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Cleaning up the cleaner wrasses: revision of the *Labroides phthirophagus* and *Labroides bicolor* species complexes, with rediagnosis of *Labroides quadrilineatus* and descriptions of two new species (Teleostei: Labridae)

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Abstract. The *Labroides phthirophagus* Randall, 1958 and *Labroides bicolor* Fowler & Bean, 1928 species complexes of cleaner wrasses are reviewed. The former comprises three colourful, phylogenetically intractable species confined to tropical coral reefs in the Indo-Pacific, viz., *Labroides phthirophagus* from the Hawaiian Islands, *Labroides rubrolabiatus* Randall, 1958 from the central and southeastern Pacific, and *Labroides pectoralis* Randall & Springer, 1975 from the western Pacific. Our phylogenomic analysis of genome-wide ultraconserved elements and mitochondrial DNA resolves four taxa within this complex, with one taxon, *Labroides flammulatus*, new species, described as a new, cryptic species from the eastern Indian Ocean. *Labroides flammulatus*, new species, is described on the basis of eight specimens, the holotype and four paratypes from Christmas Island, and three paratypes from the Cocos (Keeling) Islands. A second species, *Labroides inopinatus*, new species, is described on the basis of six specimens, the holotype and two paratypes from Flora Reef, Coral Sea, and one paratype each from the Izu Oceanic Park in Japan, Holmes Reef in the Coral Sea, and Boulari Pass in New Caledonia. *Labroides inopinatus*, new species, appears to be widespread across the western Pacific but is restricted to deep mesophotic coral reefs below 40 m. The new species is highly distinctive and appears to be only distantly related to *Labroides bicolor*. The recent synonymy of *Larabicus quadrilineatus* within *Labroides* is corroborated by morphological and phylogenomic evidence, and the species is reinstated as *Labroides quadrilineatus* (Rüppell, 1835)**,** following the historical combination first established by Günther in the nineteenth century. New ecological and field observations are provided for *Labroides*, and phylogenetic relationships for the new species, congeneric species of *Labroides*, and related genera of labrichthyine wrasses are explored. *Labroides* is rediagnosed and a key to species is provided.

Key words. Australia, eastern Indian Ocean, systematics, taxonomy, mesophotic, cryptic species

INTRODUCTION

The cleaner wrasses from the labrid genus *Labroides* are among the most conspicuous fishes on coral reefs, known for their recognisable colouration and cleaning behaviour. Categorically, most cleaning fishes either exhibit cleaning in their juvenile stages or facultatively across their ontogeny (Côté, 2000). *Labroides*, however, are among a small handful of specialist teleost fishes exhibiting obligate, or near-obligate cleaning behaviour through to adulthood, notable for ingesting ectoparasites found on other fishes (Randall, 1958; Vaughan et al., 2017; Huie et al., 2020). In addition to their diagnostic colour patterns, cleaner wrasses advertise their services by swimming in a peculiar, oscillating fashion, often in prominent, localised areas known as cleaning stations (Randall, 1958; Potts, 1973). The genus is perhaps the best-known example of cleaner-client mutualism on coral reefs in the Indo-Pacific (Ros et al., 2011). In the Western Atlantic and Eastern Pacific where *Labroides* does not occur, this niche is filled by cleaning gobies from the genera *Elacatinus* and *Tigrigobius*, whose species also establish cleaning stations and advertise to their clients with blue or yellow lateral stripes, convergent with those found in *Labroides* (Cheney et al., 2009; Huie et al., 2020). Because of the ecosystem services they provide, *Labroides* are amongst the most well-studied coral reef organisms, forming the basis for numerous studies centred around their ecology (Randall, 1958; Bshary, 2003; Waldie et al., 2011; Sun et al., 2015; Triki et al., 2017), ethology (Bshary & Würth, 2001; Bansemer et al., 2002; Tebbich et al., 2002; Grutter & Bshary, 2003; Bshary &

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Grutter, 2005; Oates et al., 2010; Wismer et al., 2014; Côté & Mills, 2020; Aellen et al., 2022), and mimetic associations with other fishes (Randall & Randall, 1960; Wickler, 1966; Côté & Cheney, 2005; Robertson, 2013).

Despite the multitude of studies directed at *Labroides*, the taxonomy of this emblematic group is surprisingly nebulous, though this might be explained in part by the dearth of taxonomic interest in relation to the disproportionately large number of ecological and behavioural studies. In the last significant review of the genus, Randall (1958) recognised four species. The most common and widespread of the genus, *Labroides dimidiatus*, ranges across the tropical Indo-Pacific, from the east African coast eastward to the Cook Islands and French Polynesia, including the Red Sea, and absent only from the Hawaiian Islands. Presently, only a single widespread species is recognised for *Labroides dimidiatus* (Randall, 1958), though earlier authors have recognised at least one other species (see Bleeker, 1851). Molecular phylogenetic studies have complicated matters, suggesting that *Labroides dimidiatus* sensu lato constitutes a polyphyletic, cryptic species complex (Drew et al., 2008; Sims et al., 2014).

The second species, *Labroides bicolor*, is the largest member of the genus, with mature specimens easily approaching and sometimes exceeding 100 mm in standard length (SL). The species possesses a slightly longer snout than its congeners and is further unusual in that the typical stripe pattern of the genus is obvious only in juveniles and initial phase (IP) specimens (Randall, 1958). It attains a widespread distribution similar to *Labroides dimidiatus* sensu lato but is absent from the Red Sea and the Hawaiian Islands. In addition to providing species accounts for *Labroides dimidiatus* and *Labroides bicolor*, Randall (1958) described a third and fourth species of *Labroides* as new, viz., *Labroides phthirophagus* from the Hawaiian Islands, and *Labroides rubrolabiatus* from French Polynesia and the surrounding islands of central and southeast Oceania. Both of his new species were more colourful than *Labroides dimidiatus* and *Labroides bicolor* and appear to be more closely related to each other than either were to the preceding species. In Randall's (1985) key to species, *Labroides phthirophagus* and *Labroides rubrolabiatus* could only be reliably separated by differences in colouration.

Only one additional species of *Labroides* has been recognised since Randall's (1958) review of the genus. Randall & Springer (1975) described *Labroides pectoralis* based on 20 specimens collected from shallow coral reefs across the western Pacific. Their new species is closely allied to *Labroides phthirophagus* and *Labroides rubrolabiatus*, more so with the latter, and is similarly separable only on the basis of colouration. Most notably, *Labroides pectoralis* possesses a large elliptical spot on the lower pectoral fin base not found in congeners. *Labroides pectoralis* has since been reported from elsewhere in the Indo-Pacific, including Christmas Island, the Cocos (Keeling) Islands, and northwest Australia in the eastern Indian Ocean. The Christmas Island and Cocos (Keeling) Islands population of *Labroides pectoralis* differs from those elsewhere in the Pacific Ocean in several aspects of live colouration, yet its putative status as a distinct species has only been superficially addressed by previous authors (Kuiter & Debelius, 2006; Kuiter, 2010; Allen & Erdmann, 2012, 2024).

More recently, a second, putative species of *Labroides* unassignable to any of the presently valid species has been discovered across the western Pacific. It most superficially resembles *Labroides bicolor*, but the species differs remarkably in colouration and is known only from a handful of specimens photographed and collected from deep mesophotic coral reefs between 40 to 145 m. Notwithstanding the paucity of recent, exhaustive taxonomic scrutiny, *Labroides* continues to be the subject of numerous ecological and behavioural studies across the Indo-Pacific. This, coupled with the already nebulous taxonomy established for *Labroides dimidiatus* sensu lato provided the impetus in addressing the systematics for the remaining species.

The broader relationships within the labrichthyine wrasses are similarly problematic, with the following problems identified based on molecular phylogenetic studies: (i) *Labroides* is paraphyletic with respects to the monotypic *Larabicus quadrilineatus* (Brownstein et al., 2025; Near et al., 2025); (ii) *Labropsis* is paraphyletic with respects to the monotypic *Diproctacanthus xanthurus* (Baliga & Law, 2016; Brownstein et al., 2025; Near et al., 2025); (iii) *Labroides dimidiatus* sensu lato constitutes a polyphyletic species-complex (Sims et al., 2014).

In a recent molecular study, Near et al. (2025) placed *Larabicus quadrilineatus* and *Diproctacanthus xanthurus* in synonymy with *Labroides* and *Labropsis*, respectively. However, both nomenclatural changes were not supported by accompanying taxonomic or morphological assessment. We further note that *Diproctacanthus* Bleeker, 1862 has nomenclatural priority over *Labropsis* Schmidt, 1930, rendering *Diproctacanthus* the senior synonym of *Labropsis*. Here we corroborate recent molecular findings with a systematic treatment of the genus *Labroides*. We reconstruct a phylogenetic framework for all species of *Labroides* and related genera by employing an integrative phylogenomic approach that combines 1,019 genome-wide ultraconserved elements (UCEs), mitochondrial cytochrome oxidase I (COI), and morphological assessments.

Our results indicate that species in the *Labroides phthirophagus* complex exhibit very shallow interspecific divergences and their relationships could not be inferred from mitochondrial DNA alone. However, these relationships were fully resolved with a phylogenomic approach, demonstrating the resolving power of UCEs and their effectiveness in capturing recent evolutionary history that may be misrepresented by mitochondrial data. We describe specimens from the eastern Indian Ocean previously confused for *Labroides pectoralis* as a new species, *Labroides flammulatus*. A second new species, *Labroides inopinatus*, is described based on specimens collected from deep mesophotic coral ecosystems from across the western

Pacific. *Labroides inopinatus*, new species, is highly distinct from all presently known species of *Labroides*, differing by 8.9–9.8% in mitochondrial COI to *Labroides bicolor*, which it appears to be only distantly related. *Larabicus quadrilineatus* is restored as *Labroides quadrilineatus* (Rüppell, 1835), following the historical combination first established by Günther in 1862. The genus *Labroides* is rediagnosed, and a key to all species is provided.

MATERIAL AND METHODS

Nomenclature. The Labrichthyini, first proposed by Russell (1980), comprise a lineage of wrasses with feeding specialisations toward coral feeding and parasite- or mucous-cleaning. Recent molecular phylogenetic studies have significantly improved our understanding of labrid relationships, in some instances radically challenging long-held concepts of monophyletic groups. One example is the nesting of the Labrichthyini within the Julidini, the latter representing a large radiation comprising several genera that themselves do not appear to be monophyletic (Westneat & Alfaro, 2005; Hughes et al., 2023; Brownstein et al., 2025). Notwithstanding their nesting within the Julidini, the Labrichthyini have been consistently recovered as a monophyletic lineage comprising the genera *Diproctacanthus*, *Labrichthys*, *Labroides*, *Labropsis*, and *Larabicus* (Westneat & Alfaro, 2005; Hughes et al., 2023; Brownstein et al., 2025). However, given the numerous unresolved crown-group radiations within the Julidini (Westneat & Alfaro, 2005; Hughes et al., 2023), the paraphyly of the Julidini with respect to the Labrichthyini, and the recent adoption of rank-free phylogenetic nomenclature by several authors (de Queiroz, 2007; de Queiroz & Cantino, 2020; Brownstein et al., 2025), we refer to the Labrichthyini sensu Russell (1980) informally as the descriptive clade "labrichthyine wrasses".

The monotypic *Larabicus quadrilineatus* has been recovered as nested within *Labroides* in previous molecular studies (Brownstein et al., 2025) and was subsequently placed in this genus as *Labroides quadrilineatus* (Near et al., 2025). Here, we corroborate the nomenclatural changes proposed by Near et al. (2025) with both molecular and morphological evidence. To avoid confusion in the following phylogenetic discussion, we refer to the species as *Larabicus quadrilineatus* in all instances prior to the formal taxonomic discussion. Similarly, we use the taxonomic qualifier aff. (from Latin 'affinis', meaning 'related to') to refer to putative new species prior to their formal descriptions.

Meristics, morphometrics, and specimen deposition. Measurements were made with digital callipers, recorded to the nearest 0.1 mm. All measurements to the snout tip were made to the mid-anterior tip of the upper lip. Standard length (SL) was measured from the snout tip to the posterior end of the hypural plate. Predorsal, preanal, and prepelvic lengths were measured from the snout tip to the base of the anteriormost spine of the relevant fin. Head length (HL) was measured from the snout tip to the upper attachment of the opercular membrane. Body depth was the vertical distance between origin of first dorsal fin and pelvic fins. Body width was measured at the pectoral-fin bases. Snout length was measured from the snout tip to the anterior orbital rim. Orbit diameter was the horizontal width of the orbit. Bony interorbital width was the least measurement. Caudal-peduncle length was measured from the base of the posteriormost anal-fin ray to the ventral edge of the caudal peduncle at the vertical through the posterior edge of the hypural plate. Caudal-peduncle depth was the least depth. Pectoral-fin length was the length of the longest ray. Other measurements are self-explanatory. Morphometric values are presented in Tables 1–7, expressed as percentage of SL.

Counts of principal caudal-fin rays follow Gill et al. (2016) and are presented in the form upper + lower, where the upper rays are those associated with hypurals 3–5, and lower rays are those associated with hypurals 1–2 and the parhypural; procurrent caudal-fin rays are those anterior (dorsal and ventral) to the principal rays; pectoral-fin rays are the total number of rays presented in Arabic numerals, and including the first, unbranched and unsegmented ray).

Distinction between the ceratobranchial and epibranchial on the first gill arch is often difficult to interpret in *Labroides*. As such, gill-raker counts are presented as total counts, and include all elements on the outer face of the first arch. Lateral-line scale counts include the last expanded pored or tubed scale overlapping the hypural crease. Additional tubed or pored scales may occasionally be present and displaced above or below the lateral line. These are not included in the counts. Scale rows above lateral line are the rows of non-pored scales counted from between the lateral line and the first segmented dorsal-fin ray and includes the row of leaf-like scales extending onto the dorsal-fin. Scale rows below lateral line are the rows of non-pored scales counted from between the lateral line and the first segmented anal-fin ray. Specimens were temporarily stained in Cyanine Blue 5R to facilitate examination of cephalic pores (Akihito et al., 1993; Saruwatari et al., 1997). Where counts were recorded bilaterally, both counts are given and separated from each other by a slash where different; the first count presented is the left count. Osteological details were determined from radiographs or micro-CT scans. In the following description of the new species, data are given first for the holotype, followed, where different, by data for the paratypes in parentheses.

Accounts of live colouration are provided for all species, based on colour photographs of individuals taken in the field, in aquaria, or immediately after death. For species exhibiting markedly different colouration in their juvenile, initial (IP), and terminal phases (TP), separate colouration accounts are provided for each. Occurrence data used for distribution mapping were derived from examined vouchered specimens, including type material, as well as verified underwater photographs sourced from public and citizen-science repositories, including the Global Biodiversity Information Facility (GBIF) and iNaturalist.

Type specimens of the new species are deposited in the Australian Museum, Sydney (AMS), the Academy of Natural Sciences of Philadelphia, Philadelphia (ANSP), the Kanagawa Prefectural Museum of Natural History, Odawara (KPM), the Natural History Museum of Los Angeles County, Los Angeles (LACM), and the Western Australian Museum, Perth (WAM). Type specimens and additional non-type material of comparative species were examined from specimens deposited at AMS, ANSP, the Natural History Museum, London (BMNH), the Bernice Pauahi Bishop Museum, Honolulu (BPBM), the California Academy of Sciences, San Francisco (CAS), the Muséum national d'Histoire naturelle, Paris (MNHN), the Senckenberg Research Institute and Natural History Museum, Frankfurt (SMF), the National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM), WAM, the Museum für Naturkunde, Berlin (ZMB), and the Zoological Reference Collection of the Lee Kong Chian Natural History Museum at the National University of Singapore (ZRC). We used colour images of comparative species deposited at the Kanagawa Prefectural Museum of Natural History (KPM-NI). These images are assigned unique numbers with the prefix KPM-NR. Note that owing to zero-padding, a seven-digit number is used for the catalogue number in the fish specimen and the fish image collections of KPM, but zero suppression is adopted for expression of essential numbers here. Institutional codes follow Sabaj (2020; 2025).

Taxon sampling, sequencing, and phylogenetic analysis. Tissue samples of the putative new species resembling *Labroides pectoralis* from the eastern Indian Ocean were obtained from muscle tissue and the right pelvic fin of two paratypes (AMS I.51331-001 and AMS I.51331-002 respectively). We refer to these specimens as *Labroides* aff. *pectoralis*.

Tissue samples of the second putative new species resembling *Labroides bicolor* were obtained from gill arches taken from the right side of the holotype (AMS I.51733-001) and two paratypes (AMS I.51732-001 and 51732-002 respectively). We refer to these specimens as *Labroides* aff. *bicolor*.

Tissue samples were preserved in 100% ethanol and stored at -20°C prior to extraction. DNA was extracted using the DNeasy Blood and Tissue kit (Qiagen) following the manufacturer's protocol. Mitochondrial COI was amplified from extracted gDNA using the polymerase chain reaction (PCR). Primer sets and PCR conditions follow Ward et al. (2005). Sanger sequencing was outsourced to the Australian Genome Research Facility (AGRF; Canberra, Australia). Forward and reverse contigs were aligned and trimmed separately using Geneious Prime v 2025.2.1 (Dotmatics, Auckland). Mitochondrial COI sequences of the new species was then combined with those of nine other labrichthyine wrasses (n = 85) available from GenBank or extracted from assembled contigs of target sequence data (see Appendix in supplemental material for accession numbers).

Shallow genome sequencing was conducted by AGRF for two specimens of *Labroides* aff. *pectoralis* (AMS I.51331-001; AMS I.51331-002) while UCE targeted enrichment was conducted by Arbor Bioscience (Ann Arbor, Michigan) following the MyBaits v.5 protocol for 15 other species of labrichthyine wrasses and five closely related outgroup species (see Appendix in supplemental material). Demultiplexed Illumina reads were trimmed using fastp v.0.23.2 (Chen et al., 2018) with the specified parameters -q 25 -u 10 -l 80 -n 1 -e 20 -M 25 and --cut_by_quality_aggressive for the genome skimming data and the default parameters for the target capture data. Trimmed reads were then assembled using SPAdes v.3.15.5 with the --careful and --cov-cutoff 2 options (Prjibelski et al., 2020). Following the mapping and correction workflows implemented in Phyluce v.1.7.3, low-depth and low-quality base calls were filtered out from assembled contigs of target capture data (Faircloth, 2016; https://phyluce.readthedocs.io/en/latest/daily-use/daily-use-4-workflows.html). UCE loci and mitochondrial COI sequences were extracted from assembled contigs in Phyluce using the acanthomorph bait set comprising 1,341 UCE loci and the –phyluce_assembly_match_contigs_to_barcodes command, respectively (Alfaro et al., 2018). UCE contigs and COI sequences were aligned separately using MAFFT v.7.505 and default parameters (Katoh & Standley, 2013). UCE alignments were edge trimmed in Phyluce prior to generating a 75% species occupancy matrix. The final alignment matrices comprised 1,019 UCE loci (727,110 bp) and 90 COI sequences (652 bp).

Two independent phylogenetic reconstructions were inferred by maximum likelihood with IQ-TREE v2.2.2.2 (Nguyen et al., 2015) using best-fit substitution model and partitioning scheme selected by ModelFinder (Lanfear et al., 2012; Kalyaanamoorthy et al., 2017) on the UCE + COI alignment matrix, and the COI alignments. Branch support was assessed using ultrafast bootstrap approximation (UFBoot2) with 1,000 replicates (Hoang et al., 2018) and the Shimodaira-Hasegawa-like approximate likelihood-ratio test (SH-aLRT; Guindon et al., 2010) with 1,000 replicates. Node values were taken as robust if they were recovered with support values of UFBoot2 ≥ 95 and SH-aLRT ≥ 80 (Guindon et al., 2010; Bui et al., 2013). *Labropsis polynesica* was used as the outgroup in the phylogenetic relationships inferred from COI sequences. Uncorrected p-distances were calculated for the new species and related species of *Labroides* using Geneious Prime. Sequence alignment files, raw tree files, and accession numbers are provided in the supplemental material.

RESULTS AND DISCUSSION

Phylogenetic relationships of the labrichthyine wrasses. Our maximum-likelihood analysis of the concatenated 75% occupancy UCE + COI matrix yielded a phylogenetic tree with well-supported nodes along the backbone of the labrichthyine wrasses (Fig. 1). The monotypic *Labrichthys unilineatus* was recovered as the sister lineage to all remaining genera of labrichthyine wrasses, of which none were recovered as monophyletic.

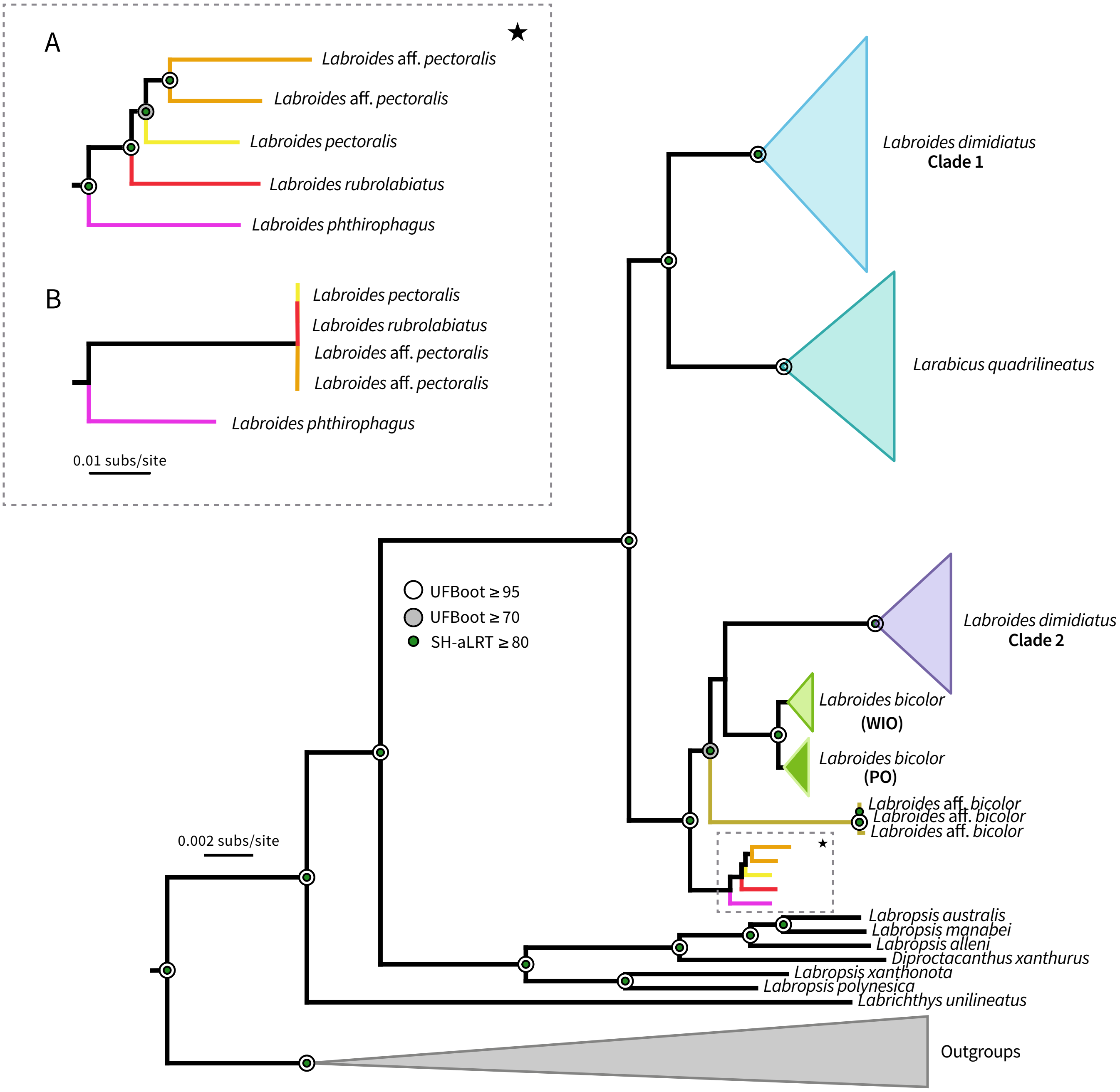

Fig. 1. Maximum-likelihood phylogenetic tree of the labrichthyine wrasses, inferred using 75% occupancy UCE + mitochondrial COI matrix. Circles at nodes indicate levels of SH-aLRT and UFB support. SH-aLRT = Shimodaira-Hasegawa-like approximate likelihood ratio test; UFBS = ultrafast bootstrapping. The expanded figure inset (marked by a star symbol) shows the A, resolved relationships among species in the *Labroides phthirophagus* species complex that were previously B, unresolved on the basis of mitochondrial COI data alone. Tree figures with uncollapsed clades are provided in the supplemental material.

