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Cirrhilabrus isosceles, a new species of wrasse (Teleostei: Labridae) from the Ryukyu Archipelago and the Philippines, with notes on the *C. lunatus* complex

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Abstract

The new labrid species, *Cirrhilabrus isosceles*, is described from six specimens, 31.0–56.7 mm SL, collected from the Ryukyu Archipelago of Japan and the northern reaches of the Philippines in the western Pacific Ocean. The holotype and a paratype were collected at 35 m depth from Funauki Bay, Iriomote-jima, Ryukyu Islands, while the four other paratypes were collected at 24–36 m from Fuga Island, Cagayan Province, northern Philippines. The new species is distinguished by features of the terminal-phase male: i.e. color pattern, a prominent long mid-dorsal-fin basal dark spot, and a broadly lanceolate caudal fin. Despite its atypical caudal-fin shape, the new species has similar color patterns to the *Cirrhilabrus lunatus* species complex, which differ in having a somewhat lunate caudal fin. Indeed, the mtDNA barcode COI sequences for the new species matches those of some other members of the *C. lunatus* complex, specifically *C. cf. lunatus*, *C. brunneus*, and *C. squirei* (shared mtDNA haplotypes among species has been documented in other *Cirrhilabrus* species complexes). *Cirrhilabrus isosceles* is sympatric with three other members of the *C. lunatus* complex, and apparently hybridizes with at



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least one of them. The new species is most often confused with *Cirrhilabrus lanceolatus*, based on the shared caudal-fin shape, however, the two species are not closely related: *C. lanceolatus* is in a different set of mtDNA lineages most closely related to *C. jordani* from Hawai'i, indicating that caudal-fin shape in this genus is not phylogenetically informative. A neighbor-joining tree and genetic distance matrix based on the COI marker is presented for a number of *Cirrhilabrus* species.

Key words: taxonomy, ichthyology, systematics, coral-reef fishes, fairy wrasse, Pacific Ocean, Japan, barcoding.

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Introduction

The labrid genus *Cirrhilabrus* Temminck & Schlegel, 1845 has seen a large increase in the number of species recognized over the last forty years (Allen, Erdmann & Dailami 2015). Prior to 1974, only six species had been described: *Cirrhilabrus cyanopleura* (Bleeker, 1851); *C. solorensis* Bleeker, 1853; *C. temminckii* Bleeker, 1853; *C. jordani* Snyder, 1904; *C. ryukyuensis* Ishigawa, 1904; and *C. exquisitus* Smith, 1957. The genus is unusual in that it was described years before a species (*C. temminckii*) was assigned to it, by Bleeker in 1853: an earlier description of *C. cyanopleura* by Bleeker in 1851 assigned the species to the genus *Chelinoides*, now a junior synonym of *Cirrhilabrus* (see Eschmeyer, Fricke & van der Laan 2016). Since then, the genus has grown to include 51 species to date (Allen, Erdmann & Dailami 2015).

This slew of discoveries can be attributed to the development of SCUBA and a focus on the genus by John E. Randall, who described almost all of the subsequent twenty or so species. More recently, the relatively new frontier of mixed-gas and rebreather diving technologies has allowed for the exploration of deep reefs in remote and isolated locations. As a result, a number of deep-dwelling species have been discovered, including *Cirrhilabrus claire* Randall & Pyle, 2001; *C. earlei* Randall & Pyle, 2001; and *C. squirei* Walsh, 2014.

The relatively recent application of molecular techniques has also opened up a previously untapped resource for taxonomists, allowing a closer examination of the relationships between populations and sometimes revealing cryptic species within nominal species (Victor 2015). Interestingly, Allen, Erdmann & Dailami (2015) found species of *Cirrhilabrus* that share mtDNA lineages, likely the result of very recent splitting of species. These discoveries have resulted in *Cirrhilabrus* containing a species number second only to *Halichoeres* Rüppell, 1835 amongst the wrasses of Labridae. Recent molecular studies have, however, suggested that *Halichoeres* is likely polyphyletic, and will be extensively subdivided (Barber & Bellwood 2005), which would make *Cirrhilabrus* unequivocally the most speciose wrasse genus.

In this study, we describe a new species of *Cirrhilabrus* on the basis of six specimens collected from the Ryukyu Archipelago and northern Philippines. It was first recognized and collected by the second author in 1998, at a depth of 35 m at Iriomote-jima in the Ryukyu Islands. Only two specimens were collected at the time, one of each sex. Recently, additional specimens have been made available, especially via the aquarium trade from the Philippines, allowing its description herein as a new species, the 52nd member of the genus.

Materials and Methods

Type specimens are deposited at the Kanagawa Prefectural Museum of Natural History, Japan (KPM-NI), Australian Museum, Sydney (AMS), Zoological Reference Collection of the Lee Kong Chian Natural History Museum at the National University of Singapore (ZRC), National Museum of Natural History, Washington, D.C. (USNM), and British Museum of Natural History, London (BMNH).

In addition to the type specimens, three fin clips were obtained from the same set of Philippines specimens in the aquarium trade and used for mtDNA sequencing. Tissue samples of comparison species were obtained for mtDNA sequencing from field-collected as well as aquarium-trade specimens, originating in the Philippines, Indonesia, the Coral Sea, and Okinawa. Comparison sequences include several from collections at the Biodiversity Institute of Ontario, Guelph, Canada as well as some of those listed in Allen, Erdmann & Dailami (2015) from specimens in the Bernice P. Bishop Museum, Honolulu (BPBM), Museum Zoologicum Bogoriense, Cibinong, Java, Indonesia (MZB), United States National Museum of Natural History, Washington, D.C. (USNM), and Western Australian Museum, Perth (WAM). Additional tissues from rare comparison species collected in the Coral Sea were provided by Fenton Walsh of Kuranda, Australia, and Tyson and Tim Bennett of Cairns, Australia, and from Hawai'i by Anuschka Faucci of the University of Hawai'i at Manoa. The mtDNA sequence from *Paracheilinus flavianalis* from the Philippines was used as the outgroup for the mtDNA analysis.

