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Lethrinus mitchelli, a new species of emperor fish (Teleostei: Lethrinidae) from Milne Bay Province, Papua New Guinea

GERALD R. ALLEN
Department of Aquatic Zoology, Western Australian Museum,
Locked Bag 49, Welshpool DC, Perth, Western Australia 6986
https://orcid.org/0000-0002-4661-4898 E-mail: gerry.tropicalreef@gmail.com

BENJAMIN C. VICTOR
Ocean Science Foundation, 4051 Glenwood, Irvine, CA 92604, USA & Guy Harvey Research Institute,
Nova Southeastern University, 8000 North Ocean Drive, Dania Beach, FL 33004, USA
https://orcid.org/0000-0002-8728-9585 E-mail: ben@coralreeffish.com

MARK V. ERDMANN
Conservation International Asia-Pacific Marine Program, University of Auckland,
23 Symonds St., Auckland 1020 New Zealand
California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118, USA
https://orcid.org/0000-0002-3644-8347 E-mail: mverdmann@gmail.com

Abstract

A new species of emperor fish, *Lethrinus mitchelli*, is described on the basis of three specimens, 109.4–111.3 mm SL, collected from 20 m at the East Cape region of Milne Bay Province, Papua New Guinea. It is similar to the sympatric relatives *L. semicinctus* and *L. rubrioperculatus*, but differs in color pattern and has a narrower cheek (cheek height 3.2–3.6 in head length vs. 2.4–2.9). Other diagnostic features include head length (2.7 in SL) greater than body depth (3.0–3.1 in SL); the snout excluding the lip 1.3–1.4 in cheek height; the snout profile nearly straight, without a prominent hump, and about 55° to the upper jaw; conical lateral jaw teeth; the interorbital area nearly flat or convex; the fourth dorsal-fin spine longest; lateral-line scales 47; transverse scale rows below and above the lateral line 15 and 4.5 rows; and a fully-scaled area adjacent to the prominent bony spine at the posteriormost margin of the opercle (excluding fleshy flap). The new species has a distinctive color pattern: brown dorsally, whitish ventrally, with a broad, brown, posteriorly tapering band on the midlateral body, partially split anteriorly by a relatively broad, ascending diagonal white band. *Lethrinus mitchelli* is 6.11% sequence divergent (pairwise) in the mtDNA COI marker from its nearest relative, *L. semicinctus*, also from the East Indies. A table of COI divergences among mtDNA lineages assigned to 27 of the 28 known species of *Lethrinus* shows a set of distinctly different lineages, from 3.32% to 20.85% divergent from each other (minimum interspecific distances).

Key words: taxonomy, ichthyology, phylogenetics, coral reef fishes, Indo-Pacific, DNA barcodes, mtDNA COI

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Introduction

The genus *Lethrinus* Cuvier, 1829 (Lethrinidae), commonly known as emperor fishes, are prominent members of Indo-Pacific reef communities and also commercially important. They are found in the tropical Indo-Pacific Ocean, ranging from East Africa and the Red Sea to the islands of French Polynesia (Carpenter 2001), except for a single species, *Lethrinus atlanticus* Valenciennes, 1830, which occurs in the Atlantic Ocean, from the shallow coastal seas of West Africa between Senegal and Gabon and the Cape Verde Islands. The genus was comprehensively reviewed by Carpenter & Allen (1989), who recognized 26 species. Subsequently, only one additional species, *Lethrinus ravus* Carpenter & Randall, 2003, has been described, from the western Pacific and eastern Indian Ocean. Most (21) of the species occur in the East Indian Archipelago, extending from the Andaman Islands to the Solomon Islands (Allen & Erdmann 2012).

We describe a new species we encountered while diving on a shoreline reef slope in the East Cape region of Milne Bay Province, Papua New Guinea during May 2018. The first author initially photographed the new species in 20 m depth and eventually three small specimens were collected by MVE. Although only subadults were collected, photographs and observations of larger adults show a distinctive color pattern.

Materials and Methods

Type specimens are deposited at the Western Australian Museum, Perth (WAM). Comparative morphological data were obtained from Carpenter & Allen (1989).

Counts and measurements follow Carpenter & Allen (1989). Pectoral-fin ray counts include the small splint-like uppermost element. Lateral-line scales include tubed scales from the upper edge of the opercle to the caudal-fin base (the line of flexure of the hypural plate), the smaller one or two tubed scales extending beyond this point are not included. Transverse scale rows above the lateral line are counted downwards and posteriorly from the base of the fifth dorsal-fin spine (the small truncated scale at the base of the fin is counted as 0.5). Transverse scale rows below the lateral line are counted upwards and anteriorly from the anal-fin origin. Parietal (supratemporal) scales are the isolated patch of scales above and behind the eye on the nape. Gill raker counts include all distinguishable elements including tiny, low-lying rudiments and are counted for the upper and lower limbs and total. Length is standard length (SL); body depth is the greatest vertical depth at the level of the pelvic-fin origin; body width is the greatest width behind the head at the level of the pectoral-fin base. Head length (HL) is measured from the snout tip to the posteriormost extension of the opercular membrane/flap. Orbit measurements are taken from the bony rim, excluding the soft fleshy rim: snout length is from the anteriormost extension of the upper lip to the anterior edge of the orbit, in addition, snout length is presented excluding the fleshy upper lip; preorbital width is from the anterior edge of the preorbital bone to the anterior edge of the orbit; the orbit is measured horizontally; the interorbital is measured from the bony rims; cheek height is measured from the lowermost point of the orbit to the apex of the preopercle angle (meeting of upper and lower limbs). The upper jaw is measured from snout tip to the posterior margin. Pectoral and pelvic-fin lengths are from the base to the tip of the longest ray. Caudal-peduncle depth is the least depth and caudal-peduncle length is the horizontal distance between the caudal-fin base and a vertical at the level of the last anal-fin ray. Caudal-fin length is a horizontal distance from the vertical line of flexure of the hypural plate to a vertical at the level of the tip of the longest ray; caudal concavity is the horizontal distance between verticals at the tips of the shortest and longest rays.