The genus *Labroides* was recovered as paraphyletic with respect to *Larabicus*, with its sole species, *Larabicus quadrilineatus*, forming a sister-group relationship with a subset of *Labroides dimidiatus* (hereafter *Labroides dimidiatus* clade 1), thereby rendering *Labroides dimidiatus* non-monophyletic. *Labroides dimidiatus* clade 1 includes topotypical representatives of *Labroides dimidiatus* sensu stricto from the Red Sea, the type species of the genus.

A second subset of *Labroides dimidiatus* (hereafter *Labroides dimidiatus* clade 2) was recovered sharing a sister-group relationship with *Labroides bicolor*, with both together sharing successive sister relationships to *Labroides* aff. *bicolor* and the *Labroides phthirophagus* species complex. The polyphyly of *Labroides dimidiatus* sensu lato and the relationships of clades 1 and 2 are congruent with relationships recovered in Sims et al. (2014) based on phylogenetic analyses of mitochondrial control region. We note, however, that node support for this portion of the tree is relatively low, and further studies are needed to assess the intraspecific relationships of *Labroides dimidiatus* sensu lato.

We were able to resolve the relationships among species in the *Labroides phthirophagus* complex, with the eastern Indian Ocean *Labroides* aff. *pectoralis* recovered as monophyletic and sharing successive sister relationships to

Fig. 2. Feeding strategies employed by *Labroides*. A, *Labroides dimidiatus* sensu lato cleaning *Ostorhinchus aureus*. Underwater photograph taken in Yakushima Island, southern Japan; B, *Labroides pectoralis* picking on *Pocillopora* spp. Underwater photograph taken in Minna Island, Okinawa, Ryukyu Archipelago, Japan; C, *Labroides dimidiatus* sensu lato feeding on coral mucus strand. D, close up inset showing the mucus strand passing between the gap on the lower lip. Underwater photograph taken in Yakushima Island, southern Japan. Photographs by (A, C, D) S. Harazaki and (B) U. Satoshi.

Labroides pectoralis, *Labroides rubrolabiatus*, and *Labroides phthirophagus* (Fig. 1A). In contrast, maximum-likelihood analysis of mitochondrial COI alone could not resolve the relationships among these species, with *Labroides pectoralis*, *Labroides rubrolabiatus*, and *Labroides* aff. *pectoralis* sharing identical COI haplotypes (Fig. 1B).

The genus *Labropsis* was also recovered as paraphyletic with respect to *Diproctacanthus*, with its sole species, *Diproctacanthus xanthurus*, forming a sister-group relationship with a subset of *Labropsis* that includes *Labropsis manabei*, *Labropsis australis*, and *Labropsis alleni*. The remaining species, *Labropsis polynesica* and *Labropsis xanthonota*, form a group sister to the remaining species.

An explicit phylogeny of the labrichthyine wrasses with all representative genera was first proposed by Westneat & Alfaro (2005), who recovered a sister-group relationship between *Labroides* and *Larabicus*, and between *Labropsis* and *Diproctacanthus*. These relationships were later also recovered by Cowman et al. (2009) and Cowman & Bellwood (2011) with the same taxon set. Baliga & Law (2016) expanded taxon coverage for *Labropsis*, demonstrating its paraphyly with respects to *Diproctacanthus*. However, their study did not include additional sampling for *Labroides*, resulting in the recovery of the same sister-group relationship between *Larabicus* and *Labroides* first proposed by Westneat & Alfaro (2005) and later by Cowman & Bellwood (2011). Brownstein et al. (2025) expanded taxon coverage for *Labropsis* and showed the same nesting of *Diproctacanthus xanthurus* within *Labropsis*. Although taxon coverage for *Labroides* in Brownstein et al. (2025) was similar to Baliga & Law (2016), they recovered a sister-relationship between *Larabicus quadrilineatus* and *Labroides dimidiatus*, resulting in a non-monophyletic *Labroides*.

Our phylogenetic analyses, with increased taxon coverage of *Labroides dimidiatus* sensu lato, suggest that the inconsistent placement of *Larabicus*, either as the sister group to *Labroides* (Cowman & Bellwood, 2011; Baliga & Law, 2016) or nested within *Labroides* (Brownstein et al., 2025), may be an artefact of the polyphyly of *Labroides dimidiatus* sensu lato (Sims et al., 2014) and incomplete taxon sampling. These results suggest that different studies have sampled representatives of each of the two distinct lineages of *Labroides dimidiatus* sensu lato, but not the entire complex—for example, clade 2 in Cowman & Bellwood (2011) and Baliga & Law (2016), and clade 1 in Brownstein et al. (2025).

Trophic ecology of the labrichthyine wrasses. Brownstein et al. (2025) reconstructed ancestral states to investigate the evolution of the cleaning trophic guild in the labrichthyine wrasses, allocating species to three discrete categories: non-cleaner, facultative adult cleaner, and obligate cleaner.

However, their coding of character states are inconsistent with the published literature and ecological field observations.

For example, in their study, Brownstein et al. (2025) regarded *Diproctacanthus* and *Larabicus* as obligate cleaners, a category they also allocated to all species of *Labroides* at the exclusion of *Labroides dimidiatus* sensu lato. The latter was regarded as a facultative adult cleaner, together with *Labropsis polynesica*. All other *Labropsis* and *Labrichthys* species were coded as non-cleaners. These trophic categorisations are in contrast with previous studies in which *Labroides* is recognised as the sole obligate cleaning genus within the labrichthyine wrasses, with all other genera except *Labrichthys* either exhibiting facultative cleaning or juvenile associated cleaning (Baliga & Law, 2016; Floeter et al., 2017).

In contrast to their taxonomy, trophic ecology of the labrichthyine wrasses is comparatively well established. Except for *Labroides*, whose species are obligate or near-obligate cleaners (Randall, 1958; Vaughan et al., 2017; Floeter et al., 2017; Huie et al., 2020), all other members of the labrichthyine wrasses are notable corallivores, specialising in picking at coral polyps or coral mucus (see Cole, 2010; Cole et al., 2010; Huertas & Bellwood, 2017; Floeter et al., 2018). The ancestral reconstructions of Cowman et al. (2009), and later Baliga & Law (2016), proposed that obligate cleaning in *Labroides* likely evolved from an ancestral condition of corallivory within labrichthyine wrasses, with cleaning behaviour being relatively labile and potentially arising from morphological or physiological specialisations originally associated with coral-mucus feeding. This hypothesis is supported by facultative or ontogenetic shifts in feeding ecology observed in other labrichthyine genera, including transitions from juvenile cleaning or fish-mucus feeding to adult-associated corallivory in species such as *Labropsis alleni*, *Diproctacanthus xanthurus*, and *Larabicus quadrilineatus*. (Abel, 1960; Randall & Springer, 1973; Cole et al., 2010; Kuiter, 2010; Baliga & Law, 2016; Floeter et al., 2017).

This hypothesis is further supported by direct field observations that cleaning in *Labroides* (Fig. 2A) is supplemented with opportunistic ingestion of client-fish mucus (Grutter & Bshary, 2004; Oates et al., 2012; Triki et al., 2025) as well as coral mucus (Fig. 2B–D; also H. Sato, pers. comm., 2025; see Data Accessibility). In Okinawa, *Labroides dimidiatus* sensu lato (see Data Accessibility) and *Labroides pectoralis* (Fig. 2B) have both been observed repeatedly picking at coral tissue—the former on *Lobophytum* spp., and the latter on *Pocillopora* spp. Our molecular phylogeny supports corallivory as the ancestral condition in the labrichthyine wrasses as proposed by Cowman et al. (2009), Baliga & Law (2016), and Floeter et al. (2017). However, given the nesting of *Larabicus* within *Labroides*, our results also suggest that cleaning evolved once within *Labroides*, with one instance of secondary reversion to the ancestral condition of corallivory in *Larabicus*.

All species of the labrichthyine wrasses possess a reticulate, sometimes pitted epithelium lining the inner surface of the operculum, including the membranous free margin of the opercle and the gill chamber (see character 6 below). The same epithelium is also present posterior to the gill chamber, overlying the cleithrum, and usually concealed by the free outer edge of the opercle. We regard this feature as a synapomorphy of the labrichthyine wrasses.

The function of this epithelium is presently unknown, but they closely resemble the mucus-secreting lamellae described by Huertas & Bellwood (2017) lining the lips of *Labropsis*. Histological sections and scanning electron micrographs show that the convoluted oral epithelium in *Labropsis* functions as a high-productivity mucus gland, secreting copious amounts of mucus and acidic and/or neutral mucopolysaccharides (Huertas & Bellwood, 2017). This lip specialisation has been hypothesised to facilitate coral feeding, and the neutralisation of nematocysts present in coral tissue. It is possible that the reticulate epithelium in the oral cavity and gill chamber of labrichthyine wrasses is composed of the same mucous epithelium and provides an additional level of protection prior to ingestion of coral tissue. We interpret the retention of these characters across all species of *Labroides* as additional support for a derived cleaning trophic ecology that evolved from an ancestral condition of corallivory.

TAXONOMY

Family Labridae Cuvier, 1816

Genus *Labroides* Bleeker, 1851

Labroides Bleeker, 1851: 249 (type species *Labroides paradiseus* Bleeker, 1851 by monotypy [= *Cossyphus dimidiatus* Valenciennes, 1839])

Diagnosis. Except for *Labroides quadrilineatus* (Rüppell, 1835), which exhibits a combination of autapomorphies and secondary reversals to the plesiomorphic state, *Labroides* is diagnosed from all other labrid genera by the following combination of characters. Character states in *Labroides quadrilineatus* that differ from those of other congeners are detailed in its species account.

1. **Lower lip bilobular and prong-shaped:** Species of *Labroides* possess a fleshy, bilobular, prong-shaped lower lip, the gap formed between the two lobes about one-fourth orbit diameter and coincides with the two caniform teeth on the dentary (Fig. 3A). When the mouth is nearly closed, the upper lip touches the lower lip at the sides of the two lobes forming a small opening, which has been proposed by previous authors as a way to increase negative pressure in the buccal cavity for suctioning of small parasitic organisms (Tedman, 1980). Field photographs of *Labroides* ingesting mucus strands show the mucus passing through the gap between the lobes (Fig. 2C, D), suggesting the lobes may also guide mucus into the mouth. We consider this character a synapomorphy for *Labroides*

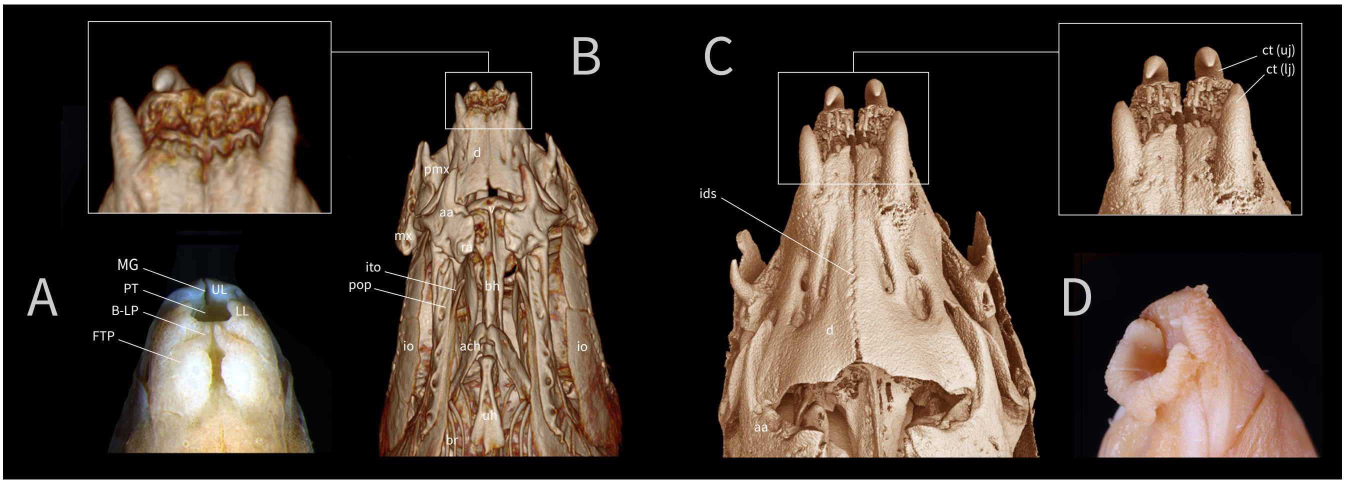

Fig. 3. A, *Labroides rubrolabiatus*, BPBM 42155, 55.6 mm SL. Ventral view of head showing prong-shaped lower lip typical of the genus; B, *Labroides rubrolabiatus*, USNM 423439, 65.1 mm SL. Micro-CT scan of head in ventral view, with expanded inset showing canine teeth in upper and lower jaws and gap between dentaries; C, *Labroides quadrilineatus*, BPBM 17886, 59.1 mm SL. Micro-CT scan of head in ventral view, with expanded inset showing canine teeth in upper and lower jaws and gap between dentaries; D**.** *Labroides quadrilineatus*, BPBM 17886, 59.1 mm SL. Ventral view of head showing U-shaped lower lip and fringing of anterior lip margin. B-LP = barbel-like projection; FTP = fleshy tissue pad; LL = lower lip; MG = median groove; PT = papillose tissue; UL = upper lip; aa = anguloarticular; ach = anterior ceratohyal; bh = basihyal; br = branchiostegal rays; d = dentary; ct = canine teeth; ids = interdigitating suture; io = infraorbitals; ito = interopercle; lj = lower jaw; mx = maxilla; pmx = premaxilla; pop = preopercle; ra = retroarticular; uh = urohyal; uj = upper jaw; v = vomer. Scale bars are 2 mm. Photographs by (A) I. Riley and (D**)** L. Hodgson. Micro-CT scans by (B) J.M. Huie and (C) K. Parkinson.

2. **Fleshy tissue pads on chin:** The chin of *Labroides* is ornamented with a pair of fleshy tissue pads, one situated beneath each lobe of the lower lip, and each occasionally with an anteriorly directed, barbel-like fleshy projection, their tips converging towards the midline of the lower jaw between both lobes of the lower lip (Fig. 3A). We consider this character a synapomorphy for *Labroides*.
3. **Anterior dentary gap:** The dentaries of *Labroides* are strongly united medially by bony interdigitating sutures for most of its length, except on the anteriormost portion, where there is a gap (Fig. 3B, C). We consider this character a synapomorphy for *Labroides*.
4. **Elongate hypohyal–basihyal complex:** The hypohyal and basihyal in *Labroides* are very well developed and elongate, reaching well into the oral cavity (Fig. 3B). The combined hypohyal and basihyal are connected to the ceratohyal by several ligaments and the depressor hypohyalis muscle (sensu Tedman, 1980). This well-developed musculature and ligamentous connection has been proposed to contribute to the feeding mechanism of *Labroides*, possibly by increasing negative pressure in the buccal cavity through depression of the hypohyal and basihyal (Tedman, 1980).
5. **Papillose tissue in upper jaw:** The median groove between the upper lip in *Labroides* bifurcates posteriorly forming a free margin that surrounds a pad of fleshy papillose tissue (Fig. 3A). This character is also present in the other labrichthyine genera. We consider this character a synapomorphy diagnosing the labrichthyine wrasses.
6. **Reticulate epithelium of the opercular cavity:** All species of *Labroides* possess a reticulate, sometimes pitting epithelium (Fig. 4) covering the inner surface of the operculum (Fig. 4D), including the membranous free margin of the opercle, the gill chamber, and overlaying the cleithrum (Fig. 4A–C). This character is also present in the other labrichthyine genera. We consider this character a synapomorphy diagnosing the labrichthyine wrasses.
7. **Infraorbitals with expanded laminae:** The infraorbital bones in *Labroides* are laterally expanded and plate-like (Fig. 5G–I). The laminal expansion of the third, fourth, and fifth infraorbitals are sometimes wide enough that they cover the quadrate and preopercle nearly in their entirety. Laminal expansion of the infraorbital bones also occurs in *Labropsis* (Fig. 5D, E), but not in *Labrichthys* (Fig. 5C) and outgroup julidine taxa (Fig. 5A, B). This character is interpreted as a synapomorphy uniting *Labroides* and *Labropsis*.

Dorsal-fin rays IX,11 (rarely 10); anal-fin rays III,10–11 (rarely 9); pectoral-fin rays 13 (rarely 14); pelvic-fin rays I,5; principal caudal-fin rays 8 + 7 (rarely 7 + 7 or 8 + 8); lateral line continuous, pored scales ≤ 40 or ≥ 50 (see key to species); total gill rakers 11–14; branchiostegal rays 5; vertebrate 10 + 15; mouth small with thick lips; lips on upper jaw fleshy with a shallow median groove; median groove on upper lip bifurcating and continuing posteriorly forming a free margin surrounding a triangular pad of fleshy papillose tissue; lips on lower jaw prong like, divided into two prominent, anteriorly projecting lobes (anterior margin of lower lip in *Labroides quadrilineatus* furled ventrally); a pair of large, curved, canine teeth anteriorly in each jaw, upper pair fitting inside wide-spaced lower pair when mouth is closed; a large, anteriorly directed canine tooth at extreme posterior part of upper jaw, separated by a gap from anterior teeth; remaining teeth small. Those in lower jaw in several close-set rows between canines and those in upper jaw forming a large mass just behind anterior canines; caudal-fin truncate or slightly rounded; preopercle entire, margin

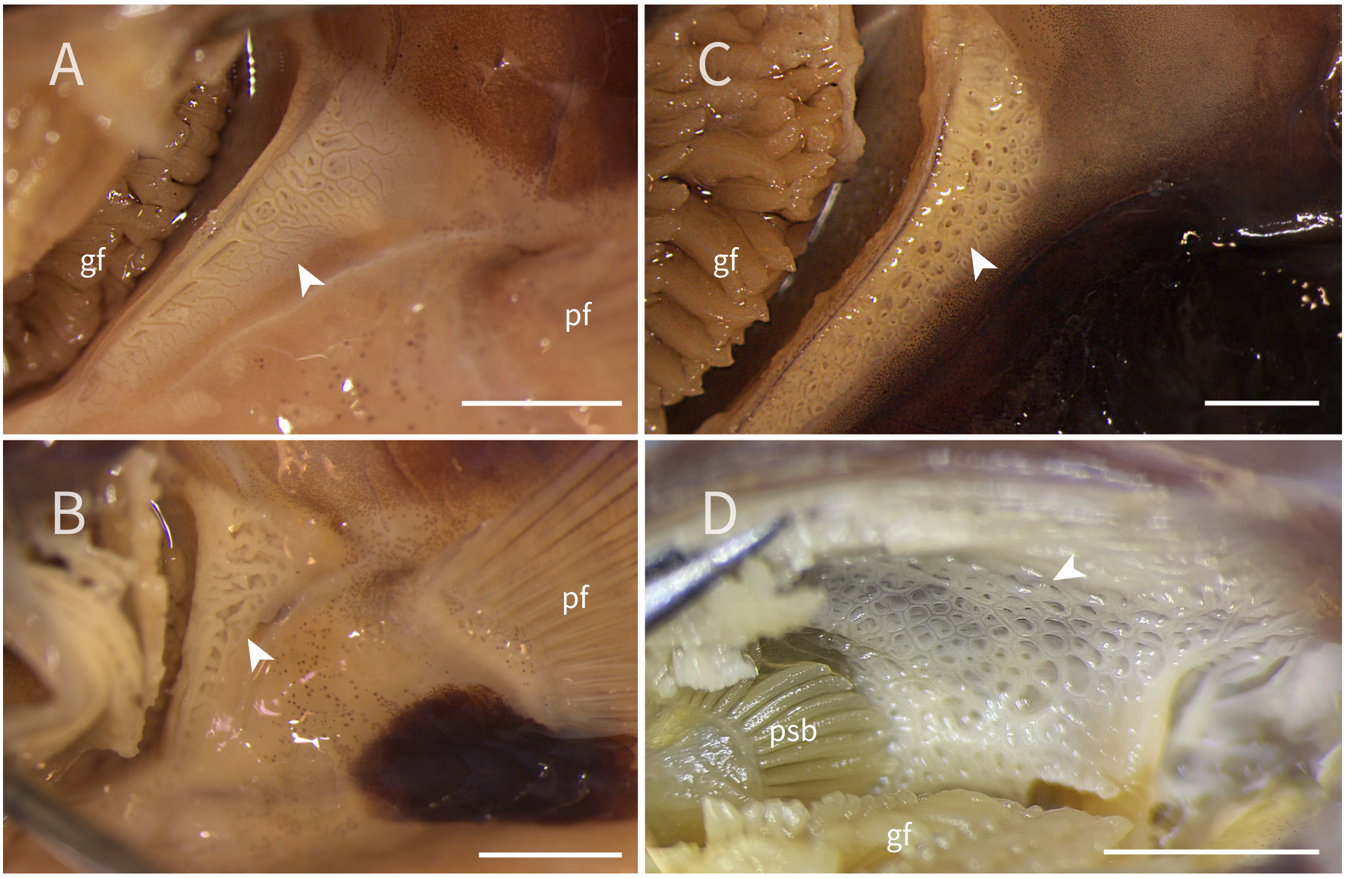

Fig. 4. A selection of labrichthyine labrids showing the reticulate and pitting epithelium (indicated by white arrow heads) overlying the cleithrum (A–C) and the inner surface of the operculum (D). A, *Labroides dimidiatus* sensu lato, AMS I.17506-002, 78.7 mm SL, Nukulau Pass, Fiji; B, *Labroides flammulatus*, new species, ANSP 133368, paratype, 53.2 mm SL, Cocos (Keeling) Islands; C, *Labrichthys unilineatus*, AMS I.44718-026, 114.6 mm SL, Lizard Island, Great Barrier Reef; D, *Labrichthys unilineatus*, AMS I.22579-046, 44.1 mm SL, Escape Reef, Great Barrier Reef. gf = gill filaments; pf = pectoral fin; psb = pseudobranch. Scale bars are 2 mm. Photographs by (A–C) T. Miskiewicz and (D) Y.K. Tea.

smooth and without serrations; gill membranes attached to isthmus; all species generally with a lateral body stripe from snout to caudal-fin with varying degrees of constriction or attenuation (see key to species).