A 652-bp segment (the "barcode" marker) was amplified from the 5' region of the mitochondrial cytochrome c oxidase (COI) gene using a variety of primers (Ivanova *et al.* 2007). DNA extractions were performed with the NucleoSpin96 (Machery-Nagel) kit according to manufacturer specifications under automation with a Biomek NX liquid-handling station (Beckman-Coulter) equipped with a filtration manifold. PCR amplifications were performed in 12.5 μ l volume including 6.25 μ l of 10% trehalose, 2 μ l of ultra pure water, 1.25 μ l of 10× PCR buffer (10mM KCl, 10mM (NH₄)₂SO₄, 20mM Tris-HCl (pH8.8), 2mM MgSO₄, 0.1% Triton X-100), 0.625 μ l of MgCl₂ (50mM), 0.125 μ l of each primer (0.01mM), 0.0625 μ l of each dNTP (10mM), 0.0625 μ l of *Taq* DNA polymerase (New England Biolabs), and 2 μ l of template DNA. The PCR conditions consisted of 94°C for 2 min., 35 cycles of 94°C for 30 sec., 52°C for 40 sec., and 72°C for 1 min., with a final extension at 72°C for 10 min. Specimen information and barcode sequence data from this study were compiled using the Barcode of Life Data Systems (Ratnasingham & Hebert 2007, Ward *et al.* 2009). The sequence data is publicly accessible on BOLD and GenBank (collection data and accession numbers are listed in Appendix 1). Sequence divergences were calculated using BOLD with the Kimura 2-parameter (K2P) model generating a mid-point rooted neighborjoining (NJ) phenogram to provide a graphic representation of the species' sequence divergence. Genetic distances were calculated by the BOLD algorithm as uncorrected p-distances and presented in a matrix.

We examined and used as illustrations here photographic records from the Image Database of Fishes (Japan), housed at KPM-NI. Images are assigned unique numbers with the prefix KPM-NR. We reviewed 29 underwater photographs tagged with location and depth (see Appendix 2).

Counts of fin spines and soft rays are given in Roman and Arabic numerals respectively, with branched rays indicated in parentheses. The lateral line is interrupted, and, as such, the count of the scales of the dorsoanterior portion is given first, followed by a plus sign and the midlateral peduncular portion. Only the tubed lateral-line scales are counted. The posterior lateral-line scale counts include all the tubed scales of the midlateral peduncular region, including the last pored scale that overlaps the hypural plate. The numbers of scales in the rows on the cheek are counted from their commencement below the front of the obit to behind the center of the orbit. Gill-raker counts include all rudiments, including the angled ceratobranchial raker.

Lengths of specimens are given as standard length (SL), with the exception of fishes photographed underwater; these are given as estimates of total length (TL). The standard length is the straight-line measurement from the front of the upper lip to the base of the caudal fin (end of hypural plate). Measurements in Table 1 are given as percentages of the standard length. Head length is the distance from the front of the upper lip to the posterior end of the opercular membrane. Body depth is the greatest depth to the base of the dorsal fin. Body width is measured just posterior to the opercular flap. Snout length is taken from the front of the upper lip to the fleshy edge of the orbit. Orbit diameter is the greatest fleshy diameter. Interorbital width is the least bony width. Caudal-peduncle depth is the least depth; caudal-peduncle length is the horizontal measurement between verticals at the posterior base of the anal fin and the caudal-fin base. Measurements of fin spines and rays are taken to the extreme base of each element. Pectoral-fin length is taken from the tip of the longest ray to its base. Pelvic-fin length is measured from the base of the spine to the tip of the longest ray.

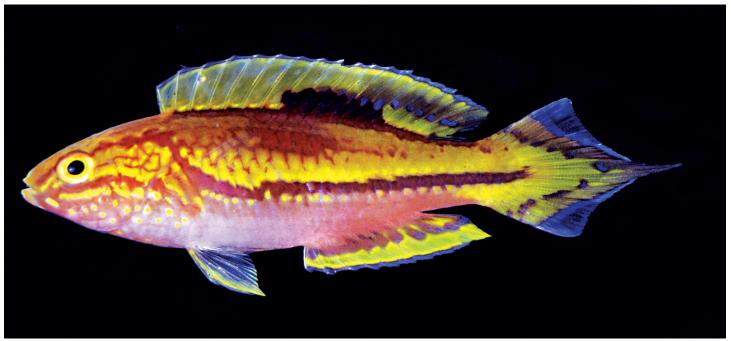


Figure 1. *Cirrhilabrus isosceles,* fresh TP male holotype, KPM-NI 5681, 56.7 mm SL, Funauki Bay, Iriomote-jima, Yaeyama Islands, Ryukyu Islands (H. Senou).

Cirrhilabrus isosceles, n. sp.

Pintail Fairy-wrasse Japanese common name: Hario-Itohikibera

urn:lsid:zoobank.org:act:529A2151-D9DB-4D03-9F7C-E51363B3C8E4

Figures 1–4, 8A, 9A & 10; Table 1.

Cirrhilabrus sp. Michael 2009: 142, 1 fig. (Japan, Taiwan, Philippines).
Cirrhilabrus cf. lanceolatus Kuiter 2010: 141, 8 figs. (Kochi, Japan, and Kumejima, Okinawa).
Cirrhilabrus sp. 3 Nishiyama & Motomura 2012: 224–225, 7 figs. (southern Japan, Izu Islands, and Ryukyu Islands).

Holotype. KPM-NI 5681, male, 56.7 mm SL, Funauki Bay, Iriomote-jima, Yaeyama Islands, Ryukyu Islands, Japan, 35 m, Hiroshi Senou, Nov. 19, 1998.

Paratypes. KPM-NI 5682, female, 31.0 mm SL, collected with holotype; AMS I.47150-001, male, 55.3 mm SL, Fuga Island, Cagayan Province, northern Philippines, 24–36 m, Aldren Delegencia, Nov. 20, 2015; ZRC 54775, male, 55.1 mm SL; USNM 437595, male, 52.7 mm SL; BMNH 2016.5.27.1, male, 55.7 mm SL, all with same data as AMS I.47150-001.

