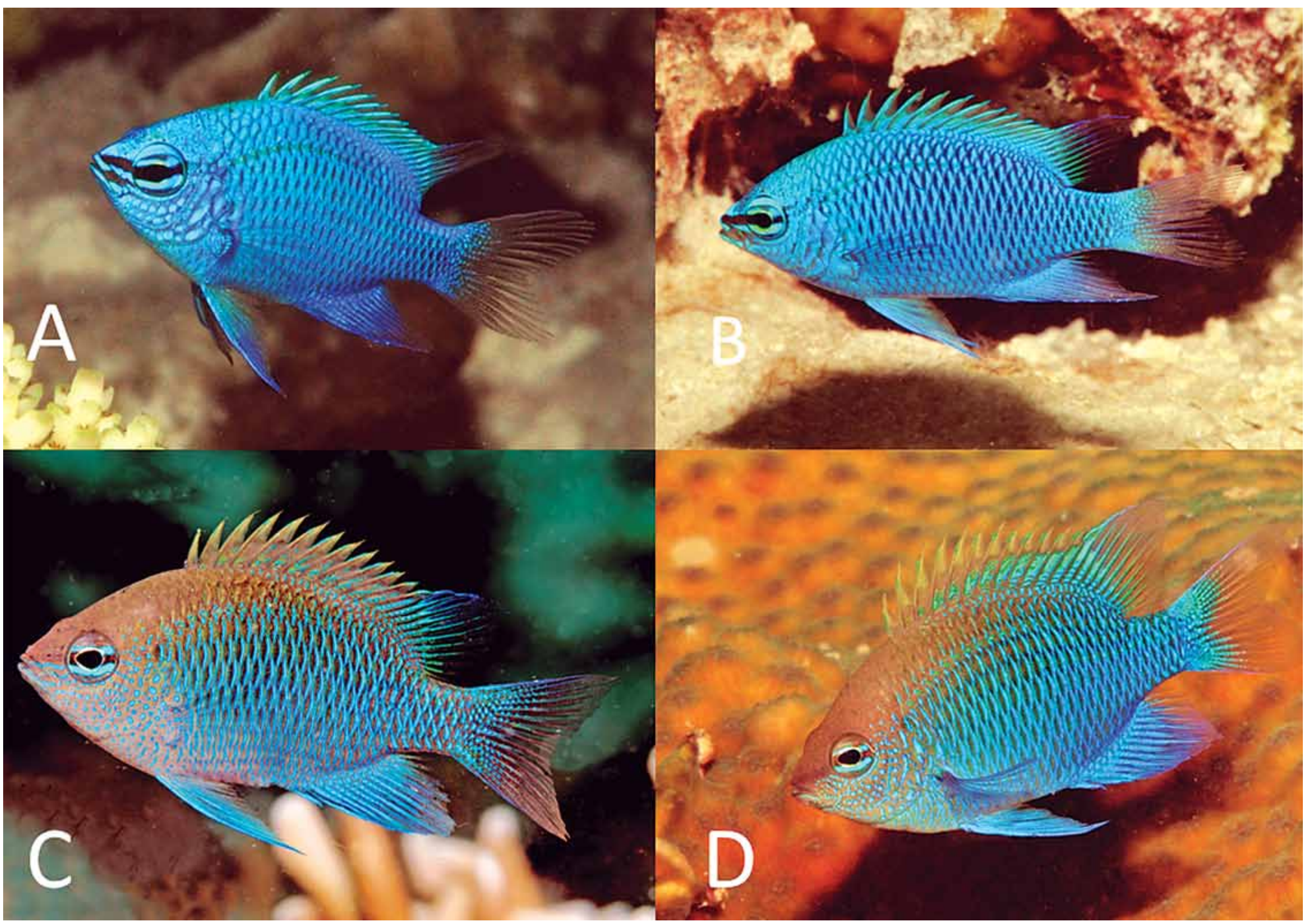

Figure 12. *Chrysiptera sinclairi*, underwater photographs, Papua New Guinea: A. juvenile, approximately 15 mm SL, Manus Island; B. juvenile, approximately 25 mm SL, Hermit Islands; C. adult, approximately 40 mm SL, Manus Island; D. adult, approximately 50 mm SL, Hermit Islands (G.R. Allen).