Description. Dorsal-fin rays IX (rarely X),11 (rarely 10), first ray unbranched, last branched to base; dorsal fin with a membranous cirrus posterior to tip of each spine; anal-fin rays III,10–11 (rarely 9), last ray branched to base; first anal-fin spine very short, sometimes embedded; pectoral-fin rays 13 (rarely 14); uppermost rudimentary, uppermost two unbranched; pelvic-fin rays I,5; principal caudal-fin rays 8 + 7 (rarely 7 + 7 or 8 + 8), upper and lowermost unbranched; upper procurrent caudal-fin rays 5–8; lower procurrent caudal-fin rays 5–8; lateral line continuous with ≤ 40 or ≥ 50 pored scales, posteriormost two slightly enlarged and beyond hypural; 3–5 scale rows between lateral line and segmented portion of dorsal-fin, third row extending onto fin base; a row of vertically elongate, leaf-shaped scales on base of dorsal fin, one to two per radial element; scales below lateral line to anal-fin origin 9–14; diagonal scale rows on cheek from eye to upper corner of preopercle 5; circumpeduncular scales 18–24; total gill rakers 11–14; branchioistegal rays 5; vertebrae 10 + 15 = 25.

Posterior edge of maxillary difficult to detect, but reaching about to a vertical at anterior nostril; mouth small, width about three-fourths orbit diameter; upper lips thick with a shallow median groove; median groove on upper lip bifurcating and continuing posteriorly forming a free margin surrounding a triangular pad of fleshy papillose tissue; lower lip distinctly bilobed, prong-shaped, gap between the lobes about one-fourth orbit diameter (anterior margin of lower lip ventrally furled and fringed in *Labroides quadrilineatus*); chin with a pair of fleshy pads of tissue, each sometimes with a forward projecting process, their tips converging towards midline of lower jaw between both lobes of lower lip (absent in *Labroides quadrilineatus*); a single pair of strongly recurved canines anteriorly in each jaw, upper canines fitting inside lower pair when mouth is closed; length of upper canines about one-fourth orbit diameter; lower canines nearly straight, angling slightly outward; a large forward-directed canine posteriorly on upper jaw at corner of mouth; remaining teeth small, those at symphysis of upper jaw in numerous close-set rows, forming a semicircular mass between canines.

Gill membranes attached to isthmus slightly posterior to a vertical at posterior edge of orbit. Snout, ventral portion of head, interorbital space, and proximal region of nape scaleless (ventral portion of head scaled in *Labroides quadrilineatus*);

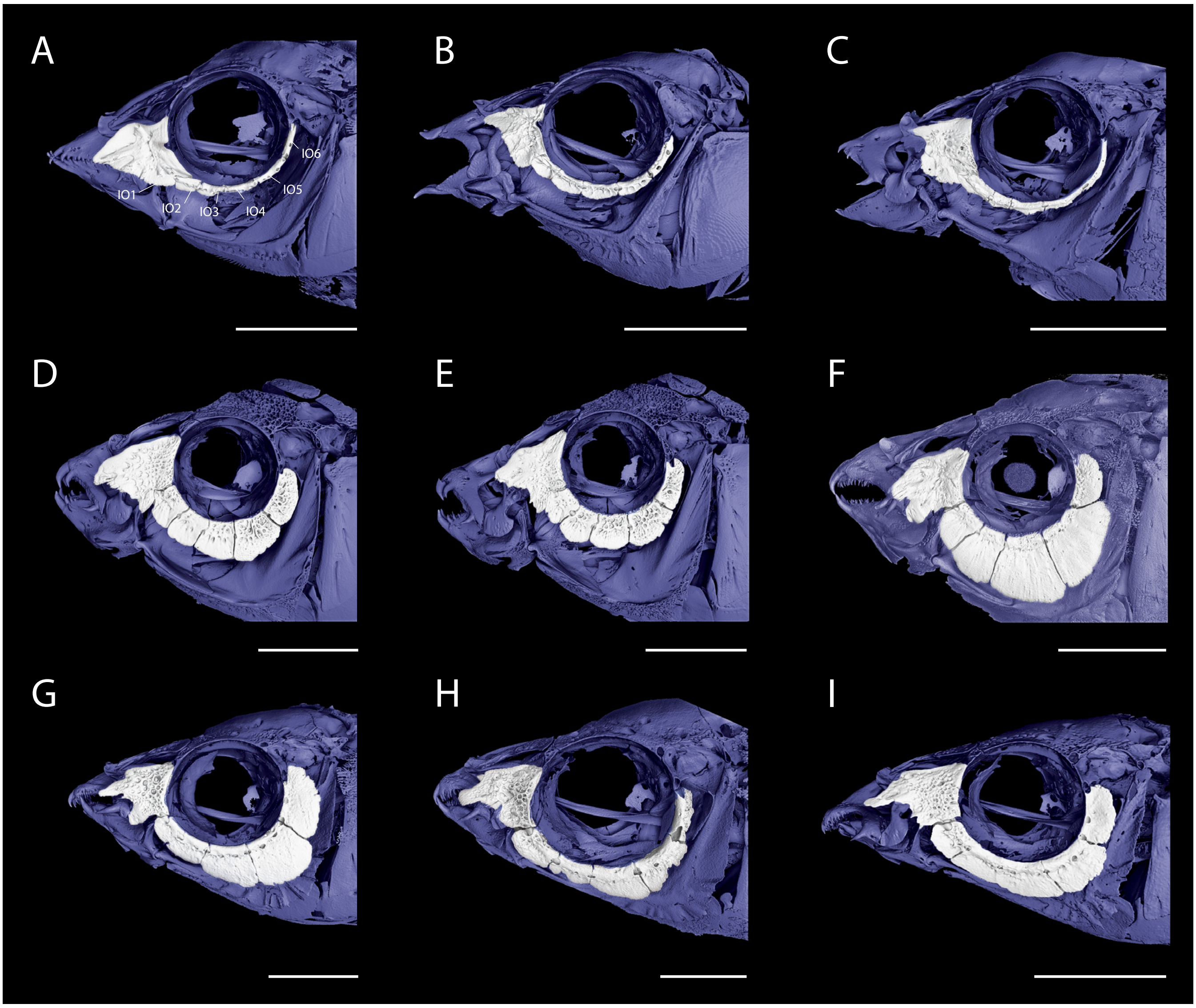

Fig. 5. Micro-CT 3D reconstruction of infraorbital (IO) bones for selected species of labrids. A, *Halichoeres hortulanus*, AMS I.28950-036, 70.9 mm SL; B, *Anampses femininus*, AMS I.46471-016, 41.1 mm SL; C, *Labrichthys unilineatus*, AMS I.15633-027, 60.6 mm SL; D, *Labropsis australis*, AMS IB.7799, 81.8 mm SL; E, *Labropsis australis*, AMS I.19462-037, paratype, 78.2 mm SL; F, *Labroides quadrilineatus*, BPBM 13400, 84.4 mm SL; G, *Labroides rubolabiatus*, AMS I.18039-013, 49.8 mm SL; H, *Labroides inopinatus*, new species, AMS I.51733-001, holotype, 49.3 mm SL; I, *Labroides bicolor*, AMS I.18034-039, 49.7 mm SL. Scale bars represent 5 mm. Head scans not to scale. Micro-CT scans by A. Mackenzie.

Fig. 6. A pair of *Labroides phthirophagus* with clients *Chaetodon lunula* and *C. quadrimaculatus* at a cleaning station. Underwater photograph from Kailua-Kona, Hawaiian Islands. Photograph by B. Fackler.

a narrow, horizontal band of scales running below eye just beneath suborbital pores, consisting mainly of a single scale row, which ends slightly anterior to a vertical at front of eye. Basal half of caudal fin scaled; dorsal and anal fin with a row of vertically elongate, leaf-shaped scales, one to two per radial element; paired fins scaled only basally; pelvic fins with a series of three enlarged scales in a median row posterior to origin.

Etymology. Combination of the labrid genus *Labrus* and the Greek suffix -oides meaning 'resembling' or 'to bear likeness to', presumably in reference to its similarity with the genus *Labrus* (or simply other members of the family Labridae). Gender is masculine. Species of *Labroides* are known by a variety of common names, including cleaner wrasse, cleaner fish, or doctor fish. To maintain consistent terminology with other members of the Labridae, and to distinguish *Labroides* from other non-labrid fishes that

Fig. 7. A juvenile *Labroides dimidiatus* sensu lato inside the gill chamber of client *Arothron hispidus*. Note visible gill filaments. Underwater photograph from Tulamben, Bali, Indonesia. Photograph by K. Steiel.

engage in cleaning behaviour, we use cleaner wrasse as the preferred common name.

Habitat and biology. Small (usually less than 70 mm TL, rarely exceedingly 100 mm SL in only one species), slender, elongate, and moderately compressed fishes most frequently found on coral reefs usually between 2–40 m (but have been reported at depths more than 100 m). Members of the genus are widespread across the Indo-Pacific, occurring from the East African coast and the Red Sea to the Hawaiian Islands and southeast Oceania, with their easternmost distributional limit in the Pitcairn Island group (Springer, 1982). Except for the corallivorous *Labroides quadrilineatus*, whose cleaning is facultative and mostly limited to juvenile and immature individuals, the diet of *Labroides* primarily consists of ectoparasites, namely caligoid copepods and gnathiid isopods (Randall, 1958; Youngbluth, 1967; Grutter, 2000) but may also opportunistically include mucus and scales of their client fishes (Grutter, 2000; Bshary & Grutter, 2005; Mills & Côté, 2010). Although sometimes encountered singly or in small groups, *Labroides* are most frequently observed in pairs at cleaning stations defined by a prominent feature, often comprising a rock, cave, or ledge easily recognised by client fishes. During cleaning, client fishes may be highly compliant and permissive, allowing the cleaner wrasse to enter their mouths and even gill chambers (Figs. 2A, 6, 7). Juveniles are less frequently encountered in the open, preferring caves, ledges, and overhangs. The stripe pattern in juveniles of all species is slightly iridescent (bright yellow in *Labroides bicolor*, blue in all remaining species), likely aiding in advertising their location for clients in more dimly lit environments which they seem to prefer. To further advertise their services, cleaner wrasses often swim in a jerky, oscillating manner interspersed with short leaps. Randall (1958) provided a more detailed account of their biology.

Key to the species of *Labroides* (adults only)

1. Lower lip U-shaped, anterior margin ventrally furled and forming a fringe; mouth tube-like when closed; lips strongly plicate internally, smooth to faintly plicate externally; ventral portion of head scaled .... ***Labroides quadrilineatus* (Rüppell, 1835)**

– Lower lip prong-shaped and bilobular with a U-shaped medial notch; anteriormost margin of lower lip not ventrally furled; mouth not tube-like when closed; upper and lower lips not plicate internally or externally, ventral portion of head naked **2**

2. Pored scales in lateral-line series ≥ 50 (usually 52–54); head and anterior body grey to ochre (usually grey); posterior body light blue; body stripe from snout, passing through orbit to end of caudal fin (this stripe gradually broadening posteriorly) .... ***Labroides dimidiatus* (Valenciennes, 1839) sensu lato**

– Pored scales in lateral-line series ≤ 40; colour not as above (body bicoloured, uniformly yellow to brown, or colourful with yellow or orange) **3**

3. Pored scales in lateral-line series 33–36; body yellowish brown with a silvery white stripe from snout to upper edge of caudal fin; caudal fin fuliginous with a narrow, white crescentic margin .... ***Labroides inopinatus*, new species**

– Pored scales in lateral-line series < 30 (usually 28); colour not as above (body bicoloured or colourful with yellow, orange, or magenta) **4**

4. Snout long, diameter of orbit usually more than 2.0 in snout length; body distinctly bicoloured, deep indigo to navy blue anteriorly, pale cream to greenish yellow posteriorly (immature specimens silvery white to pale grey); body stripe absent or, if present, attenuating at mid body; caudal fin with black crescentic margin .... ***Labroides bicolor* (Fowler & Bean, 1928)**

– Snout short, diameter of orbit contained less than 2.0 times in snout length; body colourful with yellow, orange, or magenta **5**

5. Lower pectoral fin-base without well-defined, elliptical black spot **6**

– Lower pectoral fin-base with well-defined, elliptical black spot **7**

6. Head and anterior body bright yellow; cheek unmarked; anterior body stripe narrow, expanding in width toward outer edge of caudal fin; upper and lowermost edges of caudal fin magenta .... ***Labroides phthirophagus* Randall, 1958**

– Head and anterior body pale chartreuse; cheek sometimes with narrow dusky streak running horizontally below eye to edge of opercle, rarely extending to lower pectoral-fin base as an ill-defined club-shaped blotch; body stripe restricted to head, becoming progressively attenuated or entirely absent towards middle and posterior body; middle portion of body to caudal peduncle richly suffused with bright tangerine orange .... ***Labroides rubrolabiatus* Randall, 1958**

7. Head and anterior body bright yellow orange on posterior dorsum above body stripe, posterior body above anal-fin base blue; cheek unmarked; anterior body stripe narrow (sometimes attenuated in matured individuals), expanding in width toward outer edge of caudal fin .... ***Labroides pectoralis* Randall & Springer, 1975**

– Head and anterior body grey to steely blue; cheek with narrow dusky streak running horizontally below eye to edge of opercle; posterior two thirds of body suffused with orange-brown (weakly encroaching into body stripe) .... ***Labroides flammulatus*, new species**

Nomenclature and type status of *Labrus quadrilineatus* Rüppell, 1835. Rüppell (1835) described *Labrus quadrilineatus* from Massawa, Eritrea, in the northern Red Sea. Although his description included an illustration (Fig. 8A), he neither stated the number of specimens he examined nor designated a holotype. The original material was deposited in SMF as a series of four syntypes (SMF

1588). As no holotype was designated by Rüppell, all specimens cited in the original description collectively constitute syntypes (Article 73.2 of the International Code of Zoological Nomenclature; ICZN, 1999).

Valenciennes, in Cuvier & Valenciennes (1839), erected the new genus *Cossyphus* for a group of labrids and described *Cossyphus taeniatus* (Valenciennes, 1839) from specimens collected by Ehrenberg at Massawa, Eritrea, based on Ehrenberg's unpublished manuscript name *Labrus taeniatus*. Valenciennes neither stated the number of specimens provided to him by Ehrenberg, nor designated a holotype. Ehrenberg's original material, on which Valenciennes based his description of *Cossyphus taeniatus*, consisted of two specimens deposited in ZMB (ZMB 2471). These two specimens are regarded as syntypes (Article 73.2; ICZN, 1999). In the same work, Valenciennes (1839) reassigned Rüppell's *Labrus quadrilineatus* to *Cossyphus* as *Cossyphus quadrilineatus* and noted that the two species might be conspecific. Since *Labrus quadrilineatus* predates *Cossyphus taeniatus*, the latter name is a junior subjective synonym.

Roux-Estève in Roux-Estève & Fourmanoir (1955) described a similar fish from Abu Latt, off the coast of Saudi Arabia in the Red Sea, as *Labrichthys cousteaui*, based on a holotype and four paratypes deposited at MNHN. Randall & Springer (1973) recognised that Rüppell's *Labrus quadrilineatus* did not fit in either *Labroides* or *Labrichthys* and accordingly erected the monotypic genus *Larabicus* for the species based on its unusual lip morphology. They overlooked Valenciennes' (1839) *Cossyphus quadrilineatus* in their synonymy, but since *Cossyphus* is preoccupied by a genus of tenebrionid beetle (Operation of the Principle of Homonymy, Article 52.2; ICZN, 1999), Randall & Springer's (1973) *Larabicus* remained valid as a new genus.

In their description of *Larabicus*, Randall & Springer (1973) reported that Rüppell's holotype of *Labrus quadrilineatus* at SMF had been lost; however, this is incorrect, as no holotype of *Labrus quadrilineatus* was ever fixed. They were likely referring to Rüppell's syntypic series, which is indeed probably lost and could not be located (S. Dorow, pers. comm.). According to Rüppell's handwritten notes at SMF, his syntypic series originally consisted of four specimens (S. Dorow, pers. comm.). Günther's (1862) catalogue of fishes at the British Museum included a specimen of *Larabicus quadrilineatus* (as *Labroides quadrilineatus*) "from Rüppell's collection". He provided meristic counts taken from this specimen (BMNH 1845.10.29.105), which differed from those reported in Rüppell's original description. Although the specimen is housed in the BMNH type collection (J. Maclaine, pers. comm., 2025), Günther made no mention of its type status, and Rüppell's notes at SMF made no mention to the existence of a fifth syntype (S. Dorow, pers. comm., 2025).

Randall & Springer (1973) overlooked Valenciennes' syntypes of *Cossyphus taeniatus*. However, they examined the type specimens of Roux-Estève's *Labrichthys cousteaui* and reported that the species was referrable to examples of *Labrus quadrilineatus* Rüppell (1835). We have examined photographs of Valenciennes' syntypes of *Cossyphus taeniatus* (Fig. 8B), as well as Roux-Estève's holotype and paratypes of *Labrichthys cousteaui* (Fig. 8C, D). We confirm that both these specimens are still in existence, in excellent condition, and are junior synonyms of Rüppell's *Labrus quadrilineatus*.

Notwithstanding Randall & Springer's (1973) efforts in reconciling the identity of Roux-Estève's *Labrichthys cousteaui* with Rüppell's *Labrus quadrilineatus*, Rüppell's *Labrus quadrilineatus* is still without a designated lectotype from his series of syntypes. However, since a lectotype can only be designated from among the original syntypes (Article 74.1; ICZN, 1999), and a specimen not part of the original series cannot serve as lectotype (Article 74.2; ICZN, 1999), no lectotype can presently be selected for *Labrus quadrilineatus*. The situation, however, meets the criteria for designation of a neotype. According to Article 75.2 (ICZN, 1999), a neotype should be designated only when the identity of a nominal taxon is in doubt and the absence of name-bearing types causes confusion. Given that *Labrus quadrilineatus* has been described on three separate occasions, two of which are junior synonyms themselves without lectotypes, and that the original syntypes of *Labrus quadrilineatus* have been missing since at least 1973, we herein designate a neotype, BMNH 1845.10.29.105 (Fig. 9), for Rüppell's *Labrus quadrilineatus*. The neotype, BMNH 1845.10.29.105, is designated in accordance with the qualifying conditions outlined in Article 75.3 (ICZN, 1999), as detailed herein, and on account of its topotypic affinity with Rüppell's original syntypes, and it being a purported specimen from Rüppell's collection. Specimen data for the neotype is provided in the species account immediately below.

With regards to nomenclature, the taxonomic status of *Labrus quadrilineatus* has changed several times, notably in the genus in which it has been combined. Recent phylogenetic studies have recovered *Larabicus quadrilineatus* as nested within *Labroides* (Brownstein et al., 2025; Near et al., 2025), a topology also recovered in this study. Near et al. (2025) synonymised *Larabicus quadrilineatus* within *Labroides*, as *Labroides quadrilineatus*. They were, however, incorrect in this being a new genus- and species-group combination, as it had already been long established by Günther in 1862, and adopted by Klunzinger (1871), Kossman & Räuber (1877), and Smith (1957).