Diagnosis. Dorsal-fin rays XI,9; anal-fin rays III,9 except holotype with III,8; pectoral-fin rays 14–15; lateralline scales 16–17 + 6–8; median predorsal scales 4–5; horizontal scale rows on cheek below eye 2; gill rakers 15; body depth 29–34% SL; head length 29–36% SL; snout length 9–11% SL; caudal fin of terminal-phase (TP) male broadly lanceolate, i.e. rhomboidal with an extension of central rays; pelvic fins relatively short, not reaching anal-fin origin when depressed; TP male in life orange-yellow dorsally suffusing to lavender ventrally; a bright pink-to-purplish stripe at rest and dead, but blue in life and especially when displaying, extending posteriorly from upper orbit across head before making an oblique downward slant behind pectoral-fin base, and then continuing



Figure 2. *Cirrhilabrus isosceles*, TP male, aquarium specimen from Fuga Island, Cagayan, Philippines; unusually large, approx. 100 mm TL (Y.K. Tea).

just below mid-lateral line to base of caudal fin; a prominent long mid-dorsal-fin basal dark spot, and a mostly lavender blotch on upper body below spot; initial-phase fish mainly uniformly orange with faint stripes along dorsum and weak manifestation of medial stripe. Largest specimen 56.7 mm SL.

Description. Dorsal-fin rays XI,9; anal-fin rays III,8–9, usually 9; dorsal and anal-fin soft rays branched except first ray unbranched; last dorsal and anal-fin ray branched to base; pectoral-fin rays 15 (14–15), upper two unbranched; pelvic-fin rays I,5; principal caudal-fin rays 13 (upper and lowermost unbranched), upper and lower procurrent caudal rays 4; lateral line interrupted, with dorsoanterior series of pored scales 16 (16–17) and midlateral posterior peduncular series 7 (5–8); scales above lateral line to origin of dorsal fin 2; scales below lateral line to origin of anal fin 7; median predorsal scales 4 (4–5); median preprelvic scales 5 (5–6); rows of scales on cheek 2; circumpeduncular scales 16; gill-raker counts taken only for male types, excluding smallest female paratype, 15 (14–15) gill rakers in total, with 5 epibranchial rakers on posterior surface of hyoid arch + 8 (8–9) ceratobranchial rakers (including angle raker) + 1 hypobranchial raker; pseudobranchial filaments 10 (7–10).

Body moderately elongate and compressed, depth 3.1 (3.0–3.4) in SL, width 5.7 (5.7–6.6) in SL; head length 3.4 (2.8–3.4) in SL; snout pointed, its length 3.2 (3.1–3.6) in HL; orbit diameter 3.0 (3.0–3.6) in HL; depth of caudal peduncle 2.3 (2.2–2.4) in HL. Mouth small, terminal, and oblique, with maxilla almost reaching a vertical at front edge of orbit; dentition typical of genus with three pairs of canine teeth present anteriorly at side of upper jaw, first forward-projecting, next two strongly recurved and outcurved, third longest; an irregular row of very small conical teeth medial to upper canines; lower jaw with a single stout pair of canines anteriorly which protrude obliquely outward and are slightly lateral to medial pair of upper jaw; no teeth on roof of mouth. Gill rakers small, longest on first branchial arch only less than half length of longest gill filaments.

Posterior margin of preoperculum with 34/35 (24/23–37/38) very fine serrae; margins of posterior and ventral edges of preoperculum free to about level of middle pupil. Nostrils small, located anterior to upper edge of eye in a short membranous tube. Scales cycloid; head scaled except snout and interorbital space; 10 large scales on opercle, two most anterior notably enlarged; a broad naked zone on membranous edge of preopercle; a single row of scales fully covering subopercle; a row of large, elongate, pointed scales along base of dorsal fin, one per element, longest about two-fifths length of spines, scales progressively shorter posteriorly on soft portion of fin; anal fin with a similar basal row of scales; last pored scale of lateral line (posterior to hypural plate) enlarged and pointed; one scale above and below last pored scale also enlarged; a horizontal series of greatly enlarged scales extend two-thirds distance to central posterior margin of caudal fin; pectoral fins naked except for a few small scales at extreme base; a single large scale at base of each pelvic fin, about three-fourths length of pelvic spine.

Origin of dorsal fin above second lateral-line scale, predorsal length 2.9 (2.6–3.2) in SL; first four dorsal-fin spines progressively longer, fifth to eleventh subequal, last longest, 1.8 (1.8–2.6) in HL; interspinous membranes

of dorsal fin in males extend beyond dorsal-fin spines, with each membrane extending in a pointed filament beyond spine; first dorsal-fin soft ray longest, 1.7 (1.7–2.6) in HL, remaining rays progressively shorter; origin of anal fin below base of ninth dorsal-fin spine; third anal-fin spine longest, 3.2 (3.0–3.6) in HL; interspinous membranes of anal fin extended as on dorsal fin; anal-fin soft rays relatively uniform in length, fourth to sixth longest, 1.5 (1.5–2.6) in HL; dorsal and anal-fin rays not reaching caudal-fin base; caudal fin of TP males very elongate, central rays extended, forming a rhombus broadly lanceolate, length 2.5 (2.5–3.3) in HL; pectoral fins short, reaching a vertical between bases of sixth or seventh dorsal-fin spines, longest ray 1.3 (1.3–1.8) in HL; origin of pelvic fins below lower base of pectoral fins; pelvic fins moderately long, but not reaching anal fin spine, longest ray 1.3 (1.3–2.0) in HL.

Color of TP male in life. (Figs. 1, 2, 8, 9 & 10) Dorsal aspect orange, becoming bright yellow in a broad midlateral band, suffusing to lavender ventrally; pink-to-purple stripe (blue in life, especially when displaying) along base of dorsal fin ending on caudal peduncle; large scales on upper body and adjacent head outlined in orange, in a honeycomb pattern of reticulations which converge to an elongated purplish-to-pink blotch on mid-upper body; purplish-to-pink stripes above and below orbit, upper extending rearward to above operculum, slanting down behind pectoral-fin base and continuing to caudal-fin base as a prominent purple stripe in fish at rest or dead, stripe bright blue in life, especially when displaying, lower head stripe ends at opercular flap; thorax and lower head with variable yellow spots and reticulations; dorsal fin yellow to orange, edged in blue, with a large, fuliginous, elongated spot midway just above base (from about 8th spine to 3rd soft ray in holotype); dusky-to-reddish area midway on posterior soft dorsal fin with underlying row of blue or pinkish spots; anal fin yellowish to orange, edged in blue, with blue spots basally; caudal fin mostly bright yellow with a pair of prominent blue chevrons converging at lanceolate terminus; pelvic fins bluish and translucent, edged along spine with pale yellow. Nuptial display includes a pink wash on chest, bright magenta rear body and anal-fin base; bright blue stripes on posterior body and caudal fin become iridescent blue; elongate patch on mid-upper body flashes purple to lavender.

