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Species Diversity Assessment of the Flatfish Genus *Laeops* (Carangiformes: Bothidae) in Taiwan, with the Resurrection of *L. kitaharae*

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ABSTRACT

The bothid genus *Laeops* currently comprises nine recognized species, with one to three species reported from Taiwanese waters. However, the validity of *L. kitaharae*, which was recently synonymized with *L. parviceps* based on morphology, has long been debated. This study applies integrative taxonomy to resolve the taxonomic status of *Laeops* species occurring in Taiwanese waters. A total of 57 *Laeops* specimens were collected from Taiwan and other localities across the Indo-West Pacific region and analyzed using both morphological and molecular methods. A phylogenetic tree was reconstructed from 105 mitochondrial *COI* gene sequences obtained in this study and compiled from online sources. The results reveal that *Laeops* is not monophyletic, instead forming two distinct lineages: *Laeops* I (*L. nigromaculatus*) and *Laeops* II (the remaining sampled species). Further species delimitation analyses using ASAP and bPTP consistently identified seven Operational Taxonomic Units (or inferred species), supporting *L. kitaharae* and *L. parviceps* as distinct species, with a genetic divergence of 9.7% at the *COI* locus. Morphological examinations based on available voucher specimens, including type series, indicate that *L. kitaharae* differs from *L. parviceps* by having fewer dorsal- and anal-fin rays (D: 100–103 vs. 105–109; A: 78–83 vs. 85–90) and a shorter snout (1.6–2.1% SL vs. 2.2–3.4% SL). A re-examination of the type specimens suggests that *L. tungkongensis*, a species previously described from four specimens collected in Donggang, southwestern Taiwan, is conspecific with *L. parviceps*, rather than *L. clarus*, as previously proposed. Consequently, we resurrect *L. kitaharae* as a valid species and synonymize *L. tungkongensis* with *L. parviceps*. Accordingly, three *Laeops* species (*L. kitaharae*, *L. lanceolata*, and *L. parviceps*) are confirmed to occur in Taiwan. Furthermore, genetic references and an updated identification key for *Laeops* II are provided. This research has been registered in ZooBank under the identifier: urn:lsid:zoobank.org:pub:B21F2AB6-8C06-4CE9-8024-B45C2ABDF48D.

Keywords: species delimitation, phylogeny, left-eyed flounders, West Pacific.

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1 INTRODUCTION

The flatfish genus *Laeops* from the family Bothidae was established by Günther (1880), with *Laeops parviceps* from the Arafura Sea, Australia, designated as the type species (Figure 1). This genus is characterized by an elongated body shape, small size, small mouth, being left-eyed, absence of teeth on both jaws of the ocular side, and first two dorsal-fin rays detached from the remaining fin rays, except in *L. nigromaculatus* (Amaoka, 1969; Gunther, 1880; Norman, 1934; Voronina et al., 2020). The members of the genus *Laeops* mainly inhabit the tropical Indo-West Pacific (IWP) at depths of 22–475 m (Amaoka, 1969; Amaoka, 2016; Fricke et al., 2025; Hensley & Amaoka in Carpenter & Niem, 2001; Norman, 1934; Voronina et al., 2020).

Currently, nine species are recognized within the genus (Table 1). Two species, *Laeops nigromaculatus* von Bonde, 1922 (type locality: South Africa) and *Laeops parviceps* Günther, 1880 (type locality: Australia), have a wide distribution across the IWP (Amaoka, 2016; Fricke et al., 2025; Norman, 1934; von Bonde, 1922; Voronina et al., 2020). Two species are restricted to the western Pacific: *Laeops clarus* Fowler, 1934 (type locality: Philippines) and *Laeops lanceolata* Franz, 1910 (type locality: Japan) (Norman, 1934; Amaoka, 1969, 2016; Voronina et al., 2016, 2020) (Figure 1). The remaining five species are recorded from the Indian Ocean: *Laeops guentheri* (Alcock, 1890) (type locality: Gulf of Martaban, Myanmar [Burma]), *Laeops macrophthalmus* (Alcock, 1889) (type locality: Myanmar [Burma]), *Laeops natalensis* Norman, 1931 (type locality: South Africa), *Laeops nigrescens* Lloyd, 1907 (type locality: Gulf of Aden), and *Laeops pectoralis* (von Bonde, 1922) (type locality: South Africa) (Alcock, 1889, 1890; Lloyd, 1907; Norman, 1931, 1934; von Bonde, 1922; Voronina et al., 2020). In Taiwan, two species, *L. kitaharae* and *L. parviceps*, are considered valid and present (The Fish Database of Taiwan; Shao, 2025; https:// fishdb.sinica.edu.tw/eng/home.php).