A 652-bp segment was amplified from the 5′ region of the mitochondrial cytochrome c oxidase (COI) gene using a variety of primers (Ivanova et al. 2007). After DNA extraction, PCR amplifications were performed in 12.5 µl volume including 6.25 µl of 10% trehalose, 2 µl of ultra-pure water, 1.25 µl of 10× PCR buffer (10mM KCl, 10mM $(NH_4)_2SO_4$, 20mM Tris-HCl (pH 8.8), 2mM $MgSO_4$, 0.1% Triton X-100), 0.625 µl of $MgCl_2$ (50mM), 0.125 µl of each primer (0.01mM), 0.0625 µl of each dNTP (10mM), 0.0625 µl of *Taq* DNA polymerase (New England Biolabs), and 2 µl of template DNA. Sequences were compiled using the Barcode of Life Data Systems (Ratnasingham & Hebert 2007, Ward et al. 2009) and are public (http://www.boldsystems.org) and on GenBank. Sequence divergences are BOLD p-distances. Comparison sequences for *Lethrinus* species were compiled from BOLD and GenBank records. BOLD lineages (BINs) are assigned to putative species by the senior author and will require further confirmation in future surveys of the family, since there are a number of unassigned lineages present in the BOLD database with insufficient information available to assess their true position in the family.

Figure 1. *Lethrinus mitchelli* n. sp., about 200 mm SL, East Cape Region, Milne Bay Prov., Papua New Guinea (G.R. Allen).

Lethrinus mitchelli, n. sp.

Mitchell's Emperor

urn:lsid:zoobank.org:act:AC01A248-7F13-444E-84F2-106E53AD55DC

mtDNA COI BIN BOLD:ADY6444 (https://doi.org/10.5883/BOLD:ADY6444)

Figures 1–3, 6A; Table 1

Holotype. WAM P.34850-005, 110.1 mm SL, Papua New Guinea, Milne Bay Province, East Cape region, Deakin's Reef dive site near Lawadi Village, -10.2566°, 150.6998°, 20 m, spear, M.V. Erdmann, 2 May 2018.

Paratypes. WAM P.34850-004, 2 specimens, 109.4 (DNA-sampled) & 111.3 mm SL, collected with holotype.

Diagnosis. A species of *Lethrinus* with head length 2.7 in SL, greater than body depth, 3.0–3.1 in SL; cheek height 3.2–3.6 in HL; snout length without lip 1.3–1.4 in cheek height; snout profile nearly straight without prominent hump in front of eyes, angle of snout relative to upper jaw about 55°; interorbital nearly flat or convex; fourth dorsal-fin spine longest, slightly longer than third; lateral-line scales 47; transverse scale rows below lateral line 15; transverse scale rows above lateral line 4.5; wide scaleless area on upper posterior margin of opercle; lateral teeth in jaws conical; color in life brown dorsally, whitish ventrally, with a broad, brown, posteriorly tapering band along midlateral body, partially split anteriorly by a relatively broad, ascending diagonal white band; no dark streaks radiating from eye; pelvic fins translucent with diffuse grey transverse bands; attains at least about 200 mm SL.

Description. Dorsal-fin elements X,9; anal-fin elements III,8; pectoral-fin rays 13 (except one 12); lateral-line scales 47; transverse scale rows below lateral line 15; transverse scale rows above lateral line 4.5; scale rows on predorsal nape 7 (8 on one paratype); circumpeduncular scales 9+15 (8+15); gill rakers on first gill arch 5+8=13 (5+6=11).

Body moderately elongate, greatest depth 3.1 (3.0) in SL, and laterally compressed, greatest width 2.2 (2.0–2.1) in depth; head length 2.7 in SL; snout to forehead profile straight or slightly concave; angle of snout relative to upper jaw 56° (55–56°) degrees; snout length 2.1 (2.2), snout length without lip 2.5, orbit diameter 3.6 (3.5), interorbital 5.2 (5.0–5.1), upper-jaw length 3.0 (2.8–2.9), preorbital width 3.3 (3.1–3.3), cheek height 3.4 (3.2–3.6), caudal-peduncle depth 3.8 (3.4–3.6), caudal-peduncle length 1.7 (1.8), all in HL.