Color of initial-phase in life. (Fig. 4) Uniformly fulvous orange, lightening medially in a longitudinal yellow suffusion; honeycomb pattern indistinct; dark orange-to-purple facial stripes present above and below orbit, upper running past operculum and slanting down behind pectoral-fin base and continuing to caudal-fin base, lower ends at opercular flap; ventral aspect of head and anterior body light mauve to whitish; lower head and thorax with yellow spots and reticulations; dorsal, anal, and pelvic fin(s) translucent and unmarked; caudal fin translucent, sometimes with yellowish central portion, superimposed with bluish scrawling and bluish tips. Juveniles and small initial-phase fish may have an additional pair of thread-like stripes running along upper body, spotted intermittently with small white dots; upper portion of caudal peduncle with a single black spot on most smaller individuals.

Color in alcohol. (Fig. 3) TP males in alcohol yellowish brown, becoming pale reddish brown anteriorly on head; operculum dark reddish brown; scales on dorsum dusted in grayish brown; dark grayish brown stripes along



Figure 3. Cirrhilabrus isosceles, preserved paratype, ZRC 54775, 55.1 mm SL, Fuga Island, Cagayan, Philippines (Y.K. Tea).



Figure 4. *Cirrhilabrus isosceles* Top: fresh female paratype, KPM-NI 5682, 31.0 mm SL, Funauki Bay, Iriomote-jima, Yaeyama Islands, Ryukyu Is. (H. Senou). Middle: initial phase, approx. 35 mm TL, aquarium specimen from Fuga Island, Cagayan, Philippines (K. Kohen). Bottom: fresh TP male, approx. 60 mm TL, 50-60 m, Green Island., Taiwan (B.D. Greene).

TABLE 1

	holotype	paratypes					
	KPM-NI 5681	AMS I.47150-001	ZRC 54775	USNM 437595	BMNH 2016.5.27.1	KPM-NI 5682	
	3081	1.4/130-001			2010.3.27.1		
=		TP males				IP	
Standard length (mm)	56.7	55.3	55.1	52.7	55.7	31.0	
Body depth	32.1	29.5	31.4	29.4	30.5	33.5	
Body width	17.5	15.6	16.5	17.3	15.3	16.5	
Head length	29.5	32.0	31.2	34.2	31.4	35.5	
Snout length	9.3	10.5	9.1	9.5	9.3	10.0	
Orbit diameter	9.7	9.2	9.4	9.5	8.8	10.3	
Interorbital width	8.8	7.2	7.8	8.3	8.3	9.4	
Caudal-peduncle depth	13.1	13.9	13.6	14.2	14.0	14.5	
Caudal-peduncle length	13.4	13.9	13.3	15.0	14.4	12.9	
Predorsal length	34.2	33.6	31.4	34.9	33.4	38.7	
Prepelvic length	37.7	40.7	36.8	40.8	38.8	41.3	
Preanal length	59.4	61.1	61.2	62.4	63.7	66.1	
Dorsal-fin base	58.2	56.1	59.3	57.7	59.8	56.8	
1st dorsal-fin spine	6.0	4.9	5.3	5.5	6.1	5.8	
2nd dorsal-fin spine	10.1	8.5	8.3	9.1	10.1	7.4	
Longest dorsal-fin spine	16.2	16.3	14.5	15.2	17.1	13.5	
Longest dorsal-fin ray	17.6	14.8	15.8	17.1	17.8	13.9	
Anal-fin base	26.8	26.6	26.5	28.8	29.3	26.1	
1st anal-fin spine	5.3	6.1	5.8	6.3	5.4	5.2	
2nd anal-fin spine	7.8	8.0	6.5	8.2	7.5	10.0	
3rd anal-fin spine	9.2	10.5	8.7	10.4	10.4	11.3	
Longest anal-fin ray	19.4	18.3	16.5	17.5	19.0	13.5	
Caudal-fin length	40.6	38.3	33.9	34.3	35.9	30.0	
Longest pectoral ray	22.8	18.1	21.8	21.4	21.5	21.9	
Pelvic-fin spine	10.1	10.3	10.2	11.8	9.5	12.6	
Longest pelvic-fin ray	22.4	21.7	19.1	20.8	20.6	18.1	

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

base of dorsal fin and along midlateral body onto caudal-fin base; dorsal fin largely translucent with light tan stripe on outer edge and dark brown elongated spot midway near base; posterior soft-dorsal fin with dark brown shading, punctuated with translucent spots; caudal fin mainly transluscent with prominent dark brown chevrons converging at tip; anal fin, pectoral and pelvic fins translucent.

Etymology. The species is named *isosceles* for the distinctive triangle of color on the midportion of the caudal fin. The specific epithet is a noun in apposition.

Distribution and habitat. *Cirrhilabrus isosceles* is currently known from Izu-Oshima, Japan, south to the Ryukyu Archipelago (Yaeyama Islands and Okinawa), Taiwan (Green Island), and the Philippines (Fig. 5). In addition to the paratypes from Cagayan Province on the northern tip of the Philippines, Aldren Delegencia reports collections from the Verde passage south of Luzon, although he notes that the new species is significantly less common there. The range is reported to extend to Cebu in the central Philippines, where it is rare; this likely represents the southernmost limit of its distribution. The new species is found in depths ranging from 24–60 m, although, based on habits of other closely related species, it should also be expected to occur in deeper waters. The third author described the habitat in Green Island, Taiwan, to be similar to that of most other *Cirrhilabrus* species, consisting of flat or gently sloping bottoms with scattered low outcrops of rock or coral. This species is apparently most common in the Ryukyu Archipelago, where it occurs in groups of about a dozen or more individuals, often in the company of *C. lunatus*.