Chen and Weng (1965) first reported the genus *Laeops* from Taiwan, listing seven species (*L. guentheri, L. kitaharae, L. lanceolata, L. nigrescens, L. parviceps, L. variegata,* and *L. sp.*) and described a new species, *L. tungkongensis,* based on four specimens collected from Tungkong (=Donggang) off southwestern Taiwan (Figure 1). Later, Shen (1983) reassessed these records and concluded that five of the species reported by Chen and Weng (1965)—*L. guentheri* [not of Alcock], *L. lanceolata* [not of Franz], *L. nigrescens* [not of Lloyd], *L. variegata,* and *L.* sp.—were either synonyms of *L. kitaharae* or misidentifications. Shen (1983) ultimately recognized only three species from Taiwan: *L. kitaharae, L. tungkongensis,* and *L. parviceps.* Similarly, Shen (1993) maintained these three species in the later work *Fishes of Taiwan.*

In 2011, Shen and Wu published a new edition of the *Fishes of Taiwan,* listing four *Laeops* species—*L. guentheri, L. kitaharae, L. parviceps,* and *L. tungkongensis*—along with brief descriptions, illustrations, and photographs. However, no voucher specimens were provided, and the photograph of *L. kitaharae* in Shen and Wu (2011) was a misidentification of *Plagiopsetta glossa* Franz, 1910, a tongue flatfish. Later, Amaoka (2019b) and Amaoka and Ho (2019) documented only a single species, *L. kitaharae,* existing in Taiwan, with the latter study proposing *L. tungkongensis* as a junior synonym of *L. kitaharae*. Subsequently, Voronina et al. (2020) revised the taxonomy of *Laeops,* redefining its species based on original descriptions and examined specimens. They recognized nine valid species and proposed *L. kitaharae, L. sinusarabici,* and *L. tungkongensis* as synonyms of *L. parviceps, L. natalensis,* and *L. clarus,* respectively. Following this revision, the authors listed two *Laeops* species from Taiwanese waters: *L. clarus* (senior synonym of *L. tungkongensis*) and *L. lanceolata.* However, their examination of *L. tungkongensis* was based on photographs, radiographs, and previous references to the type series rather than direct specimen analysis.

Despite recent advances in *Laeops* taxonomy, previous studies, based primarily on morphological data and literature reviews, have faced challenges and controversy. These issues stem from deficiencies in the original descriptions and limited material for comparative examination. Some type specimens have either disintegrated or been lost (Voronina et al., 2020). Furthermore, morphology-based taxonomy often struggles to detect subtle

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differences in morphological features, particularly in the Bothidae (Amaoka, 1969; Chen & Weng, 1965; Norman, 1934; Voronina et al., 2020). Flatfishes exhibit high variability in both meristic and morphometric traits within a species, and diagnosing morphological traits can be difficult in poorly preserved, damaged, or juvenile specimens (Norman, 1934; Tongboonkua et al., 2018; Voronina et al., 2020). These limitations underscore the importance of adopting an integrated taxonomic approach that considers multiple lines of evidence, including molecular phylogeny, genetics, and additional criteria such as geographical and depth distributions, to delimit species and propose a stable taxonomic hypothesis (Hung et al., 2017; Hurzaid et al., 2020; Kekkonen & Hebert, 2014; Lee et al., 2022; Lo et al., 2017).