***Labroides quadrilineatus* (Rüppell, 1835)**

Blue Four-line Wrasse
(Figs. 8–12; Table 1)

Labrus quadrilineatus Rüppell, 1835: 6, pl. 2, fig. 1 (original description; Massawa, Eritrea, Red Sea [syntypes possibly lost])
Cossyphus quadrilineatus Valenciennes in Cuvier & Valenciennes, 1839: 134 (generic reassignment *Cossyphus*)
Labroides quadrilineatus Günther, 1862: 120 (generic reassignment *Labroides*); Klunzinger, 1871: 1362 (fishes of the Red Sea); Kossman & Räuber, 1877: 26 (fishes of the Red Sea); Smith, 1957: 107 (checklist; western Indian Ocean); Near et al. 2025: 272 (nomenclatural change)

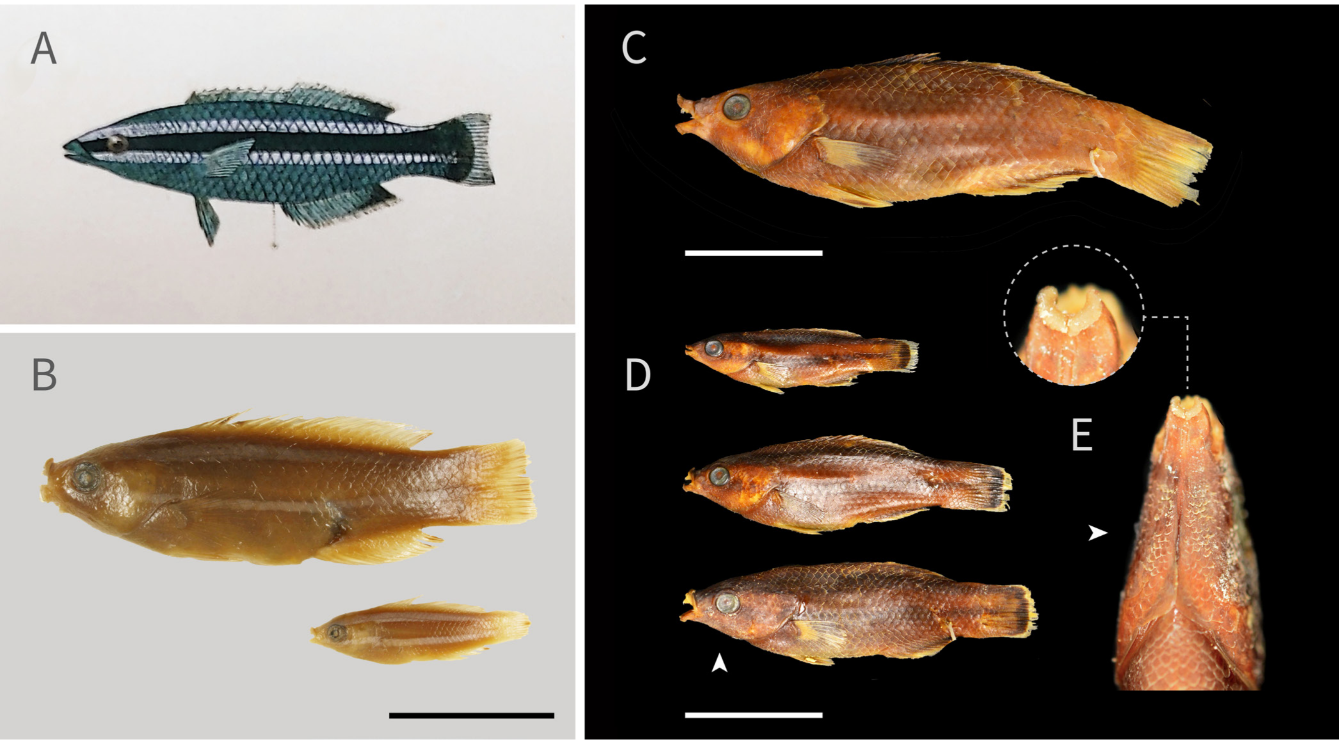

Fig. 8. A, Rüppell's (1835) illustration of *Labrus quadrilineatus*, likely based on one of the syntypes from Massawa, Eritrea, Red Sea; the specific specimen illustrated was not indicated. B, Syntypes of *Cossyphus taeniatus* Valenciennes, 1839 — ZMB 2471 (2), 22.5–51.5 mm SL, Massawa, Eritrea, Red Sea. C, Holotype of *Labrichthys cousteaui* Roux-Estève, 1955 — MNHN 1952-0254, 58.3 mm SL, Abu Latt Island, Saudi Arabia, Red Sea; D, Paratypes of *Labrichthys cousteaui* Roux-Estève, 1955 — MNHN 1986-0561 (3), 26.1–41.1 mm SL. E**,** Ventral view of 41.1 mm SL MNHN 1986-0561 paratype (white arrowheads) showing squamation of the lower head and fringed lower lip, not to scale. Scale bars represent 20 mm. Illustration reproduced from (A) Rüppell (1835). Photographs by (B) E. Aßel, **(**C, D) J. Pfliger, and (E) L. Hodgson.

Labrichthys cousteaui Roux-Estève in Roux-Estève & Fourmanoir 1955: 199 (original description; Abu Latt, Saudi Arabia, Red Sea); Clark et al., 1968 (Red Sea distribution)

Labrichthys cousteani Bauchot, 1963: 77 (type catalogue of the MNHN; misspelling of *L. cousteaui* Roux-Estève)

Larabicus quadrilineatus Randall & Springer, 1973: 291 (type species by monotypy); Parenti & Randall, 2000: 29 (checklist; Labridae); Debelius, 2007 (field guide; Red Sea); Kuiter & Debelius, 2006: 607 (underwater photographs from the Red Sea); Kuiter, 2010: 360 (colour photographs); Bogorodsky & Randall (2018): 254 (Red Sea and Gulf of Aden distribution); Golani & Fricke, 2018: 127 (checklist; Red Sea and Gulf of Aqaba); Heemstra et al., 2022: 223 (field guide; western Indian Ocean); 550 (colour photograph from the Red Sea)

Neotype. BMNH 1845.10.29.105, 44.3 mm SL, Red Sea, specimen from Rüppell's collection (Fig. 9).

Diagnosis. Dorsal-fin rays IX,11; anal-fin rays III,10; pectoral-fin rays 13; upper procurrent caudal-fin rays 6–7; lower procurrent caudal-fin rays 7–8; principal caudal-fin rays 8 + 7; circumpeduncular scales 22–24; body depth 3.4–3.8 in SL; head length 2.6–3.3 in SL; snout length 2.4–4.2 in HL; orbit diameter 2.5–5.5 in HL; orbit diameter 0.6–1.9 in snout length; caudal-peduncle length 1.6–5.1 in HL; pored lateral-line scales 27–28; scale rows above lateral line 4–5; scale rows below lateral line 10–12; total gill rakers 12–14; lower lip U-shaped, its anterior margin ventrally furled, occasionally split medially; inner surface of upper and lower lips plicate; juveniles and IP with two electric blue stripes, posterior dorsal and anal fins with a conspicuous black ocellus; TP males uniformly navy blue with pale blue boomerang shaped stripe on cheek.

Colouration of TP in life. Upper portion of head and nape dusky blue grey; lower half of head and body uniformly deep navy blue; cheek with a pale blue, boomerang shaped stripe, from corner of mouth, recurving at ventral most edge of orbit and extending towards corner of operculum; second, shorter stripe occasionally present parallel to first, at 4 o'clock position of orbit; iris pale blue; dorsal fin deep navy blue, pale translucent blue on distalmost edge of segmented portion; anteriormost spinous portion of dorsal fin sometimes with up to five golden-yellow roughly triangular spots, one in each interspinous membrane space; anal fin similar to dorsal fin but without golden-yellow markings; caudal fin deep navy blue with a translucent central margin between upper and lower lobes, resulting in an emarginate appearance; central rays of caudal fin pale blue; pectoral fins dusky blue-black; pelvic-fin spine pale blue, rest of fin deep navy blue (Fig. 10).

Colouration of IP in life. Head and body navy to cobalt blue; head and body with a pair of parallel electric blue stripes; zone between both stripes sometimes darker purplish blue; first stripe beginning from medial portion of upper lip, continuing horizontally across distalmost portion of orbit, through to distalmost edge of caudal fin and terminating at about vertical of hypural crease; second stripe beginning from

Table 1. Proportional measurements of selected specimens of *Labroides quadrilineatus* (Rüppell, 1835), expressed as a percentage of SL.

	BPBM 17886	**BPBM 13400**	**CAS 238128**	**CAS 2411988**		**CAS 241989**			**ZRC 66174**			
SL (mm)	59.1	84.4	51.6	35.5	50.3	10.7	15.1	22.0	26.5	35.5	39.7	43.4
Body depth	29.6	damaged	26.9	27.0	27.8	28.2	29.8	27.3	29.8	27.3	26.7	26.5
Body width	13.5	12.8	11.1	14.9	13.7	14.1	14.6	13.2	15.5	13.0	13.1	12.0
Head length	36.5	34.0	31.0	29.9	31.6	35.7	32.4	33.6	37.4	36.3	39.0	37.8
Snout length	13.7	11.6	12.8	9.9	11.5	8.5	8.6	8.6	10.2	10.1	11.3	10.8
Upper jaw length	5.4	4.7	6.6	4.2	5.0	3.8	4.0	5.0	6.0	5.1	5.3	6.0
Orbit diameter	7.4	6.2	7.6	8.7	7.4	14.1	11.9	10.5	10.6	9.3	8.6	9.4
Interorbital width	9.1	8.9	9.5	9.3	9.1	10.3	9.9	10.0	10.9	8.7	10.3	8.5
Caudal-peduncle depth	18.8	18.7	16.9	16.1	17.1	17.8	17.2	15.9	15.8	14.1	16.9	15.9
Caudal-peduncle length	9.5	9.4	9.9	8.7	9.5	6.6	8.6	8.6	8.3	9.6	11.8	10.4
Predorsal length	39.8	35.8	37.8	33.5	36.0	41.3	42.4	39.1	40.0	37.5	40.8	38.2
Preanal length	72.6	64.2	67.8	65.6	67.4	68.5	66.8	65.5	68.7	63.4	66.8	64.3
Prepelvic length	38.2	34.7	37.2	36.9	39.6	45.1	44.3	38.6	41.1	35.5	40.1	41.0
Dorsal-fin base	52.1	54.3	44.0	44.2	44.7	55.4	45.0	45.0	46.4	49.9	48.9	51.2
1st dorsal-fin spine	4.7	5.2	4.8	4.2	4.0	4.7	4.6	5.0	4.9	3.1	3.5	3.9
2nd dorsal-fin spine	6.6	7.9	8.7	5.6	6.2	damaged	6.6	5.9	6.8	5.4	5.5	6.2
Last dorsal-fin spine	9.0	11.0	8.9	9.3	8.9	damaged	11.9	15.0	10.6	9.6	9.6	9.9
Longest dorsal-fin ray	11.7	14.6	11.6	11.0	10.9	17.8	15.9	18.2	12.1	13.0	12.3	12.9
Anal-fin base	25.4	30.0	24.4	26.2	25.8	26.3	21.2	21.4	24.2	23.4	22.9	25.3
1st anal-fin spine	2.9	2.7	2.3	1.4	2.8	3.8	2.6	2.3	2.6	2.0	2.0	1.8
2nd anal-fin spine	6.8	6.5	6.4	5.9	7.0	7.5	6.0	6.8	5.7	6.5	6.8	6.7
3rd anal-fin spine	10.3	10.0	9.5	7.6	9.1	10.3	9.9	10.5	9.8	10.7	10.1	9.9
Longest anal-fin ray	12.9	13.6	11.0	9.9	10.7	15.0	13.9	12.7	11.3	13.5	14.4	15.9
Caudal-fin length	22.8	24.1	13.2	14.4	damaged	18.8	17.9	15.5	17.0	15.5	17.9	18.9
Pectoral-fin length	18.4	17.4	17.4	18.0	18.5	18.8	19.2	damaged	17.0	19.2	18.6	19.8
Pelvic-spine length	10.0	9.6	8.9	10.4	9.9	10.3	11.3	10.9	10.2	9.6	9.6	10.4
Pelvic-fin length	14.2	16.7	14.0	16.6	15.3	14.1	15.2	14.5	14.7	15.8	15.4	15.9

Fig. 9. Neotype of *Labrus quadrilineatus*, BMNH 1845.10.29.105, 44.3 mm SL, Red Sea, specimen from Rüppell's collection. Photograph by L. Goodayle, copyright 2025 The Trustees of the Natural History Museum, London (used with permission).

Fig. 10. *Labroides quadrilineatus*, underwater photograph of TP individual taken in the Red Sea, off Jeddah, Saudi Arabia. Photograph by R. Field.

corner of mouth, continuing horizontally across ventral most portion of orbit and continuing across body and terminating at caudal-fin base at level of hypural crease; both stripes sometimes joined by a vertical stripe of similar colour at caudal-fin base; remainder of caudal fin black with a narrow translucent margin; dorsal fin deep navy blue, becoming slightly translucent posteriorly; anteriormost spinous portion of dorsal fin sometimes with up to five golden-yellow roughly triangular spots, one in each interspinous membrane space; posteriormost segmented portion of dorsal fin with a conspicuous black ocellus; anal fin similar to dorsal fin but without golden-yellow markings; anal fin also with a conspicuous black ocellus on posteriormost segmented portion; pectoral and pelvic fins translucent blue-grey (Figs. 11,12).

Colouration in preservation. Freshly preserved specimens similar to colouration in life, except ground colour very dark blue, almost black; electric blue stripes in IP specimens bluish grey; black markings on dorsal, anal, and caudal fin persisting but difficult to discern against ground colouration of fins. Ground colouration eventually fading to dark tan over time; blue-grey stripes becoming dusky (Fig. 8B–E).

Remarks. *Labroides quadrilineatus* is endemic to the Red Sea basin, occurring throughout the Red Sea proper, including the Gulf of Aqaba, and extending southward to the Gulf of Aden (Bogorodsky & Randall, 2018), but not beyond into the wider Indian Ocean. It has also been photographed in the Gulf of Tadjoura off Djibouti.

Fig. 11. *Labroides quadrilineatus*, underwater photograph of IP individual with clients *Parupeneus macronemus*, Gulf of Aqaba, Red Sea, off Eilat, Israel. Photograph by R. Amar.

Fig. 12. A juvenile *Labroides quadrilineatus* with client *Pseudanthias squamipinnis*. Underwater photograph from Gulf of Aqaba, Red Sea, off Dahab, Egypt. Photograph by K. Steiel.

The species is unusual in possessing a combination of characters that depart from all other species of *Labroides*, some of which served as the basis for its previous placement in the genus *Larabicus* (Randall & Springer, 1973). The U-shaped lower lip of *Labroides quadrilineatus* is unusual in having its anterior margin ventrally furled, forming a fringe that is most conspicuous along the midline (Figs. 2D, 8E). Occasionally, the midline of the lower lip is split anteriorly. We consider the furling of the anterior lower lip margin to be an autapomorphy of *Labroides quadrilineatus*.

In addition to the unique lower lip morphology, *Labroides quadrilineatus* possesses several character conditions more typical of the labrichthyine wrasses but at the exclusion of other *Labroides*. These include extensive squamation on the lower head (Fig. 8E), plicate inner surface of the upper and lower lips, mouth tube-like when closed, and corallivory as a trophic resource in adults. *Labroides quadrilineatus* is typically encountered in close association with stony corals to depths of about 25 m. The species exhibits facultative cleaning in its juvenile and immature stages, but does not appear to establish well-defined cleaning stations (Figs. 11, 12).

Etymology. From the Latin 'quadri' meaning 'four', and 'linea' meaning 'line', possibly in reference to the four bright blue stripes (two on each side) in the juvenile and immature stages.

Material examined. BMNH 1845.10.29.105, 44.3 mm SL, neotype of *Labrus quadrilineatus*, Red Sea, specimen from Rüppell's collection; BPBM 13400, 84.4 mm SL, off Dahab, Egypt, Gulf of Aqaba; BPBM 17886, 59.1 mm SL, off Eilat, Israel, Gulf of Aqaba; CAS 238128, 51.6 mm SL, Al Lith, Saudi Arabia, Red Sea; CAS 241988 (2), 35.5–50.3 mm SL, Farasan Islands, Saudi Arabia, Red Sea; CAS 241989 (4), 10.7–26.5 mm SL, Farasan Islands, Saudi Arabia, Red Sea; MNHN 1952-0254, 58.3 mm SL, holotype of *Labrichthys cousteaui*, Abu Latt Island, Saudi Arabia, Red Sea (photographic examination only); MNHN 1986-0561 (3), 26.1–41.1 mm SL, paratypes of *Labrichthys cousteaui*, Abu Latt Island, Saudi Arabia, Red Sea (photographic examination only); ZMB 2471 (2), 22.5–51.5 mm SL, syntypes of *Cossyphus taeniatus*, Massawa, Eritrea, Red Sea; ZRC 66174 (3), 35.5–43.4 mm SL, aquarium specimens from the Red Sea.

Labroides phthirophagus Randall, 1958
Hawaiian Cleaner Wrasse
(Figs. 6, 13–15, 37A; Table 2)

Labroides dimidiatus (non Valenciennes, 1839): Günther, 1881: 243 (Hawaiian distribution record); Brock, 1954: 307 (Hawaiian distribution record)

Labroides phthirophagus Randall, 1958: 337; fig. 6; pl. 1A (holotype USNM 164466, Oahu, Hawaiian Islands); Parenti & Randall, 2000: 26 (checklist; Labridae); Kuiter & Debelius, 2006: 607 (underwater photograph from Hawaii); Randall, 2007: 339 (underwater photographs from Hawaii); Kuiter, 2010: 359 (underwater photograph from Hawaii)

Diagnosis. Dorsal-fin rays IX,11; anal-fin rays III,10; pectoral-fin rays 13–14; upper procurrent caudal-fin rays 6; lower procurrent caudal-fin rays 7; principal caudal-fin rays 8 + 7; circumpeduncular scales 18–20; body depth 3.3–4.5 in SL; head length 2.9–3.1 in SL; snout length 3.0–3.7 in HL; orbit diameter 3.9–5.1 in HL; orbit diameter 1.2–1.5 in snout length; caudal-peduncle length 2.4–3.9 in HL; pored lateral-line scales 25–29; scale rows above lateral line 3; scale rows below lateral line 9–10; total gill rakers 12–14; head and anterior body bright yellow; median lateral black stripe constricted to about origin of anal fin, expanding past this point toward outer edge of caudal fin; upper and lowermost edge of caudal fin magenta.

Colouration in life. Head and anterior half of body bright yellow; nape and predorsal region with a black stripe, from midline of upper lip to dorsal-fin origin; snout with narrow horizontal black stripe, from upper lip to anterior edge of orbit, its width about diameter of pupil; stripe continuing horizontally through orbit, expanding in width slightly to about diameter of iris and continuing to free upper edge of opercle, continuing as horizontal body stripe posteriorly, its width gradually expanding towards distalmost edge of caudal fin; upper and lower portion of iris above black stripe yellow to grey; pupil ringed in bright yellow; posterior portion of body above and below body stripe dusky indigo to black, sometimes indistinguishable from stripe; anterior spinous portion of dorsal fin dusky yellow; segmented portion of posterior dorsal fin indigo to violet on proximal third, translucent distally; middle portion of segmented dorsal fin with a nondescript dusky yellow stripe; anal fin similar to

Fig. 13. *Labroides phthirophagus* with client *Triaenodon obesus*. Underwater photograph from O'ahu, Hawaiian Islands. Photograph by O. Turner III.

Fig. 14. *Labroides phthirophagus*, freshly euthanised specimen, KPM-NI 22694 (=KPM-NR 59904), 53.4 mm SL, O'ahu, Hawaiian Islands. Photograph by H. Senou.

Fig. 15. *Labroides phthirophagus*, underwater photograph from Midway Atoll. Photograph by G.R. Allen.

Table 2. Proportional measurements of selected specimens of *Labroides phthirophagus*, expressed as a percentage of SL.

	BPBM 33961	**BPBM 7941**		**BPBM 29641**		**BPBM 34829**	
SL (mm)	55.4	63.9	55.7	41.5	38.2	40.3	31.2
Body depth	27.4	26.3	28.5	30.1	damaged	24.1	22.4
Body width	11.7	9.9	10.8	11.1	12.3	10.2	11.5
Head length	31.9	33.2	35.4	37.1	33.8	33.5	34.9
Snout length	10.1	10.2	10.4	10.1	10.2	11.2	10.3
Upper jaw length	4.9	3.6	5.6	4.8	5.0	3.7	3.5
Orbit diameter	7.0	6.9	7.0	8.4	8.1	8.7	8.3
Interorbital width	9.2	8.9	8.8	8.9	8.6	9.4	8.7
Caudal-peduncle depth	18.2	17.2	17.4	17.1	15.2	14.9	14.4
Caudal-peduncle length	9.6	13.8	10.1	9.9	8.6	9.7	9.6
Predorsal length	30.9	33.3	38.4	34.5	37.4	37.7	36.5
Preanal length	59.0	63.2	69.7	66.3	damaged	63.8	68.3
Prepelvic length	absent	36.3	40.4	35.2	39.5	36.5	37.8
Dorsal-fin base	51.6	53.5	48.3	51.8	47.9	51.4	49.7
1st dorsal-fin spine	2.2	3.0	2.5	2.9	3.1	3.2	2.9
2nd dorsal-fin spine	4.2	3.4	4.1	4.1	4.5	4.7	3.5
Last dorsal-fin spine	9.2	7.5	8.1	7.5	6.5	8.2	7.1
Longest dorsal-fin ray	11.7	13.6	12.0	8.9	damaged	13.9	12.2
Anal-fin base	31.0	26.9	29.8	28.4	21.5	31.8	24.4
1st anal-fin spine	2.3	2.0	1.6	1.9	2.6	2.7	1.9
2nd anal-fin spine	5.4	3.6	5.0	5.5	4.5	6.0	3.8
3rd anal-fin spine	9.2	8.1	8.8	9.6	7.6	8.2	8.3
Longest anal-fin ray	13.7	12.4	14.2	14.9	damaged	13.2	14.4
Caudal-fin length	19.5	19.2	22.6	22.9	26.2	28.8	24.7
Pectoral-fin length	19.0	19.7	20.3	19.5	18.8	21.6	18.9
Pelvic-spine length	absent	11.0	9.9	10.4	damaged	10.2	9.9
Pelvic-fin length	absent	14.6	14.4	15.2	damaged	17.6	15.1

dorsal fin; caudal fin black, except distal and ventral edge of caudal peduncle bright magenta, expanding in width along upper and lower caudal-fin lobes toward distalmost edge of caudal fin; pelvic fins translucent, slightly yellow at the bases; pectoral fins translucent (Figs. 6, 13–15, 37A).

Colouration in preservation. Similar to colouration in life except ground colouration uniformly pale tan; body stripe and predorsal region dark brown; magenta accents on upper and lower caudal fin now translucent tan.

Remarks. *Labroides phthirophagus* is the only representative of its genus occurring in the Hawaiian Islands, including the Northwestern Hawaiian Islands and Midway Atoll (Fig. 15) in the Papahānaumokuākea Marine National Monument. Previous reports of *Labroides dimidiatus* from the Hawaiian Islands likely refer to this species (Günther, 1881; Brock, 1954). It also occurs in Johnston Atoll (Randall, 1993; 2007; Chave & Mundy, 1994). Although species of *Labroides* are most frequently observed in shallow coral reefs, Chave & Mundy (1994) reported *Labroides phthirophagus* at depths of up to 122 m in Johnston Atoll and the Hawaiian Islands.

One examined specimen of *Labroides phthirophagus* (BPBM 33961; 55.4 mm SL) is unusual in lacking pelvic fins and all externally visible associated structures. An X-ray image taken of the same specimen however revealed the presence of a pelvic girdle. Except for species that naturally lack pelvic fins, these abnormalities have been occasionally reported in other labrid fishes (Tea et al., 2022).

Etymology. From the Greek 'phtheiros' meaning 'louse', and 'phagus' meaning 'to eat', in reference to its diet consisting of external parasites of fishes.

Material examined. BPBM 7941, (2), 55.7–63.9 mm SL, Kaneohe Bay, Oahu, Hawaiian Islands; BPBM 29614, (2), 38.2–41.5 mm SL, Johnston Atoll; BPBM 33961, 55.4 mm SL, Johnston Atoll; BPBM 34829, (2), 31.2–40.3 mm SL, Midway Atoll.

Labroides rubrolabiatus Randall, 1958

Red-lipped Cleaner Wrasse
(Figs. 16–19; 37B; Table 3)

Labroides rubrolabiatus Randall, 1958: 342; pl 1B (holotype USNM 164603, Moorea, Society Islands); Parenti & Randall, 2000: 26–27 (checklist; Labridae); Allen et al., 2003: 237 (underwater photograph); Lobel & Lobel, 2004: (checklist; Wake Atoll); Randall, 2005: 422 (underwater photographs from the Line Islands); Kuiter & Debelius, 2006: 606 (underwater photograph from Cook Islands); Kuiter, 2010: 359 (underwater photographs from Cook Islands and Tuvalu).