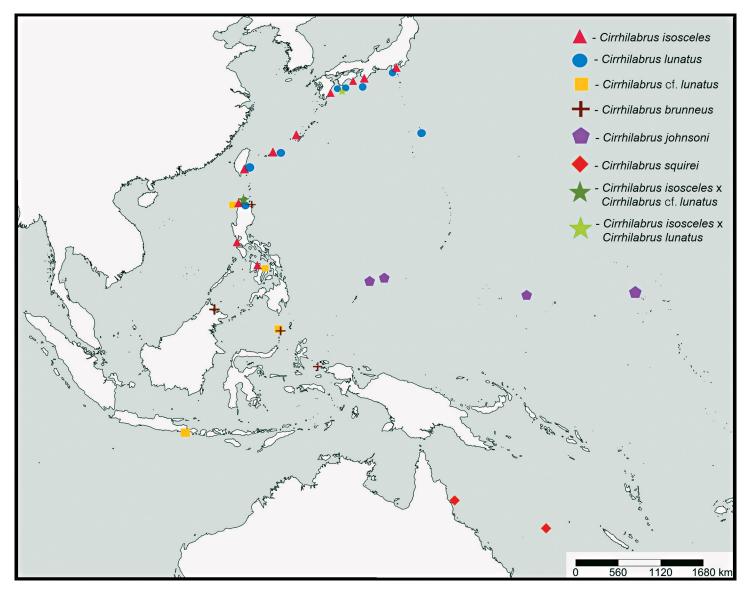


Figure 5. Distribution map showing locality records for *Cirrhilabrus isosceles* and other members of the *C. lunatus* complex. Star-shaped symbols denote hybrid phenotypes found in the Ryukyu Islands and the northern Philippines.

Genetic analysis. We resolved relationships among a set of *Cirrhilabrus* species including the new species using the mitochondrial DNA barcode marker COI. GenBank accession numbers and associated collection data are presented in Appendix 1. Genetic distances are low within species, 0.3% or less, and often large between species, usually from 12–18%, but several species are very close or have the same sequences (Table 2). The neighbor-joining tree of these sequences shows mostly deep interspecific divergences, but two independent sets of species share mtDNA sequences, even sharing haplotypes (Fig. 6). The *C. marinda/condei* shared lineage has been described and discussed by Allen, Erdmann & Dailami (2015). Notably, we find that *C. isosceles* shares a lineage with *C. cf. lunatus, C. brunneus*, and *C. squirei*, and all but *C. squirei* share identical haplotypes. Only *C. bathyphilus* is on the same branch and *C. lanceolatus* and a set of related species comprise a distant set of lineages.

Comparisons. *Cirrhilabrus isosceles* clearly belongs in the *C. lunatus* complex, based on genetics, coloration, and habitat preference. Based on observations by the authors, documented photographs, and records from the KPM-NI and the literature, the range of species in the complex is centered largely within the Coral Triangle, with the majority of species co-occurring in the Philippine Archipelago; only two species have completely allopatric distributions (Fig. 5). The closest match to the range of *C. isosceles* is *C. lunatus*; the former occurring from the Izu Peninsula south to Cebu, the latter more restricted, ranging from the Ryukyu Archipelago and Ogasawara Islands, south only to the northernmost tip of the Philippines. *Cirrhilabrus* cf. *lunatus* replaces *C. lunatus* to the south, over the remaining islands of the Philippines, south to Bali, Indonesia. The range of *C. isonaneus* broadly overlaps that of *C. cf. lunatus*. The greatest overlap occurs at the northernmost tip of the Philippines, where four species of the *C. lunatus* complex co-occur. The two members with allopatric distributions are *C. johnsoni* and *C. squirei*. The former was thought to occur only on Kwajalein Atoll in the Marshall Islands, but the third author has since encountered the species through most of the Caroline Islands: in Pohnpei, Grey Feather Bank (Chuuk), Yap, and Ngulu Atolls. *Cirrhilabrus squirei* is restricted to the Coral Sea and the Great Barrier Reef on the northeastern coast of continental Australia.

TABLE 2

	bat	bru	cf. lu	con	hum	iso	jor	lan	mar	ros	rub	squ
C. bathyphilus	NA						-					-
C. brunneus	12.0	0.2										
C. cf. lunatus	12.1	0	0.2									
C. condei	15.7	15.5	15.8	0.2								
C. humanni	15.6	15.2	15.2	8.1	NA							
C. isosceles, n. sp.	11.8	0	0	15.8	15.2	0.3						
C. jordani	16.6	17.5	17.5	13.4	14.1	17.5	NA					
C. lanceolatus	16.0	16.0	16.0	13.5	13.5	16.0	6.7	NA				
C. marinda	15.7	15.8	16.0	0	8.1	16.0	13.4	13.7	0.2			
C. roseafascia	16.6	17.5	17.5	12.3	14.4	17.5	6.5	5.1	12.4	NA		
C. rubrimarginatus	17.7	17.8	18.0	13.8	14.7	17.8	13.6	11.2	14.0	10.4	0.2	
C. squirei	12.3	0.2	0.2	16.0	15.4	0.2	17.5	16.0	16.1	17.5	17.8	NA

Minimum Interspecific and Maximum Intraspecific P-distances (uncorrected pairwise) for mtDNA COI sequences of 12 species of *Cirrhilabrus*

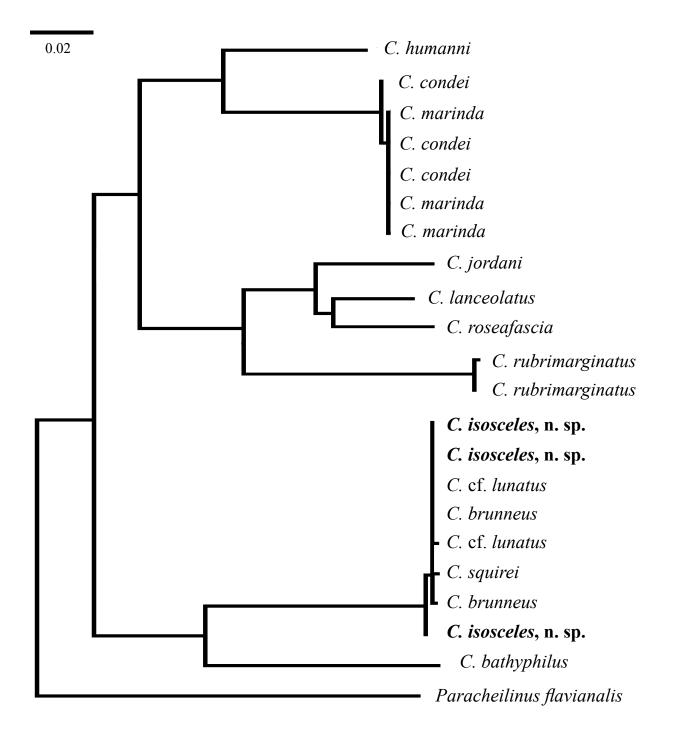


Figure 6. The neighbor-joining phenetic tree of *Cirrhilabrus* following the Kimura two-parameter model (K2P) generated by BOLD (Barcode of Life Database). The scale bar at left represents a 2% sequence difference and *Paracheilinus flavianalis* is used as an outgroup. GenBank accession numbers and collection data for the sequences in the tree are listed in Appendix 1.