In this study, comprehensive sampling of *Laeops* was conducted in Taiwan, along with additional samples from the Indo-West Pacific, to explore species diversity. A total of 57 collected samples, along with available homologous sequences retrieved from public databases such as the National Center for Biotechnology Information (NCBI) (GenBank; Sayers et al., 2025; http://www.ncbi.nlm.nih.gov/genbank/), and the Barcode of Life Data System (BOLD Systems; Ratnasingham et al., 2024; https://v4.boldsystems.org/), were analyzed using molecular species delimitation at the *mitochondrial Cytochrome c oxidase subunit I (COI)* locus, employing two widely used methods: Assemble Species by Automatic Partitioning (ASAP; Puillandre et al., 2021; https://bioinfo.mnhn.fr/abi/public/asap/) and Bayesian-based Poisson Tree Processes (bPTP; Zhang et al., 2013; https://species.h-its.org/). These analyses resulted in the proposal of a primary species hypothesis, which was then evaluated using morphological characteristics and other criteria for species delimitation (Lee et al., 2022). Special emphasis was placed on assessing the validity of *L. kitaharae* and *L. tungkongensis,* which had previously been synonymized with other species. Following our revision, we provide accurate genetic references and an improved species identification key for the genus *Laeops.*

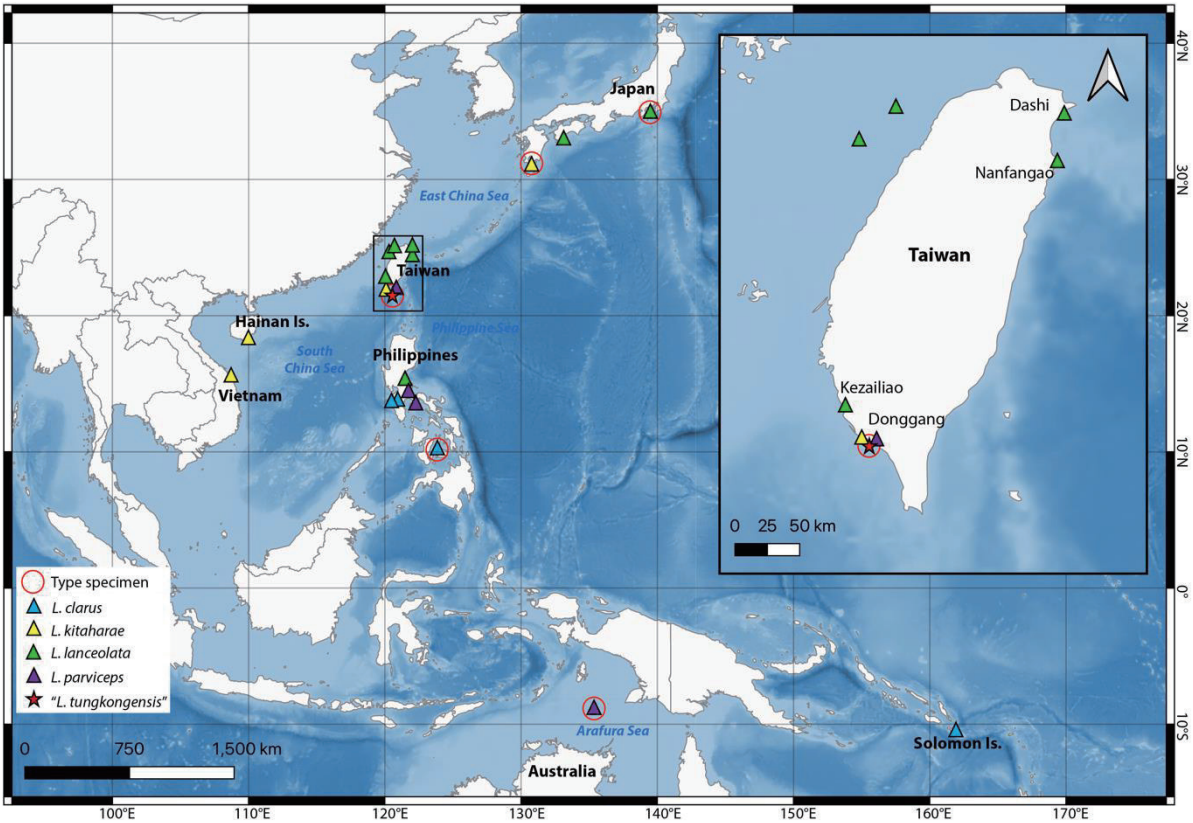

Figure 1. Distribution map of *Laeops* Günther, 1880 from Taiwan and adjacent waters, as examined in this study. Triangles represent valid *Laeops species: L. clarus* (blue); *L. kitaharae* (yellow); *L. lanceolata* (green); and *L. parviceps* (purple). The star represents the invalid name "*L. tungkongensis*" (red). Red circle: type locality.