Body depth 2.0–2.1 in SL; maximum body width 2.6–2.7 in depth; HL contained 3.0–3.1 in SL; snout 3.5–4.0, eye 2.3–3.0, interorbital width 3.3– 3.6, least depth of caudal peduncle 2.2–2.3, length of caudal peduncle 2.3–3.1, all in HL; first dorsal-fin spine 4.0–5.6, seventh dorsal-fin spine 1.8–2.2, last dorsal-fin spine 1.8–2.2, longest dorsal-fin soft ray 1.2–1.5 all in HL; length of dorsal-fin base 1.7–1.8 in SL; first anal-fin spine 3.2–4.7, second anal-fin spine 1.8–2.3, longest anal-fin soft ray 1.1–1.3, all in HL; base of anal fin 2.1–2.3 in base of dorsal fin; caudal-fin length 2.5–2.3 in SL; pectoral-fin length 3.1–3.4 in SL; pelvic-fin length 2.8–3.3 in SL. Color of small juveniles entirely blue; adults mostly blue with brownish anterodorsal area (Fig. 12).

Color of adult in life. (Fig. 12 C & D) Head and nape brownish to greyish-green, side of head covered with bright blue spots or irregular lines from front edge of eye to snout tip; most of body scales with vertical, charcoal-colored streak in center and bright blue margin, imparting overall dusky blue appearance; thorax and abdomen light blue to greyish; fins mainly blue except outer half of spinous dorsal fin grey; pectoral fins, posterior portions of dorsal and anal fins, and outer half of caudal fin translucent.

Color of juvenile in life. (Fig. 12 A & B) Smallest individuals (< about 15–20 mm SL) entirely blue with greyish vertical streak on most body scales and blue spots on cheek and opercle; blackish stripe across middle of blue iris, joining black stripe from front of eye to snout tip; lips charcoal-grey with blue sections; spinous part of dorsal fin bluish with turquoise spine tips, soft portion of fin translucent grey; anal and pelvic fins mainly blue; caudal fin translucent grey with blue spots basally; pectoral fins translucent.

Color in alcohol. Head and body generally brown to greyish, darker dorsally; median fins brownish basally, dusky grey to translucent on outer portions; pelvic fins whitish or dusky tan; pectoral fins translucent.

Distribution. Known only from oceanic insular areas of northeastern Papua New Guinea, including the Hermit Islands, Manus, New Britain, New Ireland, and New Hanover (Fig. 1).

Etymology. The species is named in memory of the late Nick Sinclair, friend and loyal workmate of the first author, and a technical officer at the Western Australian Museum.

Comparisons. *Chrysiptera sinclairi* differs from all members of the *C. oxycephala* species complex in having blue juveniles and adults, clearly lacking yellow in all stages (Table 2). It also differs in having the urogenital papilla not marked differently from the remaining body vs. dark colored in the other related species. The only other member of the species complex sharing an entirely blue juvenile is *C. ellenae*, but those juveniles do not have the prominent dark vertical streaks on the body scales. Adults of *C. ellenae* develop a different adult color pattern entirely, with a greenish yellow background covered with small turquoise spots. Unlike the other members of the species complex, *C. sinclairi* exhibits some different meristics, i.e. one fewer modal soft-dorsal and anal-fin rays, fewer pectoral-fin rays and fewer lateral-line scales on average, and usually lacking preorbital+suborbital scales (occasionally a single scale present)(see Table 5).

Genetic Analysis

We resolved relationships within the *C. oxycephala* complex using a 384-base-pair segment of the mtDNA control region, of which 104 bases were parsimony informative. The neighbor-joining phenetic tree calculated following the Kimura-2-parameter model using 1000 bootstrap replicates (Fig. 13) shows a set of distinct monophyletic lineages representing a complex of five closely-related species in the *C. oxycephala* species complex and three outgroup species.

Not all populations with divergent mitochondrial lineages show phenotypic differences that justify species or subspecies status (Victor 2015). In this set of lineages, the Lembeh population of *C. oxycephala* is an example of this phenomenon: the population could be considered a genovariant population within the same species. In comparison, the two lineages representing *C. maurineae* and *C. sinclairi* diverge to a similar degree to the genovariant lineages within *C. oxycephala*, yet have marked phenotypic differences, including both color and meristic differences that clearly justify different species. Interestingly, the two species are the least similar in appearance among the species complex, emphasizing the finding that the degree of genotypic and phenotypic divergence within cryptic species complex is typically not well-correlated (Victor 2015). Indeed, the largest genetic divergence within the complex is between *C. papuensis* and *C. oxycephala*, the two species with the most similar color patterns and meristics.