Figure 7. Cirrhilabrus lunatus, fresh TP male, approx.70 mm TL, Green Island, Taiwan (Academia Sinica Digital Resources).

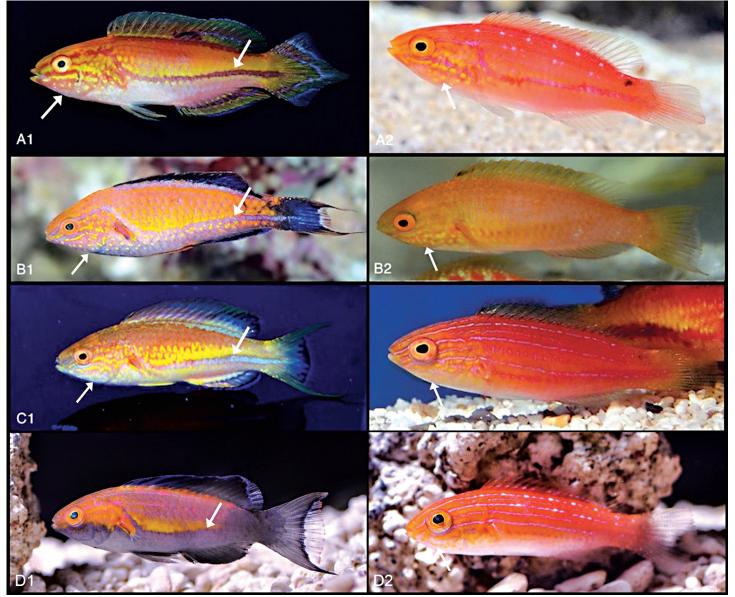


Figure 8. Live color patterns in *Cirrhilabrus* species (TP males in A1-D1, initial phase in A2-D2). A: *C. isosceles*, Fuga Island, Cagayan (A1=paratype AMS I.47150-001); B: *C. cf. lunatus*, Fuga Island, Cagayan; C: *C. squirei*, Great Barrier Reef; D: *C. lunatus*, Okinawa, Japan (A1, B1: Y.K. Tea; A2: K. Kohen; B2: B. Shutman; C1: R. Lanceley; C2: F. Walsh; D1, D2: E. Fleishauer).

The TP males of the *C. lunatus* species complex are also characterized by a set of markings; in particular, a lateral stripe from the head to caudal fin that slants down abruptly behind the pectoral fin base. This stripe is less obvious in *C. lunatus* and *C. brunneus*, but is still present as a colored delimitation separating the upper and lower body (Figs. 7, 8 & 9). The TP males also share the anastomosed reticulation of spots and short stripes on the face and lower chest (Figs. 7, 8 & 9), although these can be obscured in *C. lunatus* and *C. brunneus*. In addition, the members of this complex, except for *C. isosceles*, possess their namesake somewhat lunate or crescentic caudal fins, often with the central rays elongated to form the shape of a recurved bow (Fig. 7). These species also share similarities in the coloration during the nuptial display, specifically, the lightening and iridescence of the dorsal



Figure 9. Nuptial displays in *Cirrhilabrus* TP males A: *C. isosceles*, Fuga Island, Cagayan; B: *C. brunneus*, from Indonesia C. *C. johnsoni* Kwajalein, Marshall Islands (Y.K. Tea, Y.K. Tea, and J. Johnson).



Figure 10. Cirrhilabrus isosceles, nuptial display of TP male, KPM-NR 143313, 40 m, Otsuki-cho, Shikoku, Japan (H. Ueno).

"epaulette" above and behind the pectoral fin (Figs. 9 & 10). This feature is particularly prominent in *C. brunneus* (Fig. 9B) and *C. johnsoni* (Fig. 9C).

Despite the similarity of color patterns and genetics, *C. isosceles* is easily distinguished from its relatives by having a broadly lanceolate caudal fin. Other differences include the elongated dark spot on the mid-dorsal fin, absent on all other members. The nuptial display of TP males is also unique: the lower rear body and anal-fin base flashes bright magenta and the prominent blue stripes on the tail are brightly iridescent (Fig. 9A & 10).

The *C. lunatus* species complex apparently share virtually all meristic and morphometric data. Some slight differences may exist (but counts and measures are by different observers), i.e. *C. isosceles* with a modal total gill raker count of 15 vs. 13 reported in *C. squirei* (Walsh 2014) and *C. brunneus* (Allen 2006), 14 in *C. johnsoni* (Randall 1988), and 16 in *C. lunatus* (Randall & Masuda 1991). Snout lengths apparently differ slightly, with *C. isosceles* with 9.1–10.5% SL vs. 7.9–8.9% SL in *C. squirei* (Walsh 2014), 8.7% SL in *C. brunneus* (Allen 2006), 8.9–10.0% SL in *C. johnsoni* (Randall 1998), and 8.6–9.3% SL in *C. lunatus* (Randall & Masuda 1991).

Like most other Cirrhilabrus, the species of the C. lunatus complex have a penchant for denuded rubble pans



Figure 11. Probable hybrid Cirrhilabrus isosceles X lunatus, Kochi, Japan, approx. 80 mm TL, image reversed ("Kiss2Sea").

adjacent to reef slopes. An exception to this general habitat preference is *C. johnsoni*, which is found almost exclusively in *Halimeda* beds instead of exposed rubble. At Ngulu Atoll, the third author recorded peak densities of the species in areas with 100% *Halimeda* cover. Where both *Halimeda* and exposed rubble were available, *C. johnsoni* preferred *Halimeda*. It only occurs in exposed rubble pans when *Halimeda* is not present, such as in Yap. All members of the *C. lunatus* complex have a proclivity for deep water and are normally found deeper than 15 m. The third author collected specimens of *C. isosceles* from 60 m in Green Island, Taiwan. Only *C. squirei* has been recorded in deeper water, at 65 m by Walsh (2014).