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2 RESEARCH METHODS

Institutional abbreviations

ASIZP Academia Sinica, Institute of Zoology, Taipei, Taiwan (R.O.C.);

BMNH Natural History Museum, London, United Kingdom;

CAS California Academy of Sciences, California, United States;

NMMBP National Museum of Marine Biology and Aquarium, Pingtung, Taiwan (R.O.C.);

NTUM National Taiwan University Museum, Taipei, Taiwan (R.O.C.);

USNM Smithsonian Institution National Museum of Natural History, Washington D.C., United States.

List and abbreviations of morphological characters analyzed

SL Standard length presented as a percentage of the standard length (% SL);

D Dorsal fin;

A Anal fin;

P Pectoral fin on ocular side;

C Caudal fin rays;

GR Gill rakers;

Vert. Vertebrae;

LLS Pored lateral line scales on ocular side;

UJL (O) Upper jaw length on ocular side length;

UJL (B) Upper jaw length on blind side length;

LJL (O) Lower jaw length on ocular side length;

LJL (B) Lower jaw length on blind side length.

Catalogue numbers for voucher specimens are followed by the number of preserved specimens in alcohol, presented in brackets [for more than one specimen]. Tissue sample voucher IDs are provided in parentheses. Information on the examined materials for morphological and molecular analyses is provided in Supplementary Table 1. Museum acronyms follow *A Guide to Fish Collections* in Eschmeyer's Catalog of Fishes by Fricke et al. (2025).

2.1 Taxon Sampling

A total of 57 *Laeops* specimens were collected, of which 47 were from fish landing sites in southern China (Hainan Island), Japan, and Taiwan. Two specimens were collected by Taiwanese fisheries research vessels. The remaining eight specimens were collected during five oceanographic surveys conducted using Philippine or French research vessels under the *Tropical Deep-Sea Benthos* (TDSB) program (2000–present): Aurora 2007 (Philippines); KAVIENG 2014 (Papua New Guinea); MAINBAZA (Mozambique); SALOMONBOA 3 (Solomon Islands); and SAYA (Saya de Malha Bank) (Supplementary Table 1).

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A small piece of muscle tissue from the blind side was collected from each individual and stored in 95% ethanol at -20 °C before DNA extraction. Freshly collected specimens were photographed before being fixed in 10% formalin and transferred to a 70% ethanol solution for long-term preservation. All newly collected specimens were deposited in the ichthyology collections at ASIZP and NTUM. Detailed information on the specimens examined in this study is provided in Supplementary Table 1.

Table 1. List of valid species in the genus *Laeops* Günther, 1880 and their geological and depth distributions. Abbreviations: IO, Indian Ocean; IWP, Indo-West Pacific; WI, western Indian Ocean; WP, western Pacific.

Species	Distribution	Depth range (m)	Remarks
L. clarus Fowler, 1934	WP: Philippines and New Caledonia	48–413	
L. guentheri Alcock, 1890	IO: Mozambique and Persian Gulf east to Myanmar	23–123	
L. kitaharae (Smith & Pope, 1906)	WP: Vietnam and China to Japan	N/A	Revalidated in this study: Previously synonymized as *L. parviceps*
L. lanceolata Franz, 1910	WP: Vietnam and Philippines north to Korea and Japan	22–290	Junior synonyms: *Laeops variegata* Franz, 1915; *Laeoptichthys fragilis* Hubbs, 1915
L. macrophthalmus (Alcock, 1889)	IO: Gulf of Oman and India to Burma	180–196	Junior synonym: *Scianectes lophoptera* Alcock, 1889; *L. lophoptera* (Alcock, 1889)
L. natalensis Norman, 1931	WI: South Africa and Red Sea	53–420	Junior synonym: *L. sinusarabici* Chabanaud, 1968
L. nigrescens Lloyd, 1907	IO: Gulf of Aden	238	
L. nigromaculatus von Bonde, 1922	IWP: South Africa to Saya de Malha Bank; Japan; Papua New Guinea to New Caledonia	183–475	
L. parviceps Günther, 1880	IWP: East Africa; Persian Gulf; Vietnam east to Philippines and Papua New Guinea, north to Taiwan, south to Australia	22–238	Junior synonym proposed in this study: *L. tungkongensis* Chen & Weng, 1965
L. pectoralis (von Bonde, 1922)	WI: South Africa, Mozambique, and Kenya	235–380	Junior synonym: *Parabothus thackwrayi* Smith, 1967