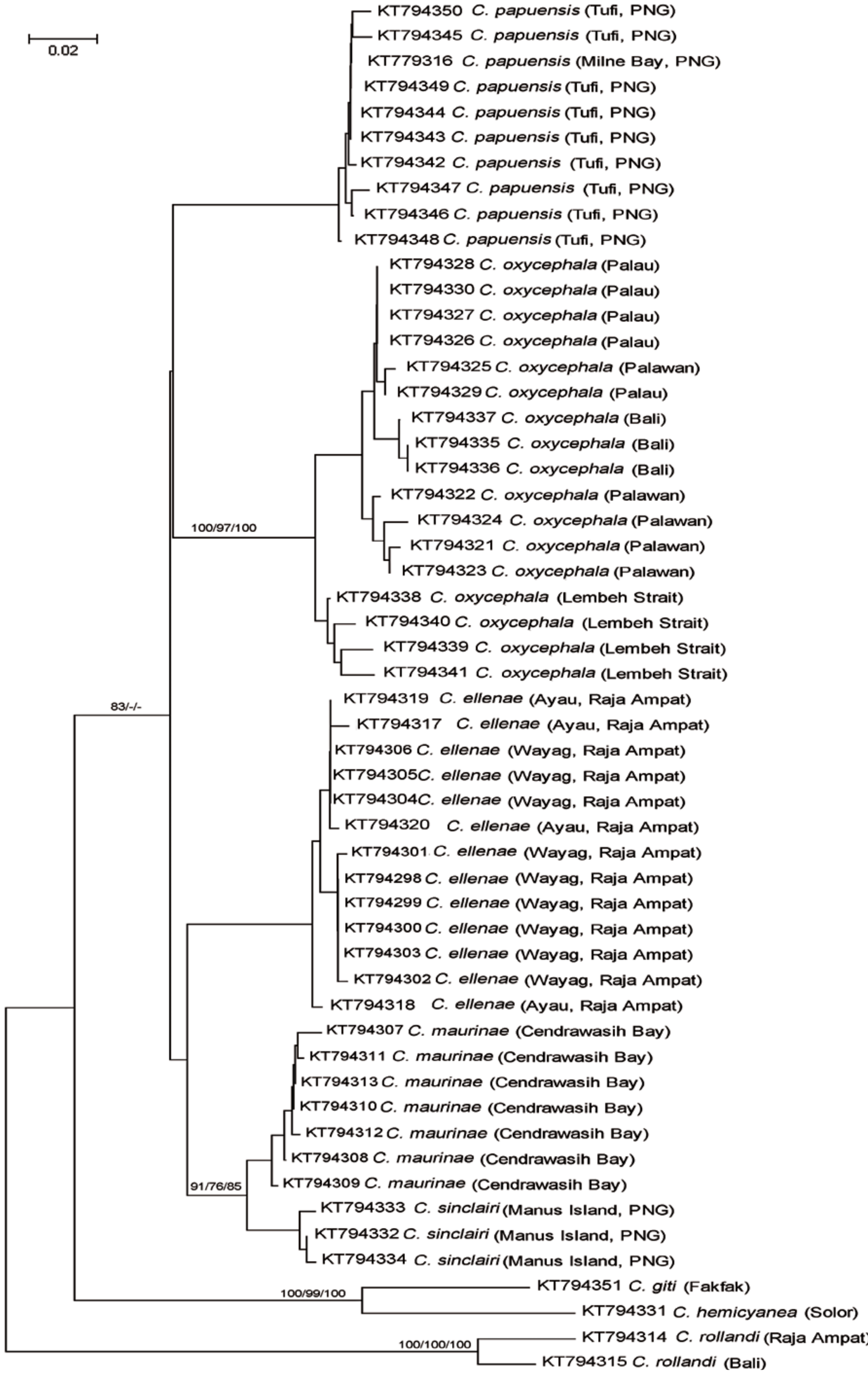

Figure 13. Neighbor Joining (NJ) topology generated from 384-bp of mtDNA control-region sequence data from *Chrysiptera* species. Numbers above the major nodes indicate bootstrap support for 1000 replicates using neighbor-joining, maximum likelihood, and Bayesian posterior probability, respectively. GenBank accession numbers and collection location are listed for each individual. Papua New Guinea is abbreviated as PNG.