Diagnosis. Dorsal-fin rays IX,11; anal-fin rays III,10; pectoral-fin rays 13–14; upper procurrent caudal-fin rays 6–7; lower procurrent caudal-fin rays 7; principal caudal-fin rays 8 + 7; circumpeduncular scales 18–20; body depth 3.7–4.1 in SL; head length 2.9–3.4 in SL; snout length 2.8–3.7 in HL; orbit diameter 3.6–5.4 in HL; orbit diameter 1.3–1.9 in snout length; caudal-peduncle length 2.0–3.8 in HL; pored lateral-line scales 24–28; scale rows above lateral line 3; scale rows below lateral line 9–10; total gill rakers 12–13; head and anterior body pale chartreuse; lower head sometimes with narrow dusky streak from corner of mouth to lower edge of opercle, sometimes extending to pectoral-fin base; median lateral black stripe distinct only to about anterior half of body, attenuating and becoming increasingly indistinct or absent towards middle and posterior body; middle portion of body to caudal peduncle (where median lateral stripe has been attenuated) suffused with bright tangerine orange; caudal fin black; upper and lowermost edge of caudal fin pale blue to lilac.

Colouration of TP in life. Head and anterior half of body chartreuse; lower portion of head sometimes with narrow dusky streak, from corner of mouth to lower edge of opercle, rarely extending to pectoral-fin base as an ill-defined, clubbed-shaped blotch; nape and predorsal region with a reddish black stripe, from midline of upper lip to dorsal-fin origin; inner margin of lips red; snout with horizontal reddish brown to grey stripe, from upper lip to anterior edge of orbit, its width subequal or slightly narrower than that of orbit; stripe continuing horizontally through orbit, expanding in width slightly before abruptly attenuating or disappearing entirely at about midbody, approximately vertical of anal-fin origin; horizontal body stripe in some specimens weakly persisting, extending toward outer edge of caudal fin; upper and lower portion of iris above black stripe yellow to grey; pupil ringed in bright yellow; posterior body from approximately vertical of anal-fin origin to caudal peduncle bright tangerine orange, anterior and posterior margins of orange body section very suffused and indistinct; anterior spinous portion of dorsal fin tangerine orange, extending to posterior segmented portion of dorsal fin only on the proximal third; remaining distal portion of segmented dorsal fin translucent; anal fin similar to dorsal fin; caudal peduncle and caudal fin black, except distal and ventral edges pale blue to lilac; pelvic fins translucent yellow; pectoral fins translucent (Figs. 16–18; 37B).

Fig. 16. *Labroides rubrolabiatus*, freshly euthanised specimen, BPBM 42155, 55.6 mm SL, Fagatele Bay, Tutuila Island, American Samoa. Photograph by B.D. Greene.

Fig. 17. *Labroides rubrolabiatus* with client *Pycnochromis margaritifer*. Note the lower cheek stripe extending to the lower pectoral-fin base. Underwater photograph from Nukulaelae, Tuvalu. Photograph by T. Sinclair-Taylor.

Colouration of IP in life. Similar to TP except body stripe complete and orange colouration on posterior body reduced (Fig. 19).

Colouration in preservation. Head and anterior body greyish tan; stripe on head and anterior body greyish brown, attenuating at about vertical level of pectoral fin; middle to posterior body pale tan and unmarked; caudal peduncle and caudal fin dark brown; pale blue to lilac edges on upper and lower caudal fin translucent; all remaining fins translucent.

Remarks. *Labroides rubrolabiatus* has a disjunct distribution across the Pacific Ocean. The species is widespread in the central and southeastern Pacific Ocean, occurring in the Gilbert Islands, the Line Islands, Tuvalu, Wallis and Futuna, American Samoa, Samoa, Niue, the Cook Islands, and the islands of French Polynesia. The species is also reported from Wake Atoll (Fig. 19) and Marcus Island (BPBM 7129)

Table 3. Proportional measurements of selected specimens of *Labroides rubrolabiatus*, expressed as a percentage of SL.

	AMS I.18039-013	**AMS I.18051-053**	**AMS I. 32739-002**	**BPBM 7129**	**BPBM 13246**	**BPBM 13682**	**BPBM 16545**		**BPBM 17168**		**BPBM 42115**	**ZRC 66202**	**ZRC 65831**
SL (mm)	49.8	44.7	45.3	65.7	65.4	50.5	57.8	43.5	57.5	57.4	55.6	66.5	57.2
Body depth	24.3	26.2	24.5	26.8	24.3	24.6	26.1	25.1	24.9	26.1	24.3	26.9	26.0
Body width	13.9	13.2	10.2	12.0	10.1	12.7	11.2	11.7	11.1	9.6	14.2	14.3	12.8
Head length	34.1	34.5	29.4	33.9	33.5	34.5	33.9	34.0	33.7	32.6	35.1	35.8	35.0
Snout length	11.4	10.5	10.6	10.8	9.2	10.3	11.1	12.0	11.5	9.8	11.0	11.4	11.2
Upper jaw length	3.8	3.4	3.1	5.2	4.6	4.2	5.2	4.6	4.9	4.5	4.1	3.6	4.0
Orbit diameter	7.8	7.8	8.2	6.2	7.2	7.3	7.1	6.4	7.0	7.1	6.5	6.2	7.2
Interorbital width	8.6	8.7	8.8	8.7	8.4	8.3	8.3	8.5	8.5	8.5	9.2	9.8	9.4
Caudal-peduncle depth	16.1	15.0	15.5	17.2	15.3	16.2	17.0	15.9	15.8	15.9	15.6	17.9	16.6
Caudal-peduncle length	16.3	14.3	14.8	10.5	9.3	11.9	9.0	9.7	9.9	9.2	11.0	6.5	6.6
Predorsal length	32.1	37.6	32.0	33.5	29.1	34.5	31.5	35.4	33.6	34.3	33.8	34.6	35.0
Preanal length	60.8	57.9	60.9	61.6	62.7	63.2	61.8	61.8	64.0	61.0	61.0	62.7	58.6
Prepelvic length	34.1	35.3	34.0	34.9	35.2	34.9	37.0	36.8	34.8	38.7	34.5	34.9	33.7
Dorsal-fin base	46.4	48.3	48.6	53.4	54.7	52.5	50.7	47.1	51.8	49.8	52.7	54.6	54.0
1st dorsal-fin spine	2.8	2.2	3.3	2.6	2.8	3.2	2.8	2.8	3.0	3.5	3.6	3.3	3.1
2nd dorsal-fin spine	3.8	3.6	4.2	3.7	3.5	4.0	4.2	3.4	4.3	4.7	4.7	4.7	3.7
Last dorsal-fin spine	10.4	10.3	damaged	7.8	7.0	7.9	8.8	6.9	7.5	8.5	10.8	9.6	10.3
Longest dorsal-fin ray	13.1	14.3	15.7	damaged	12.2	10.3	12.3	11.5	13.4	11.7	13.8	15.5	15.0
Anal-fin base	30.1	26.2	24.1	27.9	30.7	29.3	27.0	30.1	26.3	27.0	29.9	28.6	33.2
1st anal-fin spine	2.4	3.1	2.9	2.0	1.2	2.4	2.1	1.4	damaged	3.1	2.0	2.1	3.1
2nd anal-fin spine	6.2	6.3	4.6	6.4	4.4	5.1	5.9	3.9	damaged	7.7	7.0	5.1	7.3
3rd anal-fin spine	10.2	9.6	9.1	10.0	7.6	9.3	8.8	7.8	9.2	9.4	11.2	7.7	10.7
Longest anal-fin ray	15.9	14.8	13.9	damaged	13.1	15.4	13.1	14.0	15.5	12.7	15.3	13.4	15.6
Caudal-fin length	19.9	20.4	17.9	damaged	22.0	24.2	20.8	23.4	24.9	22.6	23.4	21.8	26.0
Pectoral-fin length	21.3	18.8	19.9	20.2	20.8	21.6	19.9	20.2	21.2	20.0	20.5	19.4	22.4
Pelvic-spine length	10.6	10.3	9.9	10.4	10.6	8.5	10.6	9.2	10.1	11.3	9.2	8.9	11.4
Pelvic-fin length	16.3	15.9	15.0	15.2	13.9	15.2	14.7	17.7	15.5	15.7	14.4	15.0	16.6


Fig. 18. *Labroides rubrolabiatus*, underwater photograph from Moorea, French Polynesia. Photograph by K. Stender.


Fig. 19. *Labroides rubrolabiatus* with client *Coris aygula*. Note IP specimen (left) with complete body stripe. Underwater photograph from Wake Atoll. Photograph by K. Lino, NOAA Fisheries: Pacific Islands Fisheries Science Centre.

in the northwestern Pacific (Randall & Springer, 1975). The species is replaced by *Labroides pectoralis* in the disjunct portion of its range, and in the remainder of the western Pacific Ocean.

Etymology. From the Latin 'rubro' meaning 'red', and 'labrum' meaning 'lip', in reference to the colour of the lips in life. The description of *Labroides rubrolabiatus* predates those of *Labroides pectoralis* and *Labroides flammulatus*, new species, described herein (see below), both of which also possess red lips.

Material examined. AMS I.18039-013, 49.8 mm SL, Abaiang Atoll, Gilbert Islands; AMS I.18051-053, 44.7 mm SL, Abaiang Atoll, Gilbert Islands; AMS I.32739-002, 45.3 mm SL, Parema Bank, Pago Pago, American Samoa; BPBM 7129, (2), 29.8–66.1 mm SL, Marcus Island; BPBM 13246, 65.4 mm SL, Bounty Bay, Pitcairn Islands; BPBM 13682, 50.5 mm SL, Tubuai Island, Austral Islands; BPBM 16545, (2), 43.3–57.4 mm SL, Oeno Island, Pitcairn Islands; BPBM 17168, (2), 55.5–56.8 mm SL, Ducie Atoll, Pitcairn Islands; BPBM 42155, 55.6 mm SL, Fagatele Bay, Tutuila Island, American Samoa; USNM 423439, 65.1 mm SL, Raivavae, Austral Islands, French Polynesia; ZRC 65831, 57.2 mm SL, Tahiti, Society Islands; ZRC 66202, 66.5 mm SL, Tahiti, Society Islands.

Labroides pectoralis Randall & Springer, 1975
Breastspot Cleaner Wrasse
(Figs. 20–23; 36C; Table 4)

Labroides sp. cf. *phthirophagus* – Burgess & Axelrod, 1973: 453, fig. 335 (Randall's holotype image of *Labroides pectoralis* questionably identified as *Labroides phthirophagus*)

Labroides dimidiatus (non Valenciennes, 1839): Burgess & Axelrod, 1975: 1586, fig. 368 (underwater photograph of *Labroides pectoralis* misidentified as *Labroides dimidiatus*)

Labroides pectoralis Randall & Springer, 1975: 6, pl 1 (holotype BPBM 7245, Auluptagel Island, Palau); Myers, 1989: 191; Pl 104C (checklist; Micronesia); Randall et al., 1996: 326 (underwater photograph); Myers, 1999: 204; pl 131K (checklist; Micronesia); Parenti & Randall, 2000: 26 (checklist, in part, non-Christmas Island distribution; Labridae); Allen et al., 2003: 237 (underwater photograph); Kuiter & Tonozuka (2004): 465 (underwater photographs from Flores); Randall, 2005: 421 (underwater photograph from Rowley Shoals and Papua New Guinea); Kuiter & Debelius, 2006: 607 (underwater photographs from Western Australia and Indonesia); Kuiter, 2010: 359 (underwater photographs from Western Australia and Flores, Indonesia); Allen & Erdmann, 2012: 695 (in part, underwater photograph from Halmahera); Allen et al., 2015: 239 (underwater photograph); Allen & Erdmann, 2024: 760 (in part, underwater photograph from Papua New Guinea)

Diagnosis. Dorsal-fin rays IX,11; anal-fin rays III,10; pectoral-fin rays 13; upper procurrent caudal-fin rays 6–7; lower procurrent caudal-fin rays 7–8; principal caudal-fin rays 8 + 7 (BPBM 15838 with 8 + 8); circumpeduncular scales 18–20; body depth 3.6–4.2 in SL; head length 2.5–3.1 in SL; snout length 2.9–4.0 in HL; orbit diameter 3.9–5.3 in HL; orbit diameter 1.0–1.7 in snout length; caudal-peduncle length 2.4–4.0 in HL; pored lateral-line scales 26–28; scale rows above lateral line 3; scale rows below lateral line 9–10; total gill rakers 13–14; head and anterior body bright yellow, darkening to orange posteriorly above median lateral black stripe; median lateral black stripe constricted or attenuated to about origin of anal fin, expanding past this point toward edge of caudal fin; upper and lowermost edge of caudal fin light blue to lilac; pelvic fins translucent yellow; pectoral fins translucent; lower base of pectoral fin with large elliptical spot.

Colouration of TP in life. Head and anterior half of body bright yellow; nape and predorsal region with a reddish brown stripe, from midline of upper lip to dorsal-fin origin; inner margin of lips red; snout with narrow horizontal grey to black stripe, from corner of mouth to anterior edge of orbit, its width subequal to or narrower than that of pupil; stripe continuing horizontally through orbit, expanding slightly in width slightly to about diameter of pupil and extending to free upper edge of opercle, continuing as horizontal stripe posteriorly; width of anterior portion of body stripe somewhat subequal from posterior orbit to about midbody, widening posteriorly to distalmost edge of caudal fin; anterior portion of stripe narrowed or occasionally attenuated in matured individuals; thickest posterior portion of stripe dusky brown to black, its width approximately equal to caudal-peduncle depth; upper body yellow, becoming increasingly orange

Table 4. Proportional measurements of selected specimens of *Labroides pectorali*s, expressed as a percentage of SL.

	Paratypes				**Non-types**								
	AMS I.18466-001	**BPBM 9370**	**BPBM 15838**	**BPBM 18851**	**AMS I.17496-014**	**AMS I.19171-001**	**AMS I.19472-069**		**AMS I. 51800-007**	**ANSP 137343**	**BPBM 35138**	**WAM P.27659.026**	**ZRC 62814**
SL (mm)	48.1	53.3	51.8	55.6	49.9	37.2	49.6	60.5	53.4	53.4	49.3	47.9	58.2
Body depth	26.4	23.6	27.0	24.5	26.7	26.9	27.4	26.6	24.3	27.9	25.8	24.2	24.2
Body width	13.7	13.3	14.3	11.3	15.0	10.8	13.3	12.7	13.3	10.9	13.4	11.5	14.3
Head length	32.4	34.1	33.2	35.4	35.1	39.2	35.5	35.0	35.8	31.8	36.9	31.9	27.7
Snout length	10.8	8.8	8.3	10.8	10.2	11.3	11.5	11.1	12.2	10.5	10.3	9.8	9.6
Upper jaw length	4.6	4.5	4.1	4.7	3.6	4.3	4.0	4.3	5.1	3.9	4.9	4.2	4.3
Orbit diameter	8.1	7.9	7.9	7.0	7.8	8.6	7.9	6.6	6.7	7.1	8.7	6.5	7.0
Interorbital width	8.9	8.6	9.1	9.4	8.8	9.4	9.1	8.9	9.2	9.2	9.3	7.9	8.9
Caudal-peduncle depth	14.6	16.3	17.6	15.5	15.2	17.2	16.5	17.0	16.7	15.9	15.4	17.1	15.3
Caudal-peduncle length	9.4	8.6	8.7	10.1	13.8	11.6	9.5	11.9	8.1	13.1	9.5	11.3	10.7
Predorsal length	32.2	34.1	33.8	37.6	35.1	35.5	34.3	32.6	36.9	33.0	33.3	36.5	33.2
Preanal length	63.6	60.0	63.3	55.8	59.5	57.5	59.7	62.0	64.2	59.2	62.5	62.0	59.5
Prepelvic length	41.6	34.5	36.1	33.6	34.1	38.7	34.4	32.9	36.3	32.6	34.1	37.4	35.9
Dorsal-fin base	49.5	52.7	48.5	damaged	46.3	51.1	51.4	52.7	49.1	47.9	54.4	50.5	52.2
1st dorsal-fin spine	3.1	2.8	2.3	2.7	2.4	3.2	3.2	3.0	3.6	3.6	3.0	3.5	3.1
2nd dorsal-fin spine	3.7	3.4	4.1	damaged	4.0	damaged	4.2	4.0	3.7	5.2	4.1	4.2	4.1
Last dorsal-fin spine	9.4	7.3	6.8	damaged	9.0	8.6	9.9	9.8	7.7	7.5	8.7	7.9	8.9
Longest dorsal-fin ray	15.6	11.6	12.2	damaged	13.0	14.8	13.3	14.7	13.9	11.6	13.8	12.1	15.3
Anal-fin base	29.7	29.3	30.1	25.5	30.1	33.6	30.2	27.4	29.0	26.2	28.0	29.9	27.1
1st anal-fin spine	2.3	2.1	1.9	1.4	2.0	2.4	2.2	2.1	1.7	1.5	2.0	1.5	1.7
2nd anal-fin spine	6.4	5.1	5.6	4.3	5.4	6.5	6.7	6.0	6.0	5.6	5.1	4.6	5.7
3rd anal-fin spine	10.2	7.7	8.7	7.7	8.6	10.5	9.7	9.8	10.5	9.2	9.1	7.9	9.6
Longest anal-fin ray	16.4	12.2	13.1	11.9	12.8	damaged	13.9	14.0	15.5	14.8	15.0	14.2	15.1
Caudal-fin length	25.2	22.5	20.8	22.1	18.2	25.0	25.6	24.3	21.2	20.6	25.4	25.5	21.1
Pectoral-fin length	22.2	21.6	21.2	21.6	18.2	21.2	19.8	20.5	21.0	20.2	22.1	19.2	18.9
Pelvic-spine length	13.7	10.5	10.0	9.2	10.2	11.0	11.1	11.2	12.5	7.9	12.2	8.6	6.4
Pelvic-fin length	16.8	17.3	14.8	14.0	15.6	17.7	16.5	16.2	18.2	16.1	15.8	15.2	15.1

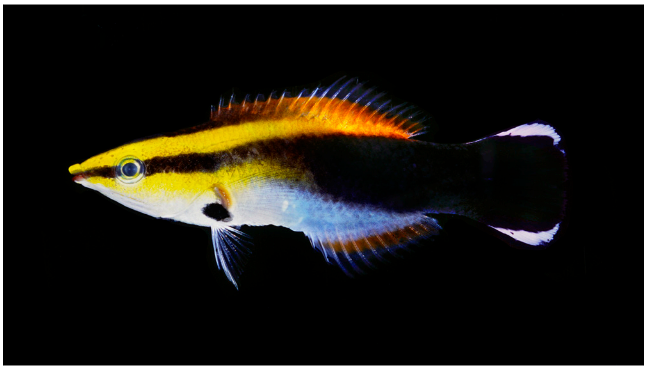

Fig. 20. *Labroides pectoralis*, freshly euthanised specimen, KPM-NI 16393 (=KPM-NR 57222), 35.4 mm SL, Bali, Indonesia. Photograph by H. Senou.

Fig. 21. *Labroides pectoralis*, underwater photograph from Flores, Indonesia. Note the red, bi-lobed lower lip visible in this photograph. Photograph by R. Stuart-Smith.

posteriorly just above body stripe; lower body silvery-grey to pale blue anteriorly, becoming azure or sky blue posteriorly just below body stripe, above anal fin; lower base of pectoral fin with a black elliptical spot; anterior spinous portion of dorsal fin dusky orange, extending posteriorly to proximal portion of segmented dorsal fin; distal portion of segmented dorsal fin translucent; anal fin similar to dorsal fin; caudal peduncle and caudal fin black, except distal and ventral edges pale blue to lilac; pelvic fins hyaline; pectoral fins translucent (Figs. 20–23; 37C).

Colouration of IP in life. Similar to TP except width of anterior body stripe wider and not attenuated.

Colouration in preservation. Similar to colouration in life except ground colouration pale tan; nape and predorsal region dusky brown; all black markings persisting in preservation, dark brown to greyish brown; pale blue to lilac edges on upper and lower caudal fin translucent; anterior portion of dorsal fin dusky brown; all remaining fins translucent.

Remarks. *Labroides pectoralis* is widely distributed across the western Pacific. In eastern Indonesia, it occurs throughout the Lesser Sunda Islands, the Banda Archipelago, the Moluccan Archipelago, Sulawesi, and west Papua. It also occurs in the Philippines, Palau, and north to the Okinawa Islands. In the western and southwestern Pacific Ocean, it occurs in the Bismarck Archipelago, the Solomon Islands, the Caroline Islands, the Marshall Islands, the Northern Mariana Islands, Ogasawara, the Great Barrier Reef in northeastern Australia, the Coral Sea, New Caledonia, and Vanuatu. Elsewhere in Oceania it is replaced by *Labroides rubrolabiatus* (see above). In the eastern Indian Ocean region, *Labroides pectoralis* is reported from Ashmore Reef and the Cartier Islands in the Timor Sea, and from Rowley Shoals, Scott Reef, and Seringapatam Reefs off Western Australia. Reports of *Labroides pectoralis* from the Christmas and Cocos (Keeling) Islands are referrable to another species (see below). *Labroides pectoralis* and *Labroides rubrolabiatus* are narrowly parapatric in the northern tip of the Gilbert Islands, around Butatitari and Makin Atolls.

Fig. 22. *Labroides pectoralis* with client *Myripristis violacea*. Underwater photograph from Wakatobi, Sulawesi, Indonesia. Photograph by W. Osborn.

Labroides pectoralis attains its northernmost distribution in the Ryukyu Archipelago, with a few photographic records taken from the Amami and Okinawa Islands (Fig. 23). Individuals from the Amami and Okinawa Islands are known to occasionally exhibit colour variation in the anterior portion of the body stripe, ranging from pale grey (Fig. 23A) to reddish-brown (Fig. 23B–D), though typically coloured examples are also known from the area (Fig. 23E, F). In the Okinawa Islands, the species has been documented engaging in what appears to be courtship behaviour with *Labroides dimidiatus* sensu lato (Fig. 23F), though hybridisation has not been reliably documented within this genus. Owing to the paucity of preserved material of *Labroides pectoralis* from these regions, it remains unclear whether these differences represent anything more than variation in colouration.