Body, predorsal nape, and opercle with finely ctenoid scales; a fully scaled area adjacent to prominent bony spine at posteriormost margin of opercle, excluding fleshy flap (see Fig. 6A); one or two vertical rows containing 12 (10–12) ctenoid scales on rear edge of postorbital series and parietal scale patch containing 10 (5–10) scales immediately above; predorsal scales occupy about half of area between dorsal-fin origin and interorbital space; interorbital, snout, chin, dentary, isthmus, preorbital, preopercle, and axil of pectoral-fin base scaleless; a pair of prominent, ovate nostril openings on each side of snout; anterior nostril with elevated rim and prominent skin flap posteriorly; preopercular and opercular margins smooth; blunt, flattened, bony spine near rear margin on upper opercle and smaller flattened spine at upper extent of opercular margin.

Upper and lower jaws, including lateral portions, with outer row of widely spaced, enlarged, conical teeth, including a few enlarged canines mainly at front of jaws, and an inner row of much smaller, closely packed, villiform teeth; palatine and vomerine teeth absent; gill rakers of lower arch low and rounded, those of upper arch more columnar and less than half size of lower-arch rakers.

Dorsal fin outline incised, fourth spine longest, slightly longer than third, remaining spines gradually decreasing in length; first dorsal-fin spine 5.7 (5.3–5.6), second dorsal-fin spine 3.3 (3.0–3.2), third dorsal-fin spine 3.0 (2.8–2.9), fourth dorsal-fin spine 2.9 (2.8), tenth dorsal-fin spine 4.1 (3.9–4.3), all in HL; first 6 or 7 soft dorsal-fin rays more or less subequal, longest ray (sixth in holotype, first one or two in paratypes), 2.8 (2.7–3.0) in HL; first anal-fin spine 8.3 (7.2–7.7), second anal-fin spine 4.7 (4.1–4.6), third anal-fin spine 3.7 (3.6–3.8), of longest (first) soft anal-fin ray 3.4 (3.1–3.6), all in HL; pectoral fins pointed, length 1.4 (1.3) in HL; pelvic fins relatively short, not reaching anal-fin origin when adpressed, length 1.8 (1.7) in HL; caudal fin moderately forked, length 4.2 (4.3–4.7) in SL, its concavity 4.6 (4.4–4.7) in HL.

Color in life. (Figs. 1 & 2) Brown dorsally and greyish white on lower half of side with a broad, brown, posteriorly tapering band along midlateral body, partially split anteriorly by a relatively broad, ascending diagonal white band; brown band with strong yellow suffusion in area above pectoral-fin base extending forward onto opercle and margined above and below by a narrow pale greyish and broad whitish area; individual scales of back and lower side brownish centrally, forming an overall reticulated appearance; nape and interorbital greyish brown, grading to bronze on snout; cheek pale greyish with a variable bronze suffusion; iris golden yellow; median fins translucent with alternating brown and white, or pale grey, areas along individual spines and segmented rays, including pronounced light and dark bands along upper and lower edges of caudal fin; pelvic fins translucent with diffuse grey transverse bands; pectoral fins mostly translucent but white basally over a rounded brown spot or band across central portion of base; a darker brown band along base in axil of fin showing as a darker spot at the origin of the first pectoral-fin ray.

Figure 2. *Lethrinus mitchelli*, blotchy pattern on rubble bottom, about 200 mm SL, East Cape Region, Milne Bay Province, Papua New Guinea (G.R. Allen).

TABLE 1

Proportional measurements of type specimens of *Lethrinus mitchelli*, n. sp. as percentages of the standard length

	holotype	paratypes	
	WAM P.34850-005	WAM P.34850-004	WAM P.34850-004
Standard length (mm)	110.1	109.4	111.3
Body depth	32.3	33.2	33.8
Body width	15.0	16.1	16.5
Head length	37.0	37.0	37.1
Snout length	17.7	17.2	17.2
Snout length excluding lip	14.6	14.6	14.6
Orbit diameter	10.3	10.5	10.6
Interorbital width	48.4	50.0	50.9
Preorbital length	11.3	11.9	11.4
Cheek height	10.7	11.5	10.4
Upper-jaw length	12.2	13.3	12.9
Caudal-peduncle depth	9.8	10.8	10.4
Caudal-peduncle length	21.3	20.3	20.8
Predorsal length	41.3	39.2	40.7
Preanal length	65.0	62.5	61.5
Prepelvic length	41.6	40.1	38.7
Length dorsal-fin base	46.6	48.9	48.0
Length first dorsal-fin spine	6.5	6.6	7.0
Length second dorsal-fin spine	11.3	11.6	12.2
Length third dorsal-fin spine	12.4	12.8	13.2
Length fourth dorsal-fin spine	12.8	13.2	13.4
Length tenth dorsal-fin spine	9.0	8.5	9.4
Length longest dorsal-fin ray	13.0	12.3	13.7
Length anal-fin base	17.2	16.8	18.0
Length first anal-fin spine	4.5	5.1	4.8
Length second anal-fin spine	7.9	8.0	9.1
Length third anal-fin spine	9.9	9.6	10.2
Length longest anal-fin ray	10.9	10.4	11.9
Length pectoral fin	27.3	27.8	27.8
Length pelvic fin	21.1	21.9	21.9
Length pelvic-fin spine	12.4	14.3	14.0
Length caudal fin	23.6	21.2	23.1
Caudal concavity	8.1	7.9	8.5

Typical of many other *Lethrinus*, individuals can quickly develop a blotchy pattern (Fig. 2), composed of a series of brown to blackish bars and large diffuse dark patches on upper body and in a row along lower body, frequently assumed when an individual swims close along the substrate or when stationary at bottom, presumably a stress-related camouflage coloration.