TABLE 6

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

No.	Species	Location	1	2	3	4	5	6	7	8	9
1	*C. papuensis*	Tufi & Milne Bay									
2	*C. ellenae*	Raja Ampat	0.090								
3	*C. sinclairi*	Manus, PNG	0.092	0.077							
4	*C. maurineae*	Cendrawasih Bay	0.072	0.072	0.029						
5	*C. oxycephala* (L)	Lembeh Strait	0.100	0.095	0.086	0.089					
6	*C. oxycephala*	Bali, Palau, Philippines	0.109	0.106	0.093	0.094	0.030				
7	*C. giti*	FakFak, West Papua	0.185	0.181	0.183	0.175	0.197	0.195			
8	*C. hemicyanea*	Solor	0.192	0.183	0.194	0.192	0.210	0.209	0.102		
9	*C. rollandi*	Raja Ampat	0.226	0.225	0.208	0.215	0.215	0.227	0.259	0.262	
10	*C. rollandi*	Bali	0.207	0.219	0.204	0.206	0.212	0.217	0.265	0.258	0.044

Average pairwise genetic distances (Table 6) between species in the *C. oxycephala* complex range from 2.9% between *C. maurineae* and *C. sinclairi* to 10.9% between *C. papuensis* and *C. oxycephala*. The two genovariant lineages within *C. oxycephala* are relatively close, only 3.0% divergent. As expected, the outgroup species of *Chrysiptera* fall outside the *C. oxycephala* clade and exhibit much greater genetic divergences than those species within the complex.

Discussion

The evolution of the *C. oxycephala* species 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). The paleogeographic reconstruction of the southwestern Pacific region by Hall (2002) incorporates a wealth of data that provides a clear picture of the complex tectonic processes that have shaped the region's ecology over the past 55 million years. According to this model (Fig. 14), an almost continuous chain of island-arc terranes extended from the Solomons Group to North Sulawesi, therefore providing a conduit for dispersal and concomitant speciation possibilities. Although more research is needed, particularly genetic investigations, there are at least 94 species (G.R. Allen, personal data), which are endemic to portions of the "Solomons-North Sulawesi conduit", although only two, *Meiacanthus crinitus* Smith-Vaniz 1987 (Blenniidae) and *Chrysiptera arnazae* Allen, Erdmann & Barber 2010 (Pomacentridae), have distributions extending over most of the conduit area.

In the case of the *C. oxycephala* species complex, this conduit appears to have facilitated the wide dispersal of the ancestral lineage, but localized isolation events have since fostered the evolution of localized species. The best-studied example of one such event is Cenderawasih Bay, the large (approximately 59,000 km^2), horseshoe-shaped bay on the north coast of New Guinea that separates the Bird's Head Peninsula and the main body of the island. The bay was effectively isolated by a combination of 100 m+ fluctuating sea levels and a migrating island-arc fragment (Tosem Block) that slid across the entrance about 2–5 million years ago (Hill & Hall 2003). Although studies are still continuing, this remarkable hotspot of endemism is home to at least 15 fish species (including *Chrysiptera maurineae*) and 18 corals that appear to be endemic (Allen & Erdmann 2012, Wallace *et al*. 2011). In addition, genetic studies by Paul Barber (University of California at Los Angeles) and his students (Barber