2.2 Molecular Analysis

All of the molecular procedures in this study were conducted at the Marine Biodiversity and Phylogenomics Laboratory, Institute of Oceanography, National Taiwan University. Total genomic DNA was extracted from all 56 *Laeops* specimens. Two outgroups (Cyclopsettidae [*Etropus microstomus*] and Bothidae [*Bothus pantherinus*]) were selected to root the phylogenetic tree, and three closely related monotypic genera. *Japonolaeops gracilis* (N=12), *Kamoharaia megastoma* (N=2), and *Neolaeops microphthalmus* (N=4), were included according to studies by Campbell et al. (2019) and Tongboonkua (2018). *COI* gene sequences were obtained through polymerase chain reaction (PCR) and Sanger sequencing using universal fish primers described by Ward et al. (2005). PCR and sequencing were performed following the laboratory protocol of Tongboonkua et al. (2018). Sequence chromatograms were visualized and edited using CodonCode Aligner v.11 (CodonCode Corporation, Dedham, MA, USA).

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An additional 21 *COI* sequences of *Laeops* and eight *COI* sequences from closely related genera were retrieved from online databases (GenBank and BOLD Systems). DNA sequences were aligned using Molecular Evolutionary Genetics Analysis version 11 (MEGA 11) software (Tamura et al., 2021). An aligned DNA data matrix of 105 sequences was utilized to reconstruct a phylogenetic tree under the maximum likelihood (ML) algorithm using RAxMLGUI 2.0 (Edler et al., 2021) with the model of nucleotide substitution GTR+I. Nodal support values were computed under the bootstrap framework with 1,000 replicates and shown as bootstrap proportions (BP). The phylogenetic tree was visualized using FigTree version 1.4.4 (Rambaut, 2018).

Interspecific and intraspecific genetic distances were determined using Kimura's two-parameter (*K2P*) model (Kimura, 1980) in MEGA 11, and species groups were defined based on both morphological and phylogenetic results (Table 2). Furthermore, two DNA-based species delimitation tools, ASAP (Puillandre et al., 2021) and bPTP (Zhang et al., 2013), were utilized to identify Operational Taxonomic Units (OTUs). ASAP is a distance-based method that detects pairwise differences (barcode gaps) between sequences. This analysis was performed on the web server (https://bioinfo.mnhn.fr/abi/public/asap/) using an aligned sequence matrix and the Kimura (K80) model (Kimura [K80] ts/tv = 2.0). For the bPTP analysis, a tree-based species delimitation tool, a rooted phylogenetic tree, was used to delimit species on the web server (https://species.h-its.org/) with the following settings: number of MCMC generations = 500,000; thinning = 100; burn-in = 0.2; seed = 123.

2.3 Morphological Analysis

Thirty-three newly collected *Laeops* II specimens, the type series of *L. tungkongensis*, and four non-type specimens from other museum collections were examined. All examined specimens were radiographed to observe osteological characters. A total of 21 morphometric and eight meristic characters were analyzed (Tables 3–5). Measurements of preserved specimens were recorded with digital calipers to the nearest 0.1 mm. Morphometric measurements are presented as a percentage of standard length (% SL). Since the type specimens of some *Laeops* species deposited in BMNH (*L. lanceolata* BMNH1931.11.16.2, syntype; *L. parviceps* BMNH1879.5.14.98, lectotype) and USNM (*L. clarus* USNM93083, holotype; *L. kitaharae* USNM55612, holotype) were not physically accessible, only their photographs and radiographs were examined. Additionally, two specimens from the SALOMONBOA 3 expedition (Solomon Islands) and one specimen from the MAINBAZA expedition (Mozambique) were lost, leaving only tissue samples and photographs available for examination: *L.* cf. *clarus* (SALOMONBOA 3, tissue voucher: WJC12332), *L. nigromaculatus* (SALOMONBOA 3, tissue voucher: SB 6), and *L. nigromaculatus* (MAINBAZA, tissue voucher: CP3131).