Color in alcohol. (Fig. 3) Generally greyish brown on back grading to tan on sides with irregular grey blotches, a large blotch below lateral line at middle of spinous dorsal fin and another below lateral line under soft dorsal fin; snout and interorbital grey, lips tannish white, and cheek and opercle pale tan to greyish with large brown patch on anterior cheek; fins translucent pale grey. A blotchy pattern is faintly evident on paratypes.

Etymology. The specific epithet honors David Mitchell, a seasoned conservationist who has dedicated his career to the spectacular nature and local indigenous communities of Milne Bay.

Distribution and habitat. The new species is currently known only from the type locality in the East Cape area of Milne Bay Province, Papua New Guinea. The habitat consists of a gully with a volcanic black sand and rubble bottom, extending from the shoreline shallows to about 30 m depth on a relatively steep slope. About 10 individuals, ranging in size from about 100–200 mm SL, were observed around a large submerged tree trunk, lying horizontally across the gully in 20–25 m depth. When pursued with a spear, the fish retreated down the slope. It is therefore possible the species is normally found in deeper water, accounting for the lack of previous observations by us despite many hours of diving near the type locality over the past two decades, routinely to depths of 40–50 m.

Comparisons. The new species is most similar to *Lethrinus semicinctus* Valenciennes, 1830 (Fig. 4) and *Lethrinus rubrioperculatus* Sato, 1978 (Fig. 5), which range throughout the East Indian Archipelago and westward to Chagos and East Africa respectively. Important characters shared by these three species include a moderately elongate body, depth 2.9–3.4 in SL; head length greater than body depth; the snout directly before the eyes straight or slightly concave without a prominent hump; the snout angle relative to the upper jaw 55–65°; conical lateral teeth; the third or fourth dorsal-fin spines longest; the axil of the pectoral-fin base scaleless; 46–49 lateral-line scales; transverse scales above and below lateral line 4.5 and 14–16 respectively; and the lower series of scales around the caudal peduncle usually 15. The only morphological feature particular to *L. mitchelli* is a narrower cheek, i.e. the cheek height 3.2–3.6 in HL vs. 2.4–2.9, and cheek height into snout length excluding lip 1.3–1.4 in HL vs. 0.8–0.9 for both *L. semicinctus* and *L. rubrioperculatus*.

Figure 3. *Lethrinus mitchelli* n. sp., preserved holotype, 110.1 mm SL, East Cape Region, Milne Bay Province, Papua New Guinea (G.R. Allen).