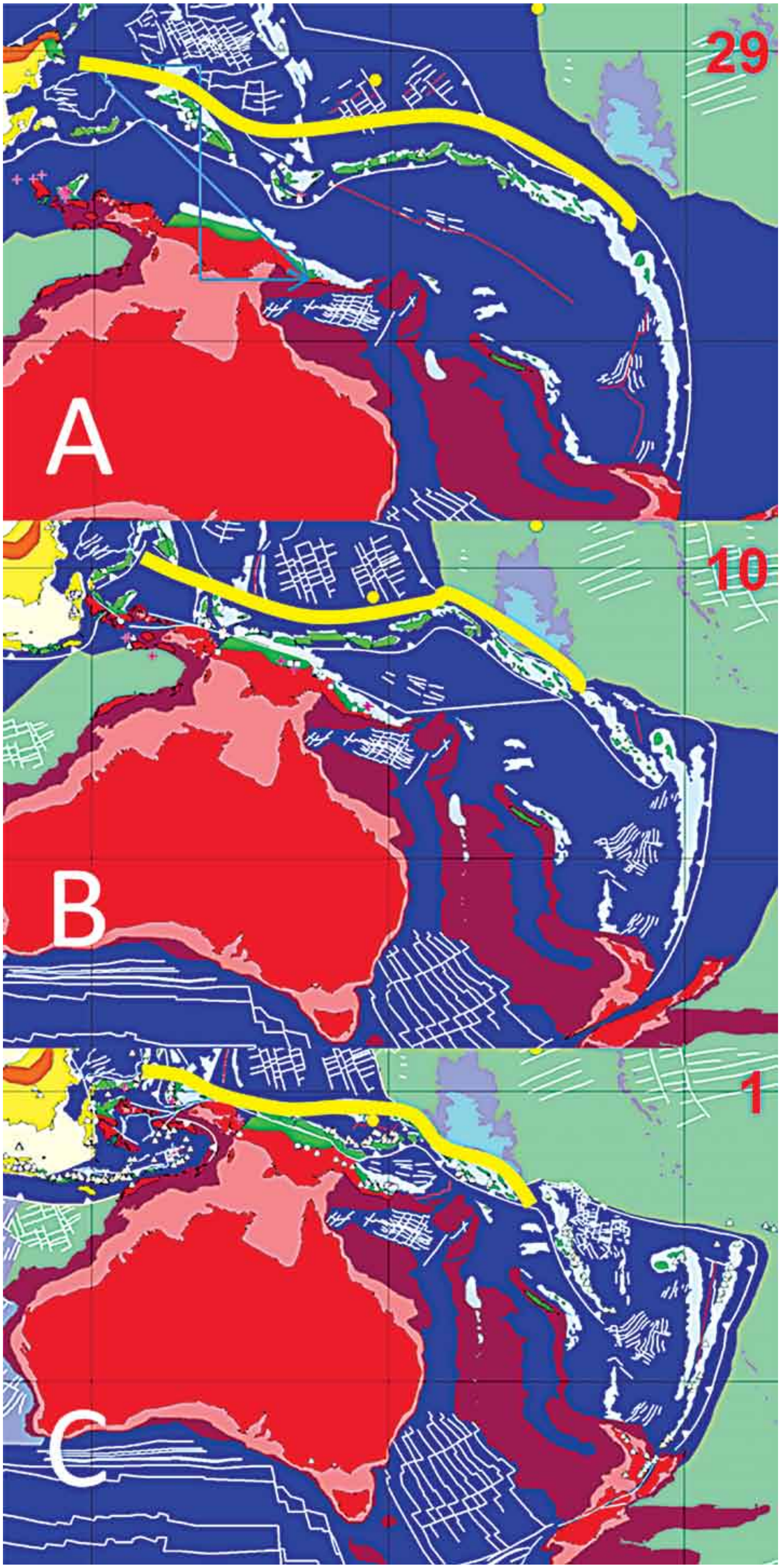

Figure 14. Paleogeographical reconstructions of the southwestern Pacific showing "Solomons-North Sulawesi conduit" (yellow line), adapted from Hall (2002): A. 29 million years ago (Mya); B. 10 Mya; C. 1 Mya.

et al. 2006, Crandall *et al*. 2008, DeBoer *et al*. 2008) have documented the presence of local DNA lineages in Cenderawasih Bay for several molluscs, crustaceans, and echinoderms. In contrast to the apparent diversification that has occurred within the *C. oxycephala* complex along the Solomons-North Sulawesi dispersal conduit, true *C. oxycephala* itself remains relatively widespread and is largely restricted to the more tectonically stable seas of the Sunda Shelf or regions connected to it by contiguous island areas (e.g. the Philippines and Lesser Sunda Islands). The Palau population is anomalous in this respect, given its geographic isolation from the Indonesian and Philippine archipelagos, nevertheless there is apparently sufficient gene flow now or in the recent past to have prevented any measurable divergence in mitochondrial DNA sequences.

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