Material examined. AMS I.17496-014, 49.9 mm SL, Alite Reef, Malaita, Solomon Islands**;** AMS I.19171-001, 37.2 mm SL, aquarium specimen from Queensland; AMS I.18466-001, paratype, 48.1 mm SL, Laura Island, Majuro, Marshall Islands; AMS I.19472-069, (2), 49.6–60.5 mm SL, Lizard Island, Great Barrier Reef, Queensland, Australia; AMS I.51800-007, 53.4 mm SL, Tydeman Reef, Great Barrier Reef, Queensland, Australia; ANSP 137343, 53.4 mm SL, Bougainville, Tautsina Island, Solomon Islands; BPBM 9370, (2), paratypes, 49.36–53.3

Fig. 23. Underwater photographs showing colour variation in *Labroides pectoralis* from A, B, Yoron Island, Amami Islands, Ryukyu Archipelago; C–F, Okinawa Island, Ryukyu Archipelago. Photographs by (A) K. Muramoto; (B) T. Nanako; and (C–F) K. and S. Imagawa (Ocean Blue Dive Shop).

mm SL, Augulupelu Reef, Palau; BPBM 15838, paratype, 51.8 mm SL, Madang, Papua New Guinea; BPBM 18851, paratype, 55.6 mm SL, Kwajalein Atoll, Marshall Islands; BPBM 35138, 47.9 mm SL, Kobusha Point, Anijima Island, Ogasawara Archipelago; KPM-NI 16394, 33.2 mm SL, Bali, Indonesia; KPM-NI 16396, 35.4 mm SL, Bali, Indonesia; WAM P.27659.026, 58.2 mm SL, Clerke Reef, Rowley Shoals, Western Australia; ZRC 62814, 58.2 mm SL, aquarium specmiens from the Philippines. ZRC 64316, (4), 39.4–45.8 mm SL, aquarium specimens from Indonesia.

***Labroides flammulatus*, new species**

Cinnabar Cleaner Wrasse
(Figs. 24–28; 37D; Table 5)

Labroides pectoralis (non Randall & Springer, 1975): Parenti & Randall, 2000: 26 (checklist, in part, Christmas Island distribution; Labridae); Allen et al., 2007: 180 (underwater photograph from Christmas Island); Allen & Erdmann, 2012: 695 (in part, underwater photograph from Christmas Island); Allen & Erdman, 2024: 760 (in part, underwater photograph from Christmas Island): Hobbs et al., 2014a (checklist; Christmas Island); Hobbs et al., 2014b (checklist; Cocos [Keeling] Islands).

Table 5. Proportional measurements of type specimens of *Labroides flammulatus*, new species, expressed as a percentage of SL.

	Holotype	**Paratypes**						
	WAM P.26083-045	**WAM P.26083.029**	**WAM P.26093.009**	**AMS I.51331-001**	**AMS I.51331-002**	**ANSP 133367**	**ANSP 133368**	
SL (mm)	55.8	21.2	29.6	63.7	53.5	68.3	51.3	53.2
Body depth	25.8	25.9	24.7	25.3	25.2	26.9	24.0	25.4
Body width	14.7	13.2	12.8	14.3	14.4	12.9	11.7	12.2
Head length	33.0	40.1	32.8	37.5	35.0	32.4	31.6	34.4
Snout length	10.8	13.2	10.5	12.4	11.0	9.8	9.6	10.7
Upper jaw length	5.0	6.6	5.1	4.9	5.0	5.3	4.1	5.1
Orbit diameter	6.8	11.8	8.4	6.4	6.2	5.9	6.4	7.0
Interorbital width	8.8	10.4	8.8	9.9	9.7	8.6	9.0	9.6
Caudal-peduncle depth	16.1	16.5	15.9	14.4	16.3	14.3	14.8	16.7
Caudal-peduncle length	12.5	14.6	16.9	11.5	13.3	14.1	10.5	14.3
Predorsal length	31.7	41.5	37.8	31.2	35.5	32.1	30.8	29.5
Preanal length	59.0	71.7	63.5	60.8	53.6	58.3	53.6	51.7
Prepelvic length	36.9	43.4	37.5	38.0	32.5	32.4	28.5	30.5
Dorsal-fin base	54.1	49.5	46.3	52.3	52.7	46.9	47.8	52.6
1st dorsal-fin spine	3.8	4.2	4.1	3.9	3.0	3.1	3.1	3.4
2nd dorsal-fin spine	4.7	6.1	5.4	4.2	3.9	4.0	4.1	3.9
Last dorsal-fin spine	7.2	9.0	8.1	6.6	7.1	8.8	8.0	7.7
Longest dorsal-fin ray	12.0	12.7	11.8	12.4	12.9	13.0	12.7	13.3
Anal-fin base	26.5	24.5	30.7	damaged	28.2	26.2	29.0	27.4
1st anal-fin spine	2.2	2.4	1.7	1.9	1.7	2.6	2.1	1.9
2nd anal-fin spine	4.1	5.7	5.4	4.6	4.5	5.6	5.8	4.7
3rd anal-fin spine	7.9	11.3	10.5	9.1	8.6	9.1	9.2	9.6
Longest anal-fin ray	13.4	14.2	15.5	12.4	13.3	14.5	12.9	13.7
Caudal-fin length	22.8	28.8	25.3	18.4	18.9	17.7	16.0	18.4
Pectoral-fin length	21.0	22.2	20.6	21.2	20.0	19.2	18.7	18.0
Pelvic-spine length	9.5	11.8	10.5	9.7	damaged	10.1	9.6	11.3
Pelvic-fin length	17.0	16.5	18.2	16.9	17.4	16.3	17.2	15.6

Fig. 24. *Labroides flammulatus*, new species, with client *Gymnothorax breedeni*. Underwater photograph from Flying Fish Cove, Christmas Island. Photograph by B. Mayes.

Fig. 25. *Labroides flammulatus*, new species. Underwater photograph from Christmas Island. Photograph by T. Sinclair-Taylor.

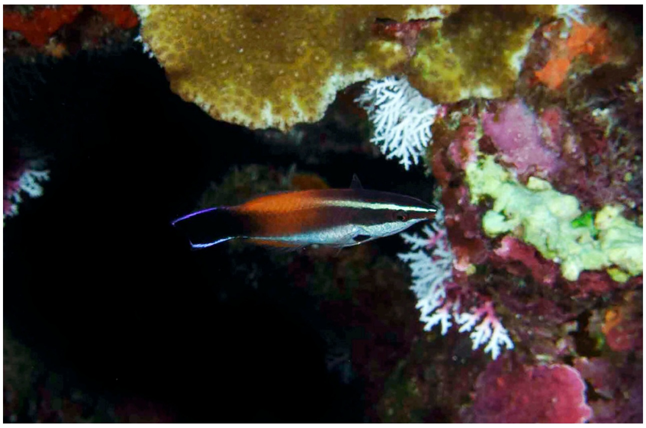

Fig. 26. *Labroides flammulatus*, new species, underwater photograph from Flying Fish Cove, Christmas Island. Photograph by P. McGee.

Labroides rubrolabiatus (non Randall, 1958): Côté & Mills, 2020: Table 1 (underwater photograph of *Labroides flammulatus*, new species, misidentified as *Labroides rubrolabiatus*).

Labroides cf. *pectoralis* – Kuiter & Debelius, 2006: 606 (underwater photograph from Christmas Island).

Labroides sp. – Kuiter, 2010: 359 (underwater photograph from Christmas Island).

Holotype. WAM P.26083-045, 55.8 mm SL, Ethel Beach, Christmas Island (10°29′S, 105°40′E), 3–6 m, G.R. Allen, 19 May 1978.

Paratypes. AMS I.51331-001, 63.7 mm SL, Ethel Beach, Christmas Island (10°27′S45.8″S, 105°42′30.8″E), 2 m, hand spear, JP Hobbs, 19 June 2023 (GenBank PZ168610); AMS I.51331-002, 53.5 mm SL, same data as AMS I. 51331-001(GenBank PZ168611); ANSP 133367, 68.3 mm SL, West Island, Cocos (Keeling) Islands (12°8′15″S, 96°48′50″E), 12 m, W.F. Smith-Vaniz et al., 26 February 1974; ANSP 133368, (2), 51.3–53.2 mm SL, between Horsburgh and Direction Islands, Cocos (Keeling) Islands (12°5′15″S, 96°51′35″E), 12–15m, W.F. Smith-Vaniz et al., 19 March 1974; WAM P.26083.029, 21.2 mm SL, same data as holotype; WAM P.26093.009, 29.6 mm SL, Margaret Beach, Christmas Island (12°29′S, 105°40′E), 10 m, G.R. Allen, 25 May 1978.

Diagnosis. Dorsal-fin rays IX,11; anal-fin rays III,10; pectoral-fin rays 13; upper procurrent caudal-fin rays 6; lower procurrent caudal-fin rays 7–8; principal caudal-fin rays 8 + 7; circumpeduncular scales 18–20; body depth 3.7–4.2 in SL; head length 2.5–3.2 in SL; snout length 3.0–3.3 in HL; orbit diameter 3.4–5.8 in HL; orbit diameter 1.1–1.9 in snout length; caudal-peduncle length 1.9–3.3 in HL; pored lateral-line scales 25–28; scale rows above lateral line 3; scale rows below lateral line 9–10; total gill rakers 12–13; head and anterior body grey to steely blue; head with narrow dusky streak on cheek below eye running from corner of mouth to edge of opercle; body with median lateral black stripe from snout, passing through orbit to end of caudal fin (this stripe broadening towards posterior); posterior two thirds of body suffused with orange brown (including the median lateral black stripe); upper and lowermost edge of caudal fin light blue to lilac; lower base of pectoral fin with black elliptical spot

Description. Dorsal-fin rays IX,11, first ray unbranched, last branched to base; dorsal fin with a membranous cirrus posterior to tip of each spine; anal-fin rays III,10, last ray branched to base; pectoral-fin rays 13; uppermost rudimentary, uppermost two unbranched; pelvic-fin rays I,5; principal caudal-fin rays 8 + 7, upper and lowermost unbranched; upper procurrent caudal-fin rays 6; lower procurrent caudal-fin rays 7 (7–8); lateral line continuous with 28/27 (25–28) pored scales, posteriormost two slightly enlarged and beyond hypural; 3 scale rows between lateral line and segmented portion of dorsal fin, third row extending onto fin base; a row of vertically elongate, leaf-shaped scales on base of dorsal fin, one to two per radial element; scale rows above lateral line to origin of dorsal fin 4 (4–5); 9 (9–10) scale rows below lateral line to segmented portion of anal fin; diagonal scale rows on cheek from eye to upper corner of preopercle 5; circumpeduncular scales 20 (18–20); gill rakers 13 (12–13); branchioistegal rays 5; vertebrae 10 + 15 = 25.

Fig. 27. *Labroides flammulatus*, new species, underwater photograph taken off Drumsite, Christmas Island. Photograph by B. Mayes.

Fig. 28. *Labroides flammulatus*, new species, underwater photograph from Bantam, Cocos (Keeling) Islands. Photograph by K. Willshaw.

Body depth 3.9 (3.7–4.2) in SL; body width 1.8 (1.8–2.1) in depth; head 3.0 (2.5–3.2) in SL; snout moderately pointed, 3.1 (3.0–3.7) in HL; orbit 1.7 (1.1–1.9) in snout length; orbit 4.8 (3.4–5.8) in HL; interorbital space convex, bony width 3.8 (3.5–3.9) in HL; caudal-peduncle depth 2.0 (2.0–2.6) in HL; caudal-peduncle length 2.6 (1.9–3.3) in HL.

Caudal fin moderately rounded, 1.4 (1.3–2.0) in HL; dorsal-fin origin above second lateral-line scale and upper pectoral-fin base; dorsal-fin spines progressively longer, first about 0.8 (0.7–0.9) length of second, ninth about 1.9 (1.7–2.9) times longer than first; first or second segmented dorsal-fin ray longest, 2.7 (2.5–3.1) in HL; anal-fin origin below base of second segmented dorsal-fin ray; first anal-fin spine very short, 15.3 (12.3–20.7) in HL, second anal-fin spine 8.0 (5.4–8.2) HL; third longest, 4.2 (3.1–4.2) in HL; fist segmented anal-fin ray longest, 2.5 (2.1–3.0) in HL; pectoral fin reaching a vertical at base of eight dorsal-fin spine, 1.6 (1.6–1.9) in HL; origin of pelvic fin slightly anterior to origin of pectoral fin; pelvic fins reaching a vertical at base of seventh or eighth dorsal-fin spine, longest ray 1.9 (1.8–2.4) in HL; pelvic-fin spine about three-fourths length of longest pelvic-fin ray, 3.5 (3.1–3.9) in HL.

Posterior edge of maxillary difficult to detect, but reaching about to a vertical at anterior nostril; mouth width about three-fourths orbit diameter; lower lip distinctly bilobed, gap between the lobes one-fourth orbit diameter; dentition typical of genus with a single pair of strongly recurved upper canines fitting inside lower pair when mouth is closed; length of upper canines about one-fourth orbit diameter; lower canines nearly straight, angling slightly outward; a large forward-directed canine posteriorly on upper jaw at corner of mouth; remaining teeth small, those at symphysis of upper jaw in numerous close-set rows, forming a semicircular mass between canines.

Gill membranes attached to isthmus slightly posterior to a vertical at posterior edge of orbit. Snout, ventral part of head, interorbital space and proximal region of nape scaleless; a narrow, horizontal band of scales running below eye just beneath suborbital pores, consisting mainly of a single scale row, which ends slightly anterior to a vertical at front of eye. Basal half of caudal fin scaled; dorsal and anal fin with a row of vertically elongate, leaf-shaped scales, one to two per radial element; paired fins scaled only basally; pelvic fins with a series of three enlarged scales in a median row posterior to origin.

Colouration TP in life. Head and anterior half body grey to steely blue; lower portion of head sometimes with narrow dusky streak, from corner of mouth to lower edge of opercle; nape and predorsal region with a brown stripe, from midline of upper lip to anterior third or half of dorsal-fin base; inner margin of lips red; snout with horizontal brown to black stripe, from upper lip to anterior edge of orbit, its width subequal or slightly narrower than that of orbit; stripe continuing horizontally through orbit, expanding in width and extending along body toward outer edge of caudal fin; orbit contained entirely within stripe; pupil ringed in bright yellow; middle to posterior portion of upper body above stripe orange-brown, sometimes encroaching ventrally and suffused with body stripe; extent of orange-brown suffusion within the body stripe generally weak, though in mature individuals it may broaden to soften or attenuate the dorsal margin of the stripe; lower body silvery grey; lower base of pectoral fin with a black elliptical spot; dorsal fin reddish brown, the posterior segmented portion more so, sometimes blending ventrally with orange brown upper body; distal portion of segmented dorsal fin translucent; base of anal fin with an orange brown stripe, remaining portion of fin translucent; caudal peduncle and caudal fin black, except distal and ventral edges pale blue to lilac; pelvic fins hyaline; pectoral fins translucent (Figs. 24–26).

Colouration of IP in life. Similar to TP except width of body stripe wider and orange-brown colouration on posterior body reduced (Figs. 27, 28).

Colour in preservation. Similar to colouration in life, except orange-brown upper body indistinguishable from tan ground colouration of body; body stripe dark brown, middle portion attenuated and pale tan; all other black markings remain; pale blue to lilac edges on upper and lower caudal fin translucent; all remaining fins translucent.

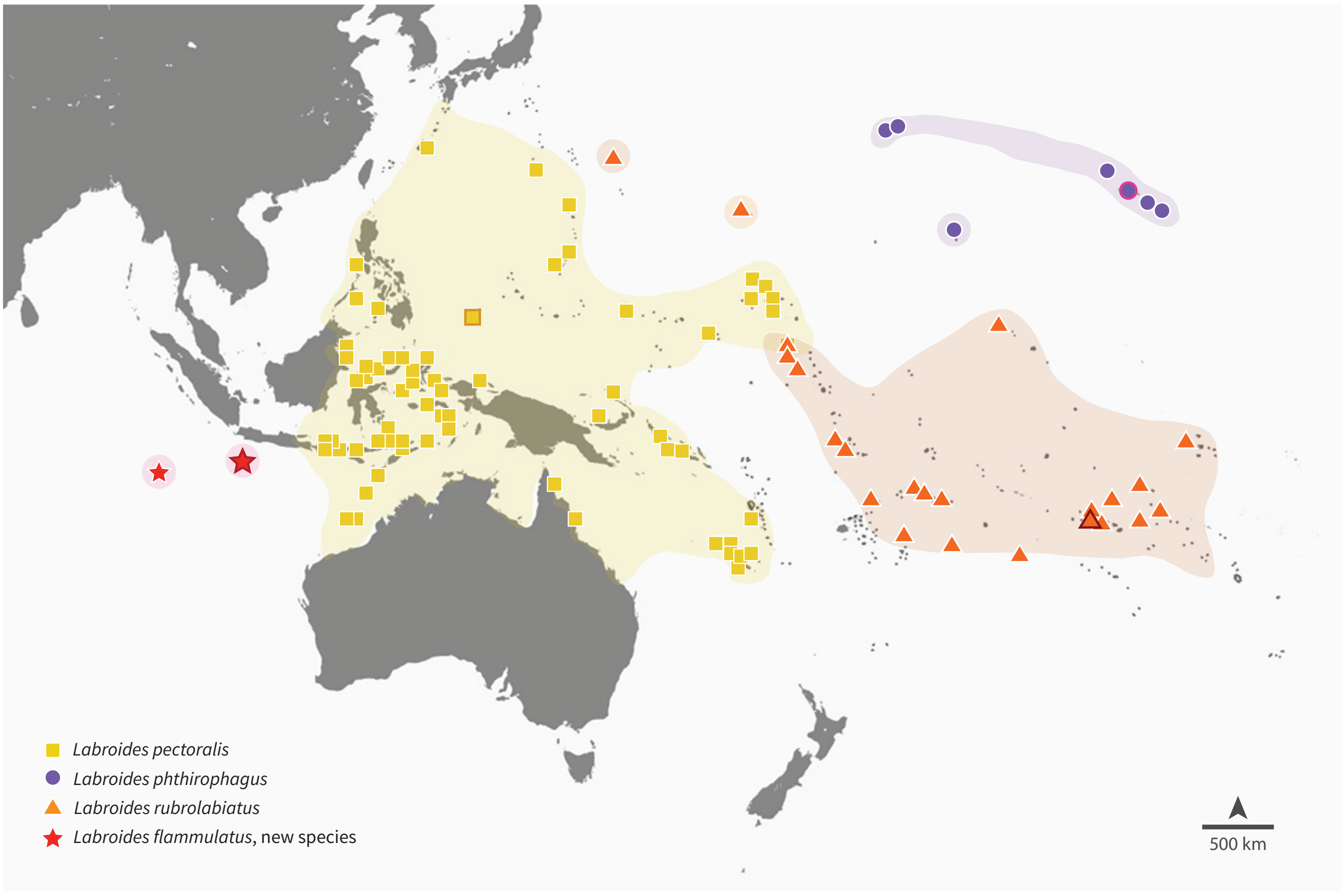

Fig. 29. Distribution map for members of the *Labroides phthirophagus* species complex. Locality data were taken from vouchered specimen data and underwater photographic records. Type localities are indicated by symbols with coloured outlines.

Habitat and distribution. *Labroides flammulatus* is known only from Christmas Island and the Cocos (Keeling) Islands (Fig. 29). It frequents shallow coral reefs at depths between 2–40 m. The species is syntopic with *Labroides dimidiatus* sensu lato and *Labroides bicolor*.

Etymology. The species name *flammulatus* is a Latin adjective derived from ‘flammula’, meaning ‘diminutive flame’ or ‘little blaze’. The adjectival form translates to ‘bearing a small flame’ in reference to the suffused orange markings on the body, which, although prominent, is rarely strong enough to obscure the lateral body stripe entirely. The name was selected as the winning vote by school students in a “Name that Fish” poll held at the Australian Museum as part of the Sydney Science Trail in 2023. To be treated as a nominative singular adjective. The common name is given after the volcanic mineral of the same name, in reference to similarities in colour, and in reference to the Christmas and Cocos (Keeling) Islands being volcanic in origin.

***Labroides bicolor* Fowler & Bean, 1928**

Bicolor Cleaner Wrasse
(Figs. 30–33, 37E, F; Table 6)

Labroides bicolor Fowler & Bean, 1928: 224 (holotype USNM 89970, Port Maricaban, Philippines); Harmelin-Vivien, 1976: 98 (checklist; Réunion Island); Parenti & Randall, 2000: 26 (checklist; Labridae); Kuiter & Tonozuka, 2004: 465 (colour photographs); Kuiter, 2010: 358 (colour photographs); Allen & Erdmann, 2012: 694 (colour photographs); Heemstra et al., 2022: 221 (field guide, western Indian Ocean); 549 (colour photographs from South Africa and Oman); Allen & Erdmann, 2024: 759 (colour photographs).

Fowlerella bicolor (Smith, 1957): 104 (type species of *Fowlerella* by original designation); Harmelin-Vivien, 1976: 97 (checklist; Réunion Island).

Diagnosis. Dorsal-fin rays X–IX,10–11; anal-fin rays III,9–11; pectoral-fin rays 13; upper procurrent caudal-fin rays 6–8; lower procurrent caudal-fin rays 7–8; principal caudal-fin rays 7–8 + 7; circumpeduncular scales 20–22; body depth 3.7–5.1 in SL; head length 2.6–3.0 in SL; snout length 2.6–3.3 in HL; orbit diameter 5.2–7.1 in HL; orbit diameter in snout length 1.6–2.5; caudal-peduncle length 3.3–4.9 in HL; pored lateral-line scales 26–29; scale rows above lateral line 4–5; scale rows below lateral line 9–11; total gill rakers 12–13; head and anterior body indigo to deep navy blue (silvery white to pale grey in IP); head with horizontal stripe from upper lip to about vertical of anal-fin origin (highly attenuated or absent in TP); posterior body yellowish green; caudal fin with black crescentic margin.

Colouration of TP in life. Head and anterior half to two thirds of body indigo to deep navy blue; snout with horizontal black stripe, from corner of mouth to anterior edge of orbit, its width subequal to slightly narrower than that of orbit; stripe continuing horizontally through orbit, subequal in width throughout and attenuating about halfway through

Table 6. Proportional measurements of selected specimens of *Labroides bicolor*, expressed as a percentage of SL.