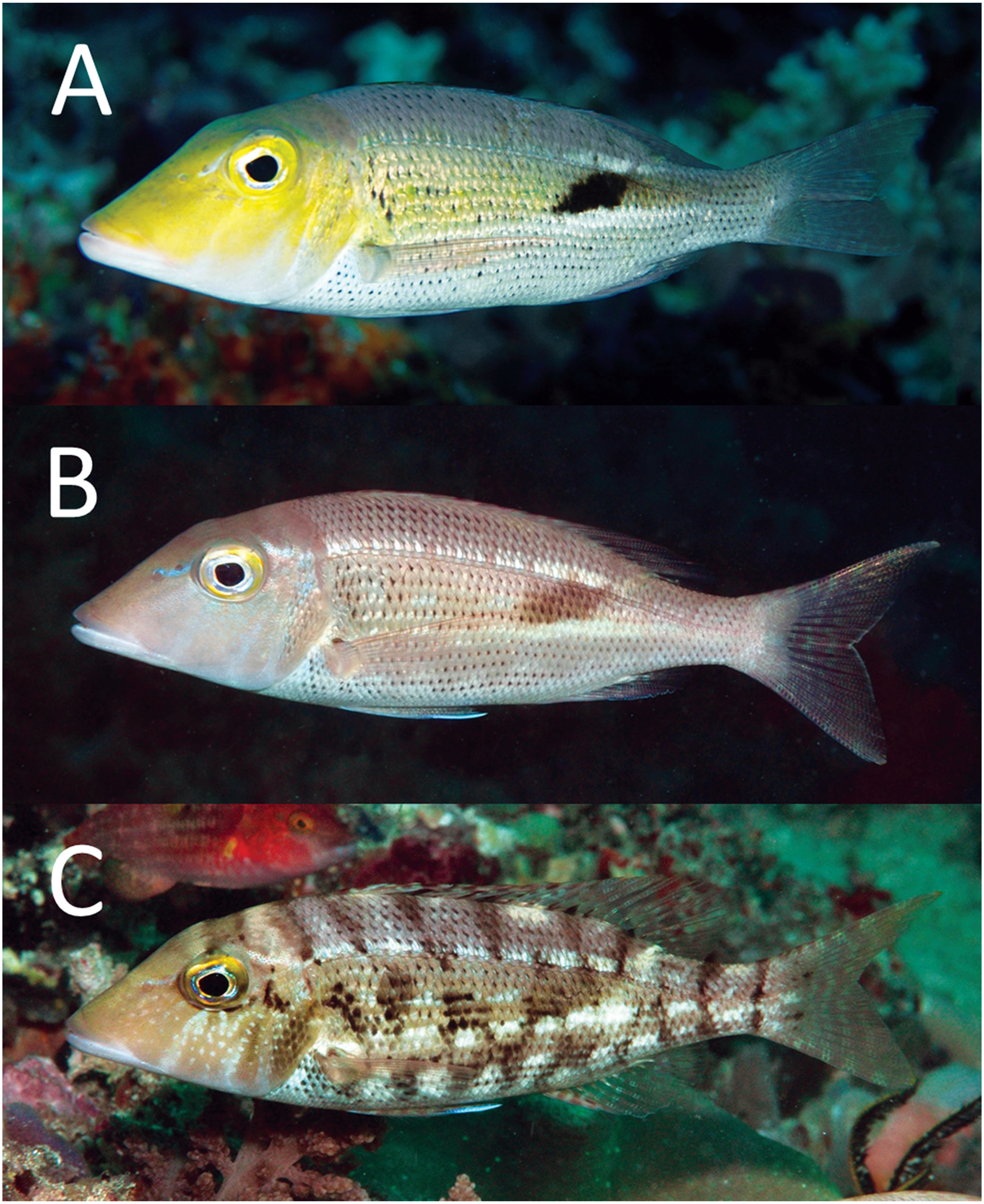

Figure 4. *Lethrinus semicinctus*, underwater photographs: A) normal pattern, approx. 250 mm SL, Fiji ; B) transitional pattern, approx. 200 mm SL, Milne Bay; and C) blotchy pattern, approx. 150 mm SL, Milne Bay Province, Papua New Guinea (G.R. Allen).

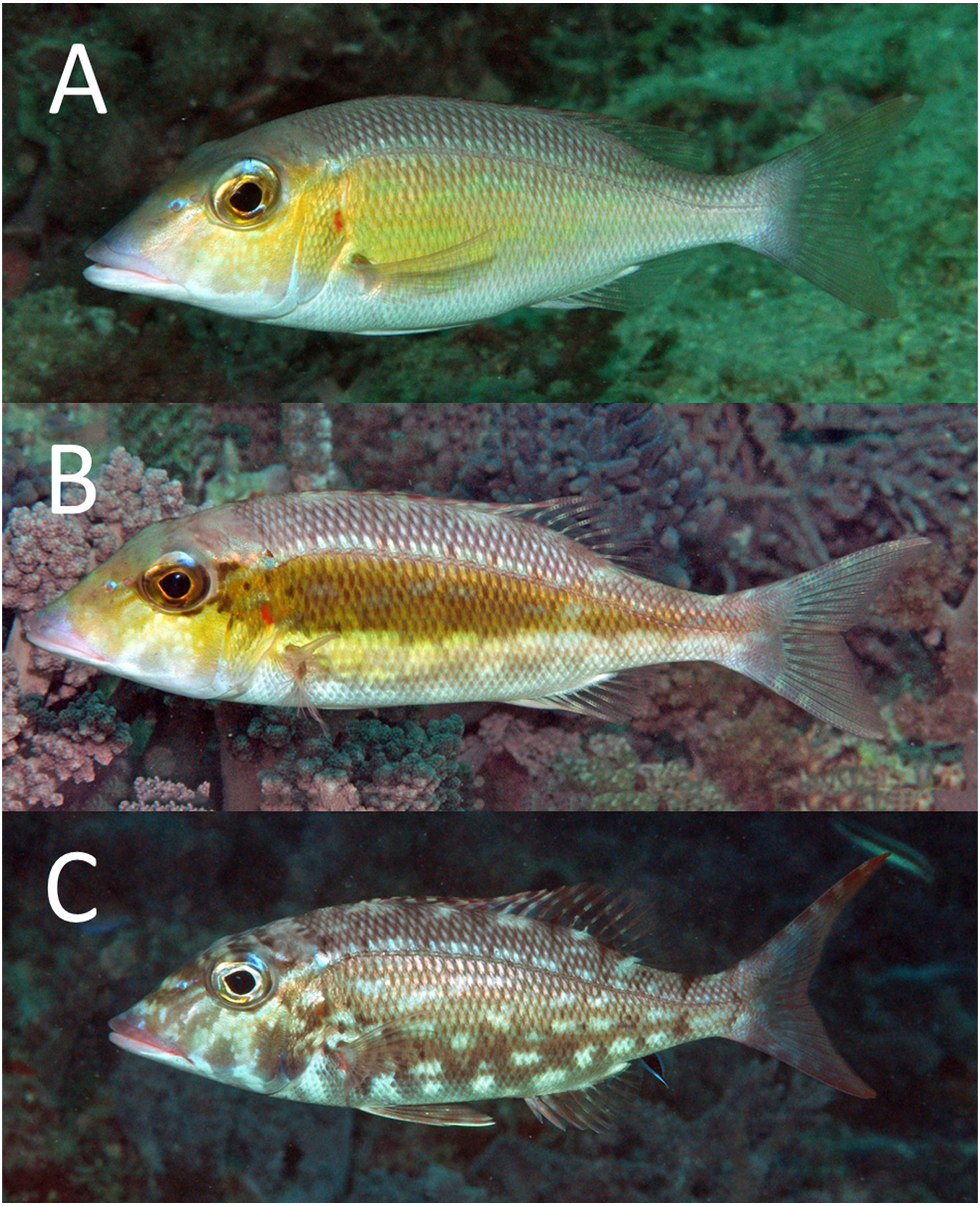

Figure 5. *Lethrinus rubrioperculatus*, underwater photographs, Milne Bay Province, Papua New Guinea: A) normal pattern, approx. 250 mm SL; B) banded pattern, approx. 200 mm SL; and C) blotchy pattern, approx. 170 mm SL (G.R. Allen). .