Moreover, several studies reporting bothid or *Laeops* records lacked voucher specimen evidence or were prone to potential misidentifications. Therefore, only literature containing species descriptions was primarily considered in the taxonomic revision. Species identification in this study was based on taxonomic descriptions and several identification keys (Hensley & Amaoka in Carpenter & Niem, 2001; Nakabo, 2002, 2013; Norman, 1934; Voronina et al., 2020).

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3 RESULTS AND DISCUSSION

3.1 Molecular Results

The phylogenetic tree inferred from *COI* gene data reveals that *Laeops* is paraphyletic, represented by two distinct clades with strong support: 1) *Laeops* I (BP=98), and 2) *Laeops* II (BP=84) (Figure 2). *Laeops* I consists of a single nominal species, *L. nigromaculatus*, with samples from different localities across the IWP (Papua New Guinea, Mozambique, Saya de Malha Bank, Solomon Islands, and South Africa), while *Laeops* II comprises the remaining six nominal *Laeops* species included in this study and can be separated into three subclades: 1) western Indian Ocean (WIO) clade, with samples of *L. pectoralis* (South Africa); 2) northern Indian Ocean (NIO) clade, with samples of *L. macrophthalmus* (India); and 3) western Pacific Ocean (WPO) clade, with samples of *L.* cf. *clarus* (Coral Sea [CS]: Solomon Islands), *L. kitaharae* (South China Sea [SCS]: Hainan Island and Taiwan), *L. lanceolata* (South China Sea: Philippines, and Taiwan, northwest Pacific [NWP]: Japan), and *L. parviceps* (South China Sea: Philippines, and Taiwan).

Laeops nigromaculatus (*Laeops* I) is resolved as the earliest branching lineage within the "*Laeops*" clade, which also includes its three related genera, *Japonolaeops, Kamoharaia,* and *Neolaeops,* in the *COI* tree, with relatively strong support (BP=84). However, monophyly of the clade grouping these four genera is not supported (BP=66). This lack of support may result from the limitations of mtDNA, such as *COI*, in inferring high-level phylogenetic relationships due to a high degree of homoplasy caused by substitutional saturation, especially at the third codon position of mitochondrial protein-coding genes (Campbell et al., 2013, 2014; Chen et al., 2008, 2014; Chen & Mayden, 2009). Nevertheless, this clade is confirmed by multi-gene phylogenetic analyses (Campbell et al., 2019; Tongboonkua et al., unpublished).

Morphological examination of available specimens indicates that *L. nigromaculatus* differs from its congeners in the *Laeops* II in several key characteristics. Unlike other *Laeops* species, the first two dorsal-fin rays of *L. nigromaculatus* are not detached from the remaining fin rays. Additionally, the origin of the first dorsal-fin ray is positioned above the anterior nostril on the blind side, whereas in other *Laeops* species, it is located above or behind the posterior nostril on the blind side. Although the *COI* gene analysis may be affected by substitutional saturation, potentially resulting in an inaccurate phylogenetic placement of *L. nigromaculatus*, genetic divergence (estimated by *K2P* distance) between *L. nigromaculatus* and its congeners ranges from 14.70 to 20.17%. This level of divergence is substantially higher than the average genetic difference of 11.62 ± 0.08% among genera reported within the flatfish family Pleuronectidae (Kartavtsev et al., 2014). Given these distinct morphological and genetic differences, the *Laeops* I (comprising only *L. nigromaculatus*) should be recognized as a distinct and potentially new genus within the Bothidae. However, further study is needed to confirm this taxonomic reassignment.

On the other hand, the *COI* gene is a suitable marker for species identification and delimitation due to its significant differences between intraspecific and interspecific variation (Allio et al., 2017; Puillandre et al., 2012, 2021; Ward et al., 2005). In the *COI* tree, all *Laeops* species involving samples collected from Taiwanese waters cluster with *L.* cf. *clarus* (one sample from the Solomon Islands) as subclade 3 (BP=99). Within this subclade, *L. parviceps* (six Taiwan individuals) is a sister species to *L. kitaharae* (one Taiwan individual), and together they form a sister lineage to two other western Pacific species: *L.* cf. *clarus* and *L. lanceolata* (36 individuals from Taiwan).

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