Discussion

Despite the differences in coloration and caudal-fin shape, the genetic analysis confirms that the group members are indeed closely related, sharing the same mitochondrial DNA lineage, even in the allopatric *C. squirei* from the Coral Sea. Several examples of this phenomenon, where species with different phenotypes exhibit nascent or no genetic divergence, dubbed "phenovariants" by Victor (2015), have been reported. This is not too surprising for



Figure 12. Probable hybrid *Cirrhilabrus isosceles* X cf. *lunatus*, from Fuga Islands, Philippines, both approx. 60 mm TL, (B. Shutman).

recently evolved, closely related taxa, particularly amongst genera such as *Cirrhilabrus* and *Paracheilinus*, where exceptionally strong sexual selection and exuberant nuptial displays serve as a driving force for speciation (Allen, Erdmann & Dailami 2015, Allen, Erdmann & Yusmalinda 2016). This is quite akin to Laman & Scholes' (2012) study of the birds-of-paradise, where they found males rapidly evolve enhanced secondary sexual characteristics as a result of very strong sexual selection. Victor & Randall (2014) reported a similar case of phenotypic change outpacing genetic divergence in the East African labrid *Pseudojuloides edwardi*.

It is quite unusual to have so many sympatric sibling species described in one small region; indeed four species in the *C. lunatus* complex co-occur at the northernmost tip of the Philippines. Traditionally, it is assumed that newly emerging species complexes speciate in allopatry (but see Rocha & Bowen [2008]); for example, the recent split between *C. walindi* and *C. cenderawasih*, proposed to be a result of the isolation of Cenderawasih Bay (Allen & Erdmann 2006). Different phenotypes corresponding to different biogeographic regions have been noted within some wide-ranging *Cirrhilabrus* species, e.g. *C. exquisitus* and *C. scottorum* (see Kuiter [2010]), and is typical of many reef fish species complexes, fitting the model of allopatric speciation. Nevertheless, more complicated patterns of sympatric species complexes have been described recently, for example in *Paracheilinus* (Allen, Erdmann & Yusmalinda 2016).

Where ranges of closely related species overlap, hybridization may occur, and, to some degree, explain the sharing of mtDNA haplotypes between species. As was found in sympatric *Paracheilinus* by Allen, Erdmann & Yusmalinda (2016), we found some hybridization occurring in zones of overlap. We base the conclusion of hybrids (vs. undescribed rare species) on the occurrence of rare individuals with an inconsistent variety of character combinations of two species known to co-occur on the same reefs (Figs. 11 & 12). These phenotypes include trident-shaped caudal fins, as well as variable darkening of dorsal, caudal, and anal fins, suggesting hybrids between *C. isosceles* x *C. lunatus* in Japan (Fig. 11). Other rare specimens from the Philippines have those hybrid markings in addition to a honeycomb pattern on the body characteristic of normal *C. cf. lunatus* (Fig. 13), suggesting hybrids between *C. isosceles* and *C. cf. lunatus* (Fig. 12).



Figure 13. *Cirrhilabrus* cf. *lunatus* (front) and *C. isosceles* (behind), aquarium specimens from Verde Islands, Philippines, both approx. 60 mm TL (B. Shutman).

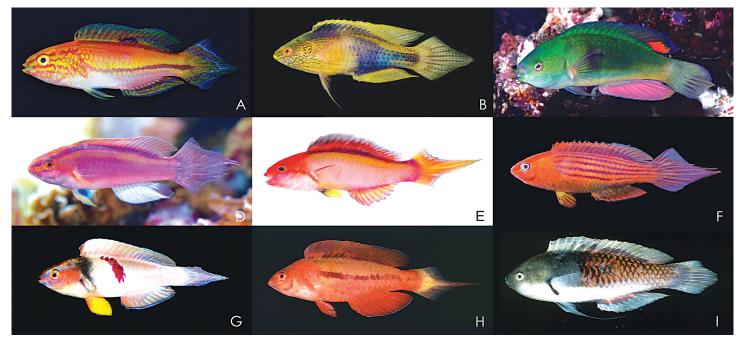


Figure 14. Lanceolate caudal fins amongst a variety of *Cirrhilabrus* species. (A) *C. isosceles* n. sp; (B) *C. rhomboidalis*; (C) *C. melanomarginatus*; (D) *C. roseafascia*; (E) *C. lanceolatus*; (F) *C. earlei*; (G) *C. sanguineus*; (H) *C. blatteus*; and (I) *C. cyanopleura* (A, C, D, & E: Y.K. Tea; B: B.D. Greene; F: B.D. Greene & R. Whitton; G: H. Tanaka; H, I: J.E. Randall).

The prominent lanceolate caudal-fin in *C. isosceles* has, in the past, led to confusion with *Cirrhilabrus lanceolatus* (Fig. 14). It would be tempting to use caudal-fin shapes as a phylogenetic character in classifying *Cirrhilabrus*, but the genetic results indicate that the lanceolate caudal fin of *C. isosceles* is an independently evolved characteristic, appearing within a species complex with somewhat lunate caudal fins. In contrast, *C. lanceolatus* shares a broad clade with the Hawaiian *C. jordani*, which has a rounded caudal fin, indicating a lanceolate caudal fin is not a synapomorphy. A wide variety of *Cirrhilabrus* have lanceolate caudal fins (Fig. 14), and it is likely they do not reflect a related group.

A parallel case is observed in the dottyback (Pseudochromidae) subfamily Pseudochrominae, where the species sport a variety of highly diverse caudal-fin shapes. These can range from strongly lanceolate in *Oxycerchthys* Gill, to deeply forked in *Pseudochromis dixurus* Lubbock. A classification of pseudochromids by Fowler (1931) used caudal-fin shape to define species groups, but a revision by Gill (2004) revealed that approach to be incorrect, and that caudal-fin shape was phylogenetically uninformative. Although caudal-fin characteristics are often useful in identifying species, it is apparently an unreliable feature for phylogenetic classifications.