	AMS I.15424-001	**AMS I.15425-001**	**AMS I.18034-039**	**AMS I.46747-030**	**AMS I.51101-001**	**AMS I.51455-023**	**AMS I.51803-007**	**SAIAB 1432**	**SAIAB 51978**	**SAIAB 77927**	**SAIAB 189203**	**ZRC 64315**	
SL (mm)	96.5	63.7	49.7	44.0	87.2	75.7	51.1	81.9	49.8	64.3	115.9	75.3	82.2
Body depth	26.8	27.2	25.2	19.5	23.2	25.2	21.7	26.0	24.3	21.9	25.5	24.6	23.6
Body width	14.3	11.8	10.5	11.1	10.6	12.5	13.3	12.6	12.9	11.7	14.2	11.0	12.0
Head length	35.4	34.5	35.4	34.3	33.3	33.7	35.2	33.7	35.1	34.8	34.2	36.8	36.9
Snout length	12.1	11.6	11.7	10.9	12.4	12.4	11.9	11.7	10.6	11.5	12.8	12.4	14.2
Upper jaw length	4.7	4.2	5.6	4.3	5.0	4.4	5.3	7.6	5.4	6.4	6.9	4.5	4.4
Orbit diameter	5.0	6.0	6.8	5.9	5.4	5.2	7.0	5.9	6.6	6.7	5.3	6.5	5.6
Interorbital width	9.5	8.9	9.1	8.9	9.3	8.9	9.6	9.8	9.2	8.9	10.4	9.3	9.5
Caudal-peduncle depth	16.8	17.6	18.5	15.0	15.8	17.0	16.2	17.6	18.1	16.0	16.5	15.1	15.0
Caudal-peduncle length	8.6	7.7	8.9	9.1	10.0	10.0	8.6	6.8	9.2	8.2	7.3	8.6	9.5
Predorsal length	34.2	32.7	37.2	33.4	33.0	34.3	34.4	33.1	32.7	38.1	32.5	35.5	34.2
Preanal length	59.3	60.8	58.4	65.5	59.1	62.5	62.0	60.7	58.8	58.8	61.4	62.4	63.6
Prepelvic length	34.3	34.2	35.8	33.2	33.1	35.1	33.1	33.6	32.7	33.3	37.2	32.8	36.0
Dorsal-fin base	58.1	53.2	55.9	50.7	53.1	52.0	51.3	58.1	60.8	54.3	56.5	53.3	51.5
1st dorsal-fin spine	1.6	2.2	2.8	2.7	2.5	2.8	2.3	2.1	4.4	2.2	3.9	2.8	3.5
2nd dorsal-fin spine	3.2	4.1	4.4	3.9	3.0	3.7	2.9	4.4	5.0	3.9	4.7	4.5	4.5
Last dorsal-fin spine	6.4	5.3	7.8	6.8	8.4	9.5	6.8	6.2	7.4	8.2	5.6	8.0	9.4
Longest dorsal-fin ray	11.5	9.9	11.3	9.8	13.4	12.9	11.2	13.1	12.0	13.2	9.6	10.9	11.6
Anal-fin base	28.2	27.5	28.8	26.6	30.7	25.6	31.3	33.1	36.1	27.7	30.5	29.3	29.7
1st anal-fin spine	0.9	1.7	2.6	1.6	2.3	1.8	1.6	2.0	2.0	2.0	1.8	2.0	1.7
2nd anal-fin spine	3.7	5.0	5.8	4.5	4.9	5.0	4.5	4.8	5.6	5.3	4.5	5.7	5.8
3rd anal-fin spine	7.5	7.2	8.9	7.7	8.1	8.3	6.7	5.9	8.6	8.7	5.9	8.4	9.0
Longest anal-fin ray	12.1	10.2	12.3	13.0	13.1	11.6	12.1	12.0	14.1	23.3	9.5	12.9	14.1
Caudal-fin length	19.9	24.5	26.2	23.6	22.9	21.0	25.6	23.6	27.1	23.8	22.7	21.4	22.7
Pectoral-fin length	20.7	22.9	23.1	23.2	21.0	21.3	21.5	21.5	23.1	21.3	21.2	20.7	19.5
Pelvic-spine length	10.2	9.4	10.3	11.8	8.7	9.5	8.6	9.8	10.6	8.7	11.6	8.2	10.5
Pelvic-fin length	15.5	17.3	16.9	18.6	15.4	17.3	15.3	13.1	17.3	15.7	14.6	11.7	12.9

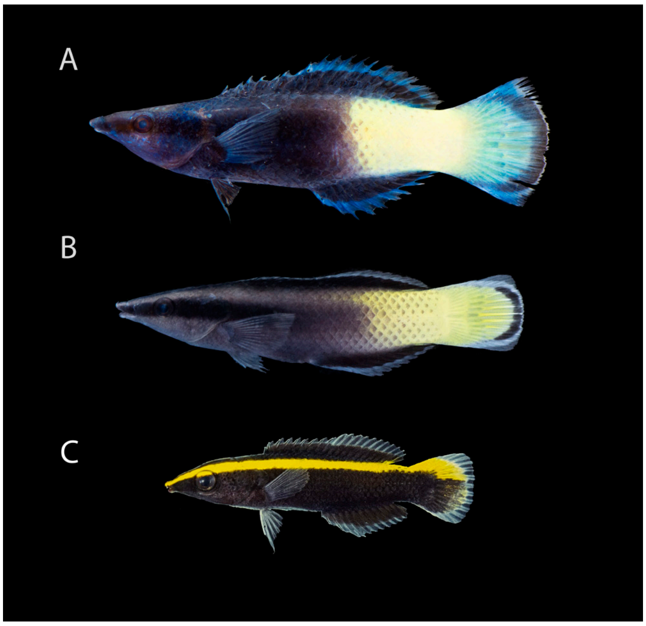

Fig. 30. *Labroides bicolor*, freshly euthanised A, TP, B, IP, and C, juvenile specimens. A, AMS I.51455-023, 75.7 mm SL, Flora Reef, Coral Sea, Queensland, Australia; B, AMS I.51803-007, 51.1 mm SL, Tijou Reef, Great Barrier Reef, Queensland, Australia; C, KAUM-I. 123553, 24.8 mm SL, Okimoerabu-jima, Amami Islands, Ryukyu Archipelago, Japan. Photographs by (A,B) Y.K. Tea and (C) H. Motomura.

Fig. 31. *Labroides bicolor*, underwater photograph of IP individual with clients *Dascyllus trimaculatus*, off Masaplod Norte, Philippines. Photograph by T. Cameron.

Fig. 32. *Labroides bicolor*, underwater photograph of spawning individuals at The Entrance, Cocos (Keeling) Islands. Note everted genital papillae. Photograph by K. Willshaw.

body (in fully matured males, stripe may be restricted to edge of opercle or absent entirely); iris orange brown with orange ring around pupil; posterior half to remaining third of body yellow to pale yellowish green; coloured interphase between anterior and posterior body very abrupt, sometimes with scattered indigo scales within posterior yellow portion of body; dorsal fin dark indigo to black, translucent sky blue on distalmost edge of segmented portion; anal fin similar to dorsal fin; caudal fin pale yellow with strong green to bluish green suffusion; distal submarginal edge of caudal fin with broad, black crescentic margin; outermost margin of caudal fin translucent sky blue; pelvic and pectoral fins translucent, their rays indigo to navy blue (Figs. 30A, 32, 33, 37E).

Colouration of IP in life. Similar to TP except anterior body silvery white to pale grey, becoming increasingly pearlescent white to yellow posteriorly; horizontal body stripe very prominent, reaching to about vertical of anal-fin origin; crescentic margin on caudal fin narrow, sometimes nascent (Figs. 30B, 31, 32, 37F).

Colouration of juveniles in life. Body dark grey to black, lightening ventrally and posteriorly with age; snout with a bright yellow stripe, from upper lip through distal portion of orbit, subequal in width throughout and confluent with distal edge of caudal peduncle and caudal fin; iris black, except distalmost portion within yellow stripe; dorsal and anal fins black, their distal most edges translucent; caudal peduncle yellowish grey; caudal fin pale yellow, its distalmost margin confluent with yellow body stripe; pelvic fins translucent grey; pectoral fins transparent (Fig. 30C).

Colouration in preservation. Similar to colouration in life except yellow to yellowish green colouration of posterior body greyish white to pale tan. Indigo to navy blue anterior body colouration in TP specimens now deep blue-black; all black markings remain; bases of segmented dorsal-, anal-, and caudal-fin rays pale blue in freshly preserved specimens, fading to translucent with age; all remaining fins translucent.

Remarks. The distribution of *Labroides bicolor* covers, in general, the entire range of the genus, from the east African coast to the Pitcairn Island group in French Polynesia. Golani & Fricke (2018) reported *Labroides bicolor* from the Red Sea, based on a record from Egypt in Debelius's guide to fishes of the Red Sea (2007). Although *Labroides bicolor* occurs in Oman and the western Indian Ocean, it is not known from the Red Sea or the Persian Gulf (Debelius, 1993; Heemstra et al., 2022). We therefore regard the Red Sea records in Debelius (2007) and Golani & Fricke (2018) as doubtful. The species is also absent from the Hawaiian Islands.

Labroides bicolor is among the largest of the cleaner wrasse species, with fully grown individuals approaching, and occasionally exceeding, 100 mm SL. Our largest specimen

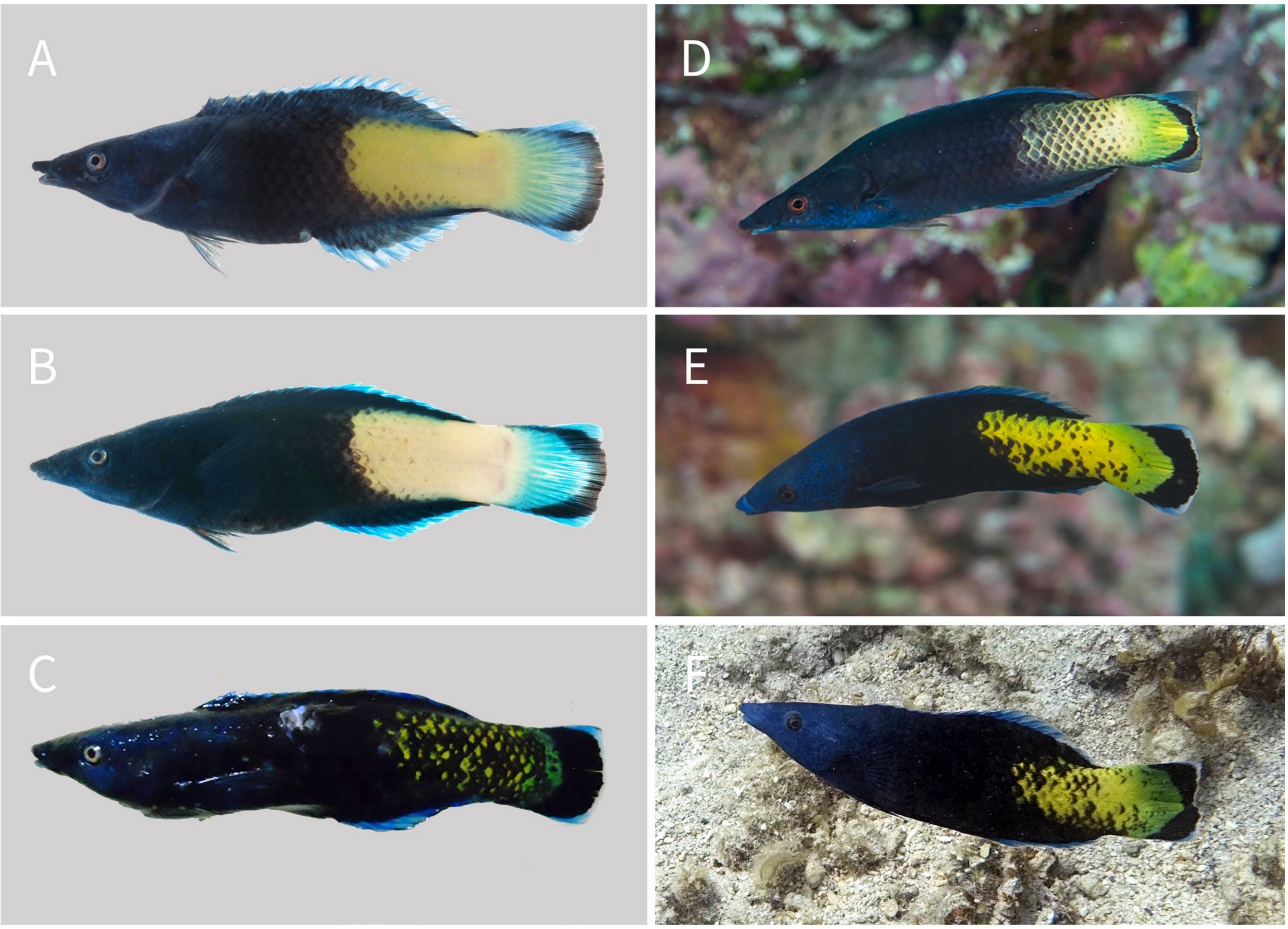

Fig. 33. Colour variation in *Labroides bicolor*. A, USNM 408732, 99.3 mm SL, Mururoa Atoll, Tuamotu Islands, French Polynesia; B, USNM 435055, 115.0 mm SL, Maupihaa Atoll, Society Islands, French Polynesia; C, SAIAB 189203, 115.9 mm SL, Sodwana Bay, KwaZulu-Natal, South Africa; D, underwater image from Pulau Luar, Cocos (Keeling) Islands; E, underwater image from Vaanee, Dhaalu Atoll, Maldives; F, underwater image taken off Flic en Flac, Mauritius. Images and photographs by (A, B) J.T. Williams, (C) A.D. Connell, (D) K. Willshaw, (E) D. Rolla, and (F) J. Gums.

examined from KwaZulu-Natal, South Africa, measured at 115.9 mm SL (140.6 mm total length). It is also the only species to display significant change in colouration across its ontogeny, with three distinct colouration patterns associated with its juvenile, IP, and TP respectively. Randall (1958) suggested that the colour patterns described for TP and IP individuals may be associated with sex. He examined two individuals (94 mm and 98 mm SL) of the two-toned "bicoloured" form and identified both as male. He examined a large 80 mm SL specimen of the paler "striped" form, identified it as female, and observed that individuals of this form in the field sometimes reached sizes comparable to the "two-toned" or "bicoloured" forms. He also noted that both colour forms often occurred as pairs in the field and, while not conclusively demonstrated, suggested that sexual dichromatism, if present in *Labroides bicolor*, is less pronounced than in other labrid species.

Reports of courtship and spawning behaviour in *Labroides* appear to be uncommon in the literature. However, the few recorded spawning events of *Labroides bicolor*, captured in underwater photographs (Fig. 32) and videos (Ueda, 2019), reveal nuptial pairs in which both individuals display the two-toned or "male-associated" colour form. While more observations are required to ascertain these hypotheses, it appears that colouration in *Labroides bicolor* is more strongly associated with ontogeny than sexual dichromatism, and reproductively active females may assume either the IP "striped form" or TP "bicoloured" form depending on age and maturity.

In some TP individuals, the anterior indigo body colouration may extend well into the posterior yellow portion, appearing mosaic-like in extreme examples (Fig. 33C–F). These variation in colour patterning appears to be more prevalent among individuals from the western Indian Ocean, though they do not appear to be regionally restricted nor consistent within populations. Such conspicuous individual variation does not appear to be common in marine fishes, particularly in the Labridae, which are better known for the constancy of their complex and often species-specific colour patterns (Wellington, 1992). Wellington (1992) reported a similar phenomenon in the Galapagos endemic *Xyrichtys victori*, where TP males exhibited pronounced individual variation in the extent of black spotting on the body. He hypothesised that the pronounced individual variation in *X. victori* may result from selective pressures linked to mate choice and dominance within its social system. Whether this applies to

X. victori, and by extension to *Labroides bicolor*, remains to be tested.

Etymology. Named in reference to its distinctive two-toned body colouration in TP individuals (Fowler & Bean, 1928).

Material examined. AMS I.15424-001, 96.5 mm SL, Heron Island, Great Barrier Reef, Queensland, Australia**;** AMS I.15425-001, 63.7 mm SL, Heron Island, Great Barrier Reef, Queensland, Australia; AMS I.18034-039, 49.7 mm SL, Abaiang Atoll, northern Gilbert Islands; AMS I.46747-030, 44.0 mm SL, North Minerva Reef (between Fiji and Tonga); AMS I.51101-001, 87.2 mm SL, Holmes Reef, Coral Sea, Queensland, Australia; AMS I.51455-023, 75.7 mm SL, Flora Reef, Coral Sea, Queensland, Australia; AMS I.51803-007, 51.1 mm SL, Tijou Reef, Great Barrier Reef, Queensland, Australia; SAIAB 1432, 81.9 mm SL, Inhaca Island, Mozambique, South Africa; SAIAB 51978, 49.8 mm SL, Flic en Flac, Mauritius; SAIAB 77927, 64.3 mm SL, Baie Ternay, Seychelles; SAIAB 189203, 115.9 mm SL, Sodwana Bay, KwaZulu-Natal, South Africa; ZRC 64315 (2), 75.3–82.2 mm SL, aquarium specimens from Indonesia.

Labroides inopinatus, new species

Goldenrod Cleaner Wrasse

(Figs. 34, 35A, B, 35D–F, 36, 37G, H; Table 7)

Holotype. AMS I.51733-001, 49.3 mm SL, Flora Reef, Coral Sea, Queensland, Australia (16°44′08″S, 147°42′04″E), 142 m, hand nets, T. Bennett, 3 August 2024 (Figs. 34, 37G) (GenBank PZ168614)

Paratypes. AMS I.51429-001, 46.7 mm SL, Holmes Reef, Coral Sea, Queensland, Australia (16°31′50″S, 147°48′10″E), 145 m, hand nets, T. Bennett, 20 January 2024; AMS I.51732-001, 45.5 mm SL, Flora Reef, Coral Sea, Queensland, Australia (16°45′03″S, 147°42′00″), 142 m, hand nets, T. Bennett, 3 December 2024 (Fig. 35D) (GenBank PZ168613); AMS I.51732-002, 40.7 mm SL, same data as AMS I.51732-001 (Fig. 35A–B) (GenBank PZ168612); KPM-NI 77429, 26.7 mm SL, Izu Oceanic Park, Jogasaki Coast, east coast of Izu Peninsula, Sagami Bay, Japan, 60 m, W. Takasei, 28 May 2023 (Fig. 35E); LACM 62086; 51.3 mm SL, Passe de Boulari, New Caledonia (22°32′00.0″S, 166°26′00.0″E), 133 m, hand nets, T. Bennett, 7 May 2025 (Fig. 35F).

Diagnosis. Dorsal-fin rays IX,11; anal-fin rays III,10–11; pectoral-fin rays 13; upper procurrent caudal-fin rays 5–6; lower procurrent caudal-fin rays 5–7; principal caudal-fin rays 7–8 + 7; circumpeduncular scales 24 (22–24); body depth 3.8–4.5 in SL; head length 2.6–3.0 in SL; snout length 2.9–3.5 in HL; orbit diameter 4.0–5.6 in HL; orbit diameter 1.3–1.8 in snout length; caudal-peduncle length 4.8–6.2 in HL; pored lateral-line scales 33–36; scale rows above lateral line 4; scale rows below lateral line 13–14; total gill rakers 11–13;

Description. Dorsal-fin rays IX,11, first ray unbranched, last branched to base; dorsal fin with a membranous cirrus posterior to tip of each spine; anal-fin rays III,11(10–11; AMS I.51429-001 paratype with III,10), last ray branched to base; pectoral-fin rays 13; uppermost rudimentary, uppermost two unbranched; pelvic-fin rays I,5; principal caudal-fin rays 8 (7–8) + 7, upper and lowermost unbranched; upper procurrent caudal-fin rays 6 (5–6); lower procurrent caudal-fin rays 7 (5–7); lateral line continuous with 35/33 (33–36) pored scales, posteriormost two slightly enlarged and beyond hypural; 5 (5–6) scale rows between lateral line and segmented portion of dorsal fin, third row extending onto fin base; a row of vertically elongate, leaf-shaped scales on base of dorsal fin, one to two per radial element; scales above lateral line to origin of dorsal fin 5 (4–5); 13 (13–14) scale rows below lateral line to anal-fin origin; diagonal scale rows on cheek from eye to upper corner of preopercle 5; circumpeduncular scales 24 (22–24); gill rakers 11 (11–13); branchioistegal rays 5; vertebrae 10 + 15 = 25.

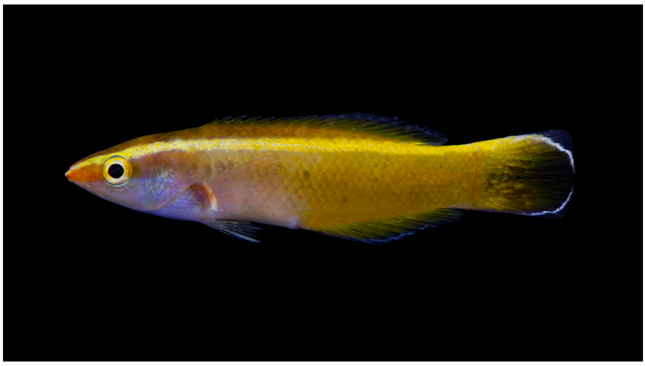

Fig. 34. *Labroides inopinatus*, new species, freshly euthanised holotype, AMS I. 51733-001, 49.3 mm SL, Flora Reef, Coral Sea, Queensland, Australia. Photograph by Y.K. Tea.

Body depth 4.5 (3.8–4.5) in SL; body width 2.0 (2.0–2.3) in depth; head 2.8 (2.0-3.3) in SL; snout moderately pointed, 3.1 (2.7–3.5) in HL; orbit 1.8 (1.3–1.8) in snout length; orbit 5.6 (4.0–5.6) in HL; interorbital space convex, bony width 4.2 (3.2–4.4) in HL; caudal-peduncle depth 2.4 (2.1–2.5) in HL; caudal-peduncle length 6.2 (3.5–6.2) in HL.

Caudal fin moderately rounded, 1.5 (1.4–1.9) in HL; dorsal-fin origin above second lateral-line scale and lower pectoral-fin base; dorsal-fin spines progressively longer, first about 0.7 (0.5–0.9) length of second, ninth about 2.4 (1.9–3.9) times longer than first; first or second segmented dorsal-fin ray longest, 2.6 (2.5–2.8) in HL; anal-fin origin below base of second or third segmented dorsal-fin ray; first anal-fin spine very short, 11.5 (11.5–17.6) in HL, second anal-fin spine 9.1 (6.6–10.5) HL; third longest, 4.7 (4.0–6.0) in HL; first segmented anal-fin ray longest, 3.1 (2.5–3.1) in HL; pectoral fin reaching a vertical at base of eight dorsal-fin spine, 1.6 (1.5–1.7) in HL; origin of pelvic fin slightly anterior to origin of pectoral fin; pelvic fins reaching a vertical at base of sixth or seventh dorsal-fin spine, longest ray 2.1 (2.1–2.8) in HL; pelvic-fin spine about three-fourths length of longest pelvic-fin ray, 3.0 (3.0–3.7) in HL.

Posterior edge of maxillary difficult to detect, but reaching about to a vertical at anterior nostril; mouth width about three-fourths orbit diameter; lower lip distinctly bilobed,

Table 7. Proportional measurements of type specimens of *Labroides inopinatus*, new species, expressed as a percentage of SL.