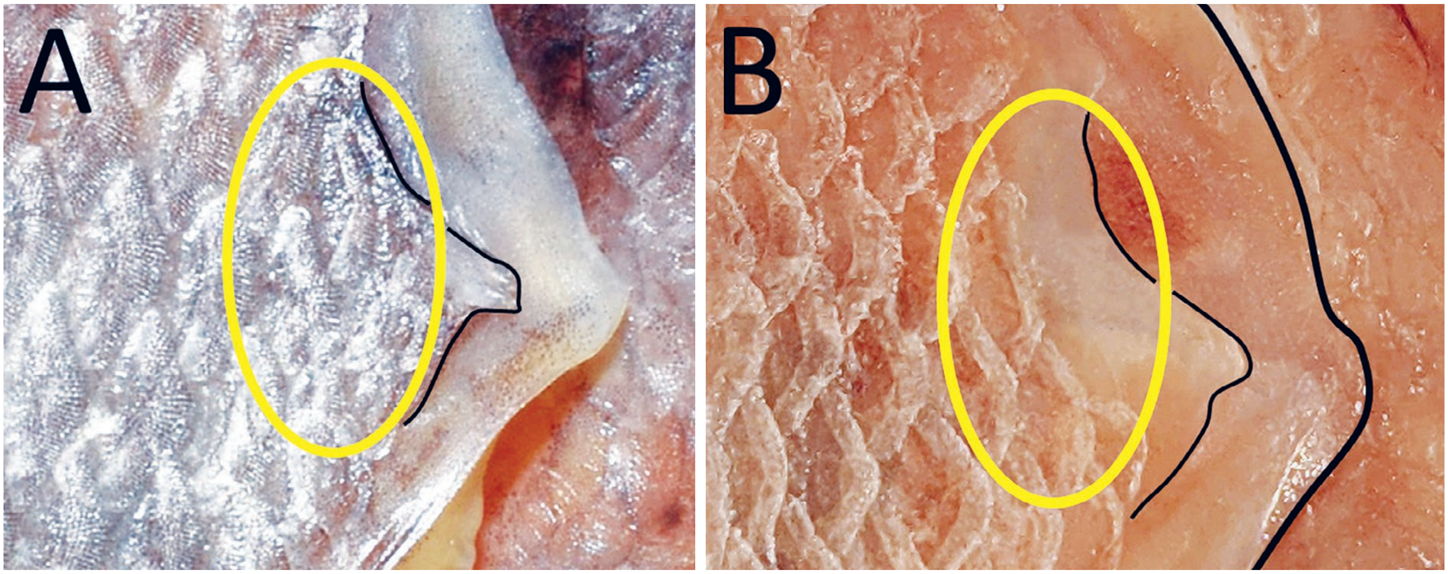

Figure 6. Comparison of scalation on the area adjacent to the opercular spine (area outlined in yellow); thin black line intersecting yellow oval is the bony opercular margin; thick black line (in B) is the edge of the soft opercular flap: A) *Lethrinus mitchelli* n. sp., preserved holotype, 110.1 mm SL; B) *Lethrinus rubrioperculatus*, WAM P.29594-003, 172.0 mm SL, Port Moresby, Papua New Guinea (G.R. & M.G. Allen).

The fully scaled condition (Fig. 6A) of the area adjacent to the prominent bony spine at the posteriormost margin of the opercle (excluding the fleshy flap) of the new species is similar to most congeners, including *L. semicinctus*. However, it differs noticeably from the wide scaleless area of *L. rubrioperculatus* (Fig. 6B). Reduced scalation in that area can also be occasionally seen in *Lethrinus crocineus* Smith, 1959 from the western Indian Ocean and *Lethrinus xanthochilus* Klunzinger, 1870 (Fig. 7), widespread in the Indo-Pacific. The latter species also has a wider cheek (cheek height 2.3–3.3 in HL and cheek height into snout length excluding lip 0.8–0.9), as well as prominent dark lines and spots radiating from the lower eye. The distinctive color pattern of *L. mitchelli*, a broad, brown, posteriorly tapering band along the midlateral body, partially split anteriorly by a relatively broad, ascending diagonal white band, distinguishes this species from all other members of the genus.

Figure 7. *Lethrinus xanthochilus*, approximately 300 mm SL, Mahe, Seychelles (G.R. Allen).