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Genus	species	Collection site	Voucher	GenBank #	Collector/Source
Cirrhilabrus	humanni	Com, Timor-Leste	MB065501	KR052205	Allen et al. 2015 IRBC
Cirrhilabrus	condei	Samarai, Milne Bay, PNG	MB0617102	KR052202	Allen et al. 2015 IRBC
Cirrhilabrus	marinda	Raja Ampat, Indonesia	MB0618401	KR052206	Allen et al. 2015 IRBC
Cirrhilabrus	condei	Samarai, Milne Bay, PNG	MB0617201	KR052204	Allen et al. 2015 IRBC
Cirrhilabrus	condei	Samarai, Milne Bay, PNG	MB0617103	KR052203	Allen et al. 2015 IRBC
Cirrhilabrus	marinda	Raja Ampat, Indonesia	MB0615701	KR052201	Allen et al. 2015 IRBC
Cirrhilabrus	marinda	Raja Ampat, Indonesia	MB0618404	KR052207	Allen et al. 2015 IRBC
Cirrhilabrus	jordani	Hawai'i	12COIFishC08	KX281112	A. Faucci/BOLD
Cirrhilabrus	lanceolatus	Japan/aq. trade	ltyk164	KU986299	Y.K. Tea/Y.Z. Tay
Cirrhilabrus	roseafascia	Holmes Reef, Coral Sea	fw16cr	KU986297	T. Bennett/F. Walsh
Cirrhilabrus	rubrimarginatus	Philippines/aq. trade	HLC-13256	FJ583239	D. Steinke/BOLD
Cirrhilabrus	rubrimarginatus	Philippines/aq. trade	HLC-10964	FJ583240	D. Steinke/BOLD
Cirrhilabrus	isosceles, n. sp.	Cagayan, Philippines	ltyk167	KU986300	Y.K. Tea/RVSFW
Cirrhilabrus	isosceles, n. sp.	Cagayan, Philippines	ltyk166	KU986286	Y.K. Tea/RVSFW
Cirrhilabrus	cf. lunatus	Philippines/aq. trade	je144cx	KX281114	J.M.B Edward/aq. trade
Cirrhilabrus	brunneus	Raja Ampat, Indonesia	MB0612901	KR052199	Allen et al. 2015 IRBC
Cirrhilabrus	cf. lunatus	Philippines/aq. trade	je13cl	KX281113	J.M.B. Edward/aq. trade
Cirrhilabrus	squirei	Harrier Reef, Coral Sea	fw15cs1	KX037922	T. Bennett/F. Walsh
Cirrhilabrus	brunneus	Raja Ampat, Indonesia	MB0612902	KR052200	Allen et al. 2015 IRBC
Cirrhilabrus	isosceles, n. sp.	Cagayan, Philippines	ltyk165	KU986296	Y.K. Tea/RVSFW
Cirrhilabrus	bathyphilus	Holmes Reef, Coral Sea	fw15cb1	KX037921	T. Bennett/F. Walsh
Paracheilinus	flavianalis	Indonesia/aq.trade	HLC-11024	FJ583815	D. Steinke/BOLD

Appendix 1: Data for specimens in the phenetic tree in Fig. 6, following the order in the tree.

Image No.	Locality	Date	Photographer	Depth
KPM-NR 16530	Kume-jima, Okinawa, Ryukyu Islands	1998	Tsuyoshi Kawamoto	35
KPM-NR 28329	Izu-Oshima, Izu Islands	19990107	Hisayuki Onuma	40
KPM-NR 28330	Izu-Oshima, Izu Islands	19990107	Hisayuki Onuma	40
KPM-NR 29057	Iriomote-jima, Yaeyama Islands, Ryukyu Islands	19981119	Keido Uchino	28
KPM-NR 29944	Izu-Oshima, Izu Islands	19990220	Satoshi Ueshima	unknown
KPM-NR 29946	Izu-Oshima, Izu Islands	19990220	Satoshi Ueshima	unknown
KPM-NR 36609	Nakanose nr. Ie-jima, Okinawa, Ryukyu Islands	19960607	Kyo Yunokawa	15
KPM-NR 62471	Izu-Oshima, Izu Islands	unknown	Hisayuki Onuma	42
KPM-NR 62472	Izu-Oshima, Izu Islands	unknown	Hisayuki Onuma	42
KPM-NR 62473	Izu-Oshima, Izu Islands	unknown	Hisayuki Onuma	42
KPM-NR 62474	Izu-Oshima, Izu Islands	unknown	Hisayuki Onuma	42
KPM-NR 62477	Izu-Oshima, Izu Islands	unknown	Hisayuki Onuma	34
KPM-NR 62497	Izu-Oshima, Izu Islands	unknown	Hisayuki Onuma	40
KPM-NR 62498	Izu-Oshima, Izu Islands	unknown	Hisayuki Onuma	40
KPM-NR 62504	Izu-Oshima, Izu Islands	unknown	Hisayuki Onuma	35
KPM-NR 71841	Kashiwa-jima, Shikoku	20100801	Hiroshi Ueno	43
KPM-NR 81100	nr. Ishigaki-jima, Yaeyama Islands, Ryukyu Islands	unknown	Junichi Nakamoto	unknown
KPM-NR 82684	Iriomote-jima, Yaeyama Islands, Ryukyu Islands	20040708	Chikako Kasuga	unknown
KPM-NR 84874	Sesoko-jima, Okinawa, Ryukyu Islands	unknown	Hajime Takano	20
KPM-NR 85755	Ishigaki-jima, Yaeyama Islands, Ryukyu Islands	2004	Junichi Nakamoto	20
KPM-NR 89951	Aka-jima, Zamami Islands, Okinawa, Ryukyu Islands	unknown	Atsushi Moriyama	17
KPM-NR 92093	Izu-Oshima, Izu Islands	unknown	Osamu Hoshino	40
KPM-NR 93226	Iriomote-jima, Yaeyama Islands, Ryukyu Islands	20060430	Chikako Kasuga	unknown
KPM-NR 93381	Iriomote-jima, Yaeyama Islands, Ryukyu Islands	200410	Rika Ikoma	unknown
KPM-NR 93407	Iriomote-jima, Yaeyama Islands, Ryukyu Islands	200505	Rika Ikoma	unknown
KPM-NR 93469	Iriomote-jima, Yaeyama Islands, Ryukyu Islands	200705	Rika Ikoma	unknown
KPM-NR 93913	Iriomote-jima, Yaeyama Islands, Ryukyu Islands	20080710	Chikako Kasuga	20
KPM-NR 143310	Otsuki-cho, Shikoku	20120212	Hiroshi Ueno	13
KPM-NR 143313	Otsuki-cho, Shikoku	20120526-27	Hiroshi Ueno	40 to 42

Appendix 2: Images examined, all registered in the Image Database of Fishes (Japan), housed at KPM-NI.