	Holotype	**Paratypes**				
	AMS I.51733-001	**AMS I.51732-001**	**AMS I.51732-002**	**AMS I.51429-001**	**KPM-NI 77429**	**LACM 62086**
SL (mm)	49.3	45.5	40.7	46.7	26.7	51.3
Body depth	22.1	25.5	24.1	26.6	25.1	23.2
Body width	11.2	13.0	12.0	12.2	12.4	9.9
Head length	35.1	35.6	38.8	33.4	37.8	30.9
Snout length	11.2	10.1	11.5	11.3	12.4	11.1
Upper jaw length	4.5	4.2	3.2	3.2	4.1	4.3
Orbit diameter	6.3	7.3	7.6	7.9	9.4	7.7
Interorbital width	8.3	8.8	8.8	9.4	10.5	9.4
Caudal-peduncle depth	14.8	15.8	15.5	14.3	18.4	13.5
Caudal-peduncle length	5.7	7.5	7.1	6.9	7.1	7.2
Predorsal length	32.0	34.7	37.3	38.1	40.1	36.1
Preanal length	62.1	63.5	65.4	64.2	65.5	67.4
Prepelvic length	32.7	35.6	37.8	38.8	39.7	37.2
Dorsal-fin base	52.7	49.0	48.9	48.0	48.3	53.6
1st dorsal-fin spine	2.6	2.0	3.7	2.8	3.4	3.5
2nd dorsal-fin spine	4.1	4.0	5.2	3.6	5.2	4.1
Last dorsal-fin spine	6.3	7.7	7.6	damaged	9.0	6.8
Longest dorsal-fin ray	13.4	12.7	15.2	damaged	damaged	11.3
Anal-fin base	28.6	32.5	31.7	29.6	30.0	28.9
1st anal-fin spine	3.0	3.1	2.2	2.1	2.6	2.5
2nd anal-fin spine	3.9	3.5	3.7	4.7	4.9	4.7
3rd anal-fin spine	7.5	5.9	7.6	7.9	9.4	7.6
Longest anal-fin ray	11.4	14.1	14.0	12.0	13.1	10.7
Caudal-fin length	22.7	21.8	20.9	20.6	21.0	21.6
Pectoral-fin length	21.5	21.8	23.6	20.8	22.8	21.1
Pelvic-spine length	11.6	9.6	10.6	9.0	10.1	10.1
Pelvic-fin length	16.4	14.1	14.7	14.3	13.5	14.6

Fig. 35. A, freshly euthanised and B, preserved paratype of *Labroides inopinatus*, new species, AMS I.51732-002, 40.7 mm SL, Flora Reef, Coral Sea, Queensland, Australia; C, cymothoid isopod, AMS P.1102936, removed from left gill chamber of AMS I.51732-002 paratype; D, AMS I.51732-001, 45.5 mm SL, Flora Reef, Coral Sea, Queensland, Australia; E, KPM-NI 77429, 26.7 mm SL, Izu Oceanic Park, Jogasaki Coast, Izu Peninsula, Sagami Bay, Japan; F, LACM 62086, 51.3 mm SL, Boulari Pass, New Caledonia. Dorsal and ventral views of isopods indicated by direction of arrowheads, respectively. Scale bar represents 5 mm. Photographs by (A, B, D) Y.K. Tea, (C) by J. Goh, (E) H. Wada, and (F) S. Ramones.

Fig. 36. *Labroides inopinatus*, new species, underwater photograph of a juvenile taken at approximately 40 m in Izu Oceanic Park, Jogasaki Coast, Izu Peninsula, Sagami Bay, Japan. Photograph by N. Kajiura.

gap between the lobes one-fourth orbit diameter; dentition typical of genus with a single pair of strongly recurved upper canines fitting inside lower pair when mouth is closed; length of upper canines about one-fourth orbit diameter; lower canines nearly straight, angling slightly outward; a large forward-directed canine posteriorly on upper jaw at corner of mouth; remaining teeth small, those at symphysis of upper jaw in numerous close-set rows, forming a semicircular mass between canines.

Gill membranes attached to isthmus slightly posterior to a vertical at posterior edge of orbit. Snout, ventral part of head, interorbital space and proximal region of nape scaleless; a narrow, horizontal band of scales running below eye just beneath suborbital pores, consisting mainly of a single scale row, which ends slightly anterior to a vertical at front of eye. Basal half of caudal fin scaled; dorsal and anal fin with a row of vertically elongate, leaf-shaped scales, one to two per radial element; paired fins scaled only basally; pelvic fins with a series of three enlarged scales in a median row posterior to origin.

Colouration of TP in life. Dorsal half of head and ground colouration of body mustard yellow to brown; lower portion of head silvery grey, fading to pale grey on isthmus and breast; snout with horizontal orange brown stripe, from lateral side of upper lip to anterior edge of orbit, its width subequal to that of pupil; stripe continuing horizontally through orbit, its width expanding slightly towards free upper edge of opercle; stripe continuing past opercle and blending with ground colouration of body; snout with a second, cream to silvery white stripe, from dorsal aspect of upper lip, curving slightly and continuing through dorsal aspect or orbit, past

Fig. 37. A selection of *Labroides* in life. A, *Labroides phthirophagus*, underwater photograph from Oahu, Hawaii. B, *Labroides rubrolabiatus*, underwater photograph from Moorea, French Polynesia; C, *Labroides pectoralis*, underwater photograph from Koror, Palau. Note attenuated and narrowed anterior body stripe; D, *Labroides flammulatus*, new species, underwater photograph from Christmas Island; E, F, *Labroides bicolor*, underwater photographs of E, TP and F, IP individuals from Kwajalein Atoll, Marshall Islands, respectively; G, H, *Labroides inopinatus*, new species, G, aquarium photograph of freshly collected AMS I.51733-001 holotype from Flora Reef, Coral Sea, Queensland, Australia, and H, underwater photograph of juvenile from Izu Oceanic Park, Jogasaki Coast, Izu Peninsula, Sagami Bay, Japan. Photographs by (A, C) K. Stender, (B) C.A. Clark, (D) J. Sommer-Knudsen, (E) N.K. Michiels, (F) M. Rosenstein, (G) S. Ramones and (H) W. Takase.

free upper edge of opercle and through to upper edge of caudal fin; dorsal fin dusky mustard yellow, dusky hyaline distally; anal fin similar to dorsal fin; caudal fin dusky yellow, becoming increasingly fuliginous distally; caudal fin with a narrow, bright white, crescentic margin; upper portion of crescentic margin continuing from terminal end of cream to silvery white body stripe; upper and lower lobes of caudal fin beyond margin translucent; pelvic fins white to translucent grey; pectoral fins hyaline (Figs. 34, 35A, 34D–F).

Colouration of IP and juveniles in life. Similar except ground colouration dusky grey to grey-brown (Figs. 36, 37H).

Colouration in preservation. Similar to colouration in life except ground colouration of body become pale tan to pale brown, dorsum above lateral stripe dark tan. Body stripe and crescentic margin of caudal fin white. Dorsal and anal fins dusky. Caudal fin very dusky, dark grey distally (Fig. 35B).

Habitat and distribution. *Labroides inopinatus* is known positively only from the type material collected at depths between 60–145 m in the Izu Oceanic Park, Sagami Bay, Japan, Holmes and Flora Reef in the Coral Sea, Queensland, Australia, and Boulari Pass in New Caledonia. Juveniles have additionally been photographed at a depth of 40 m in the Izu Oceanic Park. The species has also been observed, but not collected, from deep mesophotic reefs in Wakatobi, Southeastern Sulawesi, Indonesia, at a depth of approximately 110 m (S.J. Rowley, pers. comm., 2025).

Etymology. The specific epithet is given after the Latin adjective 'inopinatus' meaning unexpected, or unforeseen, in reference to the surprising discovery of a new, apparently deep dwelling cleaner wrasse. The common name refers to its yellowish colouration in life.

Remarks. A pair of cymothoid isopods (AMS P.1102936; Fig. 35C) was removed from the left gill chamber of one of the paratypes (AMS I.51732-002). The female appears to be gravid, although it is unclear whether the pair had mated within the host's gill chamber. No significant tissue damage was observed upon removal and examination of gill tissue.

Comparisons and phylogeography. Our maximum-likelihood phylogenetic analyses recover two distinct lineages within the genus *Labroides*, with *Labroides dimidiatus* sensu lato recovered as polyphyletic. The first lineage consists of *Labroides quadrilineatus* and *Labroides dimidiatus* clade 1, with both forming reciprocally monophyletic sister groups. The second lineage consists of all remaining species of *Labroides*, with *Labroides dimidiatus* clade 2 sharing successive sister relationships to *Labroides bicolor*, *Labroides inopinatus*, and the *Labroides phthirophagus* species complex. An expanded taxon set in Sims et al. (2014) recovered the boundary between *Labroides dimidiatus* clades 1 and 2 along the northern limits of Papua New Guinea and the Bismarck Archipelago. We note, however, that the clade comprising *Labroides bicolor* and *Labroides dimidiatus* clade 2 was not recovered with robust support. The systematics of *Labroides dimidiatus* sensu lato is beyond the scope of the present study and will be addressed in a subsequent work.

Some genetic clustering was recovered between western Indian Ocean and Pacific Ocean haplotypes of *Labroides bicolor* (Fig. 1). However, genetic divergences within and between populations appear minimal, with intraspecific variation among some Pacific Ocean haplotypes (0.2–0.9% uncorrected p-distance) exceeding that observed between Pacific and western Indian Ocean haplotypes (0.4–1.2%), suggesting little evidence of phylogeographic structuring across the species' range. We note, however, that these samples represent only a limited geographic subset, and given the widespread distribution of *Labroides bicolor*, more extensive sampling is needed to resolve patterns of population connectivity. Until such a time, we provisionally regard *Labroides bicolor* as a single widespread species.

Despite both species sharing a superficially similar crescentic caudal-fin marking, the newly described *Labroides inopinatus* appears to be only distantly related to *Labroides bicolor*, differing by 8.8–10.1% in COI. On the basis of morphology, *Labroides inopinatus* differs from all other species of *Labroides* most notably in its pored lateral-line scale count (33–36 vs ≥ 50 in *Labroides dimidiatus* sensu lato vs < 30 in all remaining *Labroides*) and in its highly distinctive colouration. *Labroides inopinatus* is also unusual in its habitat preference for deep coral reefs, with all known specimens and field observations taken from depths between 40 to 145 m. Whether this species fulfils the role as a cleaner in otherwise competition-free mesophotic coral ecosystems is not fully understood.

The *Labroides phthirophagus* species complex is resolved with four largely allopatric species, all of which are most reliably separated based on live colouration. The four species are united in having fewer than 30 pored lateral-line scales, and in having colourful bodies with yellow, orange, or magenta accents. In *Labroides phthirophagus*, the head and anterior body is bright yellow, and the distal and ventral margins of the caudal peduncle and caudal fin are richly and generously edged in magenta. The species is highly distinctive in its colouration and is the only representative of its genus in the Hawaiian Islands, and as such it is unlikely to be confused for any other species.

The remaining three species in this complex are notable in having varying degrees of orange colouration on the posterior body. The posterior orange body colouration is most extensive and conspicuous in *Labroides rubrolabiatus*, where it encroaches upon the body stripe and typically attenuates or obliterates it completely, restricting visible portions of the stripe to the head.

The remaining two species, *Labroides pectoralis* and *Labroides flammulatus*, are united by the presence of a well-defined, black elliptical spot on the lower base of the pectoral fin, a feature absent from all other congeners. In the more colourful *Labroides pectoralis*, the head and anterior body is bright yellow, and the anterior portion of the body is orange along the dorsum and blue above the anal-fin base. The body stripe of *Labroides pectoralis* is narrowed or attenuated anteriorly in mature individuals, and posteriorly, the body stripe is typically not suffused with orange (except sometimes in individuals from the Ryukyu Archipelago; see Remarks in species account). *Labroides flammulatus* can be distinguished from *Labroides pectoralis* by its grey to steely blue ground colouration on the head and anterior body, in having its anterior body stripe not conspicuously constricted or attenuated, and in having the orange body colouration encroaching and suffused within the body stripe. Character summaries for all species of the *Labroides phthirophagus* species complex are presented in the dichotomous key.

The geographical distribution of members of the *Labroides phthirophagus* complex is unusual, comprising only four species, two of which are widely distributed and two that are regional island endemics. *Labroides phthirophagus* and *Labroides flammulatus* are geographically restricted—the former is endemic to the Hawaiian Islands, Midway, and Johnston Atolls, and the latter is endemic to the Christmas and Cocos (Keeling) Islands in the eastern Indian Ocean. *Labroides pectoralis* and *Labroides rubrolabiatus* are both widespread across the Pacific Plate but occur mostly in reciprocal absence: the former ranges through much of the western Pacific, including Melanesia and Micronesia, whereas the latter replaces it in Polynesia and the remaining islands of southeast Oceania. Both species are narrowly parapatric in the northernmost Gilbert Islands. Curiously, *Labroides rubrolabiatus* is represented in the northwestern Pacific Ocean by isolated, disjunct populations in Marcus Island (BPBM 7129) and Wake Atoll (Figs. 19, 29). In their checklist of fishes from Wake Atoll, Lobel & Lobel (2004) reported *Labroides pectoralis* as present, but not *Labroides rubrolabiatus*. Since no reliable images were provided, we regard the presence of *Labroides pectoralis* from Wake Atoll as doubtful, and that Lobel & Lobel (2004) were likely referring to *Labroides rubrolabiatus* instead. This unusual distribution was noted by Randall & Springer (1975) in their description of *Labroides pectoralis*.

In his review of Pacific Plate biogeography, Springer (1982) noted the allopatric distributions of *Labroides rubrolabiatus*, *Labroides pectoralis*, and *Labroides phthirophagus*, and hypothesised that *Labroides phthirophagus* is sister to a clade comprising *Labroides pectoralis* and *Labroides rubrolabiatus*. Our phylogenetic analyses support Springer's (1982) proposed relationships, with *Labroides pectoralis* sensu lato (= *Labroides pectoralis* + *Labroides flammulatus*) recovered as more closely related to *Labroides rubrolabiatus*, and with both sister to *Labroides phthirophagus*. Divergences between *Labroides pectoralis*, *Labroides rubrolabiatus*, and *Labroides flammulatus* were, however, very shallow, suggesting that splitting of the species occurred only very recently.

Previous studies have shown evidence for niche partitioning in *Labroides dimidiatus* sensu lato, *Labroides bicolor*, and *Labroides pectoralis*, with each species evolving distinct habitat preferences and client-interaction strategies that permit stable, sympatric coexistence on reefs (Côté & Brandl, 2021). In contrast, species within the *Labroides phthirophagus* complex are not typically known to occur in sympatry. Given their close phylogenetic affinities and likely recent divergences, it is not unreasonable to assume that these species also share similarities in ecology. One possible explanation for the unusual disjunction between *Labroides pectoralis* and *Labroides rubrolabiatus* is competitive exclusion following a secondary range expansion of *Labroides pectoralis* into Micronesia.

Considerations for labrid taxonomy in the era of genomic datasets. The utilisation of large genome-scale datasets for phylogenetics has substantially improved our understanding of the evolutionary history of non-model organisms (Lemmon & Lemmon, 2013). Analyses of phylogenomic datasets have helped to resolve many long-standing questions across all nodes of the labrid tree of life (Hughes et al., 2023; Brownstein et al., 2025), ranging from the recent identification of *Centrogenys* as the sister group to the Labridae (Betancur et al., 2013, 2017; Ghezelayagh et al., 2022; Hughes et al., 2023) to the resolution of intractable shallower crown groups beset by rapid radiations and short internodes (e.g., the Cirrhilabrini and the Julidini; Tea et al., 2022; Hughes et al., 2023; Brownstein et al., 2025).

While there has been increased research effort directed at the molecular phylogenetic relationships among the Labridae, several problems persist. For one, phylogenetic relationships inferred using molecular sequence data fail to support the monophyly of several labrid genera. Some of these, such as the polyphyletic *Halichoeres* and *Coris*, have been longstanding problems identified in earlier studies (Barber & Bellwood, 2005; Westneat & Alfaro, 2005; Cowman et al., 2009), while others, such as the paraphyletic *Labroides*, have only more recently been identified (Brownstein et al., 2025). Consequently, these molecular phylogenies have important implications for labrid systematics, particularly with respect to the revision and stability of labrid taxonomy and nomenclature.

Here, we employ an integrative approach that combines newly generated genome-wide UCE data (derived from targeted enrichment and genome skimming) and mitochondrial COI sequences with morphological evidence to resolve relationships among species of *Labroides*, focusing on the *Labroides phthirophagus* species complex. While we demonstrate the efficacy of employing UCEs in systematics, we caution that this approach should not be used in isolation for implementing taxonomic changes, particularly for more recently diverged lineages where UCEs have less resolving power. In a recent study attempting to reconcile the taxonomy of the Labridae with relationships supported by molecular sequence data, Near et al. (2025) proposed a phylogenetically informed taxonomic framework through implementation of a synthetic phylogenetic tree based on genome-wide UCEs, supplemented by additional sources of data, including mitochondrial gene trees, phylogenetic relationships presented in published studies, or explicit statements of relationships in taxonomic studies and species descriptions (Near et al., 2025). The result includes the description of a new genus, elevation of 10 genera, and more than 150 nomenclatural changes to genus-species combinations, which included synonymy of 17 species (Near et al., 2025).

Curiously, the synonyms proposed by Near et al. (2025) include species explicitly identified from only two genera—*Cirrhilabrus* (fairy wrasses) and *Paracheilinus* (flasher wrasses). The authors justified these synonymies based on the following criteria: (i) lack of reciprocal monophyly in mitochondrial DNA COI gene trees; (ii) lack of reciprocal monophyly in phylogenomic UCE analyses; (iii) shared mitochondrial DNA COI haplotypes among putative species with allopatric distributions; and (iv) subtle morphological differences that are deemed phylogenetically uninformative (Near et al., 2025).

In criteria (i) and (iii), the authors argue that two or more species exhibiting COI paraphyly should be considered synonyms. Within the Labridae, this phenomenon extends well beyond *Cirrhilabrus* and *Paracheilinus*, and applying this criterion consistently across the labrid phylogeny would result in widespread taxonomic changes beyond these two genera. For example, our present study demonstrates that COI paraphyly also occurs in *Labroides*, and the phenomenon has likewise been documented in other julidine genera such as *Pseudojuloides* and *Thalassoma* (Victor & Randall, 2014). However, justification for synonymy or evidence of COI-based paraphyly were not considered or addressed in the taxonomic assessment of species in these genera by Near et al. (2025). Given the prevalence of mitochondrial introgression between closely related species, and the low phylogenetic resolution of COI in taxa with slow evolutionary rates or very recent origins (as in adaptive radiations), phylogenetic inferences based on individual gene trees should not be the sole justification for taxonomic decisions (Near & Keck, 2013). This was the point emphasised by Near et al. (2025) in their criterion (ii), which advocates the use of genomic datasets (e.g., UCEs) for delimiting species that are otherwise intractable on the basis of COI.

However, the use of UCEs in species delimitation is complex, as they do not always provide sufficient resolution to delineate species boundaries at shallow timescales (McGee et al., 2016). For example, the evolutionary timescale of *Cirrhilabrus* is very short (<10 Myr), rendering UCEs relatively uninformative (Tea et al., 2022). Tea et al. (2022) showed that while analysis of concatenated UCEs could resolve relationships among species of *Cirrhilabrus*, coalescent-based analyses yielded poor resolution. In such cases, coalescent-based approaches perform poorly compared with analyses of concatenated sequences, owing to substantial estimation error arising from individual gene trees containing few informative sites (Bryant & Hahn, 2020; Tea et al., 2022).

Brownstein et al. (2025) and Near et al. (2025) based their interpretations on a species tree estimated using the coalescent-based method in ASTRAL, but this approach offers very poor resolution within *Cirrhilabrus* for the reasons highlighted in Tea et al. (2022). Consequently, the UCE phylogeny from Brownstein et al. (2025) shows that there is very little phylogenetic resolution within *Cirrhilabrus*, and, to an extent, within the scarines, which were also characterised by short internal branches and widespread paraphyly (Brownstein et al., 2025; supplementary figure S5).

Finally, in their criterion (iv), Near et al. (2025) justified synonymy for species exhibiting subtle morphological differences that are deemed phylogenetically uninformative and show appreciable intraspecific variation. We argue that morphological characters, regardless of polarity, (i.e., autapomorphies, synapomorphies, or plesiomorphies), can be informative when they are demonstrably heritable, diagnostic, and useful for taxonomic classification at an appropriate hierarchical level. This necessitates taxonomic scrutiny, comprehensive character assessment, and an understanding of character variability based on direct examination of appropriate material prior to reaching taxonomic conclusions. For example, *Cirrhilabrus isosceles* differs morphologically from all members of the *Cirrhilabrus lunatus* complex, to which it belongs, in possessing a lanceolate caudal fin (Tea et al., 2016). This character is autapomorphic and therefore uninformative for resolving relationships within the complex; however, it is consistent within the species and provides a clear diagnostic character for species delimitation. The placement of *Cirrhilabrus isosceles* within the complex is instead supported by other shared derived characters and corroborated by molecular sequence data (Tea et al., 2016, 2022), demonstrating that autapomorphic traits need not undermine phylogenetic placement when interpreted within a broader evidentiary framework. A parallel example can be seen in *Labroides quadrilineatus*, which is placed in *Labroides* in the present study despite its possession of several autapomorphic characters.

For these reasons, we do not consider the UCE data presented in Brownstein et al. (2025) and Near et al. (2025) to be sufficiently informative in overturning the validity of species currently described in *Cirrhilabrus* and *Paracheilinus*. Essentially, justifications for synonymy within this group were based on the lack of phylogenetic resolution of UCEs at intra- and interspecific scales, without consideration of morphological characters or the examination of type material, the importance of which we show here with *Labroides*. We therefore reject the synonymy of species presented in Near et al. (2025), and caution that while large scale genomic datasets can serve as powerful tools in resolving species relationships, heterogeneity in evolutionary histories and complexities across different groups in any particular taxon's tree of life needs to be considered.

While molecular phylogenetic analyses can provide valuable insights into evolutionary histories, we emphasise that taxonomic and nomenclatural changes should ideally be supported by additional lines of evidence, accompanied by morphological evidence, detailed diagnoses, and typification. These considerations are particularly important when synonymising or resurrecting available names, describing new family-group taxa, or recombining family- and species-group names, as demonstrated in this present study.

DATA ACCESSIBILITY

Sequence alignment files, raw tree files, and accession numbers for newly generated and publicly acquired sequences are provided in the supplemental material here: https://doi.org/10.6084/m9.figshare.31808011. Underwater video of *Labroides dimidiatus* sensu lato apparently picking at and feeding on coral mucus in Okinawa is available in the Movie Archive of Animal Behaviour: http://www.momo-p.com/showdetail-e.php?movieid=momo251020ld01b&embed=on (Sato, 2025; Data No.momo2510201d01b).

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