Genetic analysis. The genus *Lethrinus* may have the highest coverage for the mtDNA-barcode marker among the larger genera of reef fishes, especially among the commercially important groups. Borsa et al. (2010) identified 16S RNA sequences for 14 *Lethrinus* species from New Caledonia and used the sequences to identify larval fishes. We have identified discrete mtDNA COI lineages for 27 of the 28 known species (including the new species) (Table 2). Fricke et al. (2021) presently list *Lethrinus punctulatus* Macleay, 1878 as valid, from the Northern Territory, Australia: however, we consider it to be a junior synonym of *Lethrinus lentjan* (Lacepède, 1802), a very broadly distributed species, occurring from the Red Sea across the Indian and western Pacific Oceans north to Japan and eastward to Tonga (Allen & Erdmann 2012). We also follow Carpenter in Carpenter & Allen (1989) as considering *Lethrinus ehrenbergii* Valenciennes, 1830 to be a synonym of *Lethrinus borbonicus* Valenciennes, 1830. We are only missing *Lethrinus enigmaticus* Smith, 1959, described from deeper waters in Seychelles and Madagascar.

We evaluated the available BINs, or algorithm-derived lineages, in the BOLD database, and identified 27 BINs for the various species based on ranges, type locations, photographs in the database, as well as from specimens from our own collections. There were a number of additional BINs labeled as *Lethrinus* by various contributors– these may represent cryptic lineages, errors, misidentifications, or undescribed species, and we do not include any of them without further information. It should be emphasized that the assignments of BINs to species is a snapshot in time and only one view of the taxonomy of the genus; in future the BINs identities will be further refined or reshuffled by additional data and by other researchers. For this reason, we list BIN codes with species assignments. We include subsets of sequences based on availability and public status and attempted to include broad geography when possible, still several species are represented by single sequences. This does not mean they are lineages made up of one sequence: in almost all cases, additional sequences form the BIN, but are private or have different labels or otherwise not available to our analysis.

The mtDNA COI lineages for the 27 *Lethrinus* species are unusually well differentiated (Table 2), the matrix showing most are more than 15% divergent from each other– all are more than 3% divergent from any other species, ranging from 3.32% to 20.85% minimum interspecific differences between pairs of species (it should be emphasized that using *mean* divergences can disguise close, or even shared, sequences). Note that there are additional unassigned lineages closer than 3% to these established species lineages, but these were not included since their status could not be confirmed.

Intra-BIN variation was available on BOLD for all sequences in each BIN, including private sequences; most of these BINs were large samples, the majority from 15–77 members. All but the two largest BINs had intra-BIN maximum variation of less than 2%. The two largest BINs, *L. borbonicus* (n=77) and *L. lentjan* (n=74), had 2.41% and 2.96% intra-BIN maximum variation (again, the mean is misleading). Thus, for the 27 BINs discussed here, inter-BIN variation was always higher than intra-BIN variation, indicating a complete barcode gap. However, it appears that if all public and private sequences of *Lethrinus* in the BOLD database were included, this neat gap would rapidly break down.

The mtDNA COI sequence for the 109.4 mm SL paratype is listed in BOLD (LIDMA2952-19) and in GenBank (MZ402607). *Lethrinus mitchelli* is apparently part of the *L. semicinctus* species complex, with a 6.11% pairwise difference from the nearest-neighbor sequence in the BOLD database, a specimen of *L. semicinctus*, from the Spratly Islands, South China Sea (MW034154).

Mekkawy (2017) used existing BOLD sequences to develop a phylogeny for a variety of lethrinids, however species identifications were accepted uncritically and included misidentifications. Afrisal et al. (2021) recently explored morphology and COI genetics of *Lethrinus harak* (Forsskål, 1775), finding small differences between Indian and Pacific Ocean populations in morphology, but with some overlap. Their two populations differed by 3–4% in COI sequence, but based on 8 sequences: additional sampling will likely reduce that gap. Afrisal et al.

Table 2. (opposite) Matrix of minimum interspecific differences pairwise among lineages for 27 species of *Lethrinus* and maximum intraspecific variation within each entire BIN (values are % sequence divergence). Within-BIN variation is based on the entire set of sequences, public and private, within the listed BIN lineage, with sample sizes (N w) often much larger than the set used for calculating interspecific distances between lineages (N b). The distances for interspecific comparisons are analyzed from a subset of sequences in each BIN: from those that could be extracted from the BOLD database and thus limited by public availability and labeling differences.

	N b	1	8	1	3	3	6	3	5	4	7	8	9	10	7	6	5	1	4	9	6	8	6	1	8	6	5	6
	N w	4	23	9	77	5	7	11	17	9	11	34	13	74	42	41	6	1	36	39	31	27	15	10	75	15	9	23
	BOLD BIN	*L. amboinensis*	*L. atkinsoni*	*L. atlanticus*	*L. borbonicus*	*L. conchyliatus*	*L. crocineus*	*L. erythracanthus*	*L. erythropterus*	*L. genivittatus*	*L. haematopterus*	*L. harak*	*L. laticaudus*	*L. lentjan*	*L. mahsena*	*L. microdon*	*L. miniatus*	*L. mitchelli* n. sp.	*L. nebulosus*	*L. obsoletus*	*L. olivaceous*	*L. ornatus*	*L. ravus*	*L. reticulatus*	*L. rubrioperculatus*	*L. semicinctus*	*L. variegatus*	*L. xanthochilus*
L. amboinensis	AAC1548	0																										
L. atkinsoni	ABY5451	19.3	1.8																									
L. atlanticus	ABX8265	16.7	13.9	0.8																								
L. borbonicus	AAB0511	19.4	8.6	14.0	2.41																							
L. conchyliatus	AAL8217	3.3	18.0	15.9	17.9	0																						
L. crocineus	AAC8224	18.5	10.1	16.3	10.7	16.8	0.6																					
L. erythracanthus	AAJ2540	13.4	15.0	16.9	14.3	14.4	12.6	0.8																				
L. erythropterus	AAE3751	16.3	15.0	16.5	14.4	16.9	14.6	13.5	1.1																			
L. genivittatus	ACK7780	17.6	17.2	20.0	18.5	16.8	18.4	17.1	15.6	1.0																		
L. haematopterus	AAC8229	19.4	16.0	17.9	17.5	19.8	17.0	16.4	18.2	19.5	0.6																	
L. harak	AAC1520	20.0	9.3	13.6	11.7	17.8	9.2	16.2	16.3	18.9	17.9	1.0																
L. laticaudus	AAB2309	18.5	11.7	15.4	13.0	16.9	11.4	15.2	15.1	17.9	17.7	10.1	1.0															
L. lentjan	AAB0508	18.1	11.2	13.8	13.9	16.4	8.7	14.5	14.7	17.4	18.2	9.8	10.8	2.96														
L. mahsena	AAB6438	16.5	3.8	12.7	8.0	15.7	10.8	14.7	13.0	16.8	16.4	9.2	11.1	10.4	0.8													
L. microdon	AAC8078	13.8	14.6	15.7	16.4	12.7	16.3	16.9	16.2	18.2	16.3	18.3	17.8	19.6	15.0	1.3												
L. miniatus	AAC8077	18.2	13.6	16.0	16.4	18.1	15.8	14.9	14.5	15.4	19.0	15.8	15.2	16.4	13.9	18.0	1.5											
L. mitchelli n. sp.	ADY6444	15.6	17.0	18.3	17.9	15.9	15.9	17.8	16.0	16.8	21.7	17.0	15.3	17.3	14.7	18.5	15.8	0										
L. nebulosus	ABY6363	18.7	7.4	12.5	9.7	17.6	7.1	12.4	13.4	17.8	17.3	7.9	9.1	7.4	7.4	17.7	14.2	15.3	1.9									
L. obsoletus	AAC1522	19.8	10.9	14.6	13.3	18.3	10.6	14.6	15.2	18.9	17.5	10.7	10.8	8.2	10.7	19.7	15.1	17.8	9.1	1.4								
L. olivaceous	AAC7352	13.4	14.9	16.7	17.7	12.3	17.3	17.2	16.1	16.2	15.7	17.4	16.5	18.8	15.4	3.3	16.9	17.8	17.7	19.2	0.9							
L. ornatus	AAK9232	17.9	8.9	13.3	11.1	16.9	6.5	13.4	16.0	19.9	19.8	7.2	10.2	7.5	8.7	19.2	15.2	16.4	6.5	8.1	19.3	1.3						
L. ravus	AAC7349	16.2	14.9	16.9	17.3	16.6	18.9	14.9	15.9	18.7	20.6	15.3	16.6	16.6	15.0	17.7	15.9	11.6	14.9	17.2	15.9	17.0	1.5					
L. reticulatus	AAB6437	13.4	17.0	18.4	16.4	12.8	15.9	14.6	15.0	17.9	18.6	16.1	16.2	15.3	15.3	14.2	17.5	13.6	15.7	16.9	13.8	17.1	14.2	0.6				
L. rubrioperculatus	AAB6439	14.2	17.8	18.0	17.5	13.4	17.7	14.6	15.4	19.3	18.8	17.8	17.2	16.1	15.9	15.0	16.4	14.3	17.2	18.6	14.4	18.4	14.9	9.0	1.3			
L. semicinctus	AAC7350	14.9	14.9	17.2	17.1	15.0	15.7	14.9	14.0	15.6	20.5	16.3	14.5	15.3	13.9	16.7	14.5	6.0	13.6	15.8	16.0	15.7	11.0	14.6	14.6	1.0		
L. variegatus	AAC7351	16.2	17.0	17.6	16.6	15.6	18.3	16.4	15.7	18.5	20.9	16.7	17.4	18.0	16.2	14.8	17.5	17.6	16.2	19.3	14.8	17.8	16.5	16.9	15.7	17.1	1.0	
L. xanthochilus	AAC1546	14.3	16.3	13.9	17.8	13.6	17.5	13.3	15.4	19.3	18.5	17.3	16.3	18.3	15.8	13.0	17.4	17.3	15.7	17.6	13.0	17.4	14.3	10.3	12.3	15.1	16.4	1.6

(2021) presented a tree based on Mekkawy's list with the addition of several species, but no corrections. Their BIN assignments and identifications mostly agreed with ours, with a few exceptions: a pair of BINs have the species identification switched; two cases are allopatric lineages, within a species, where we picked a different one, favoring the lineage from near the type location; two species were listed as sharing the same lineage, but we assign one of them to a quite different lineage; and finally one is an overlooked misidentification in GenBank (MF123939 is a sequence for a threadfin bream, *Nemipterus* sp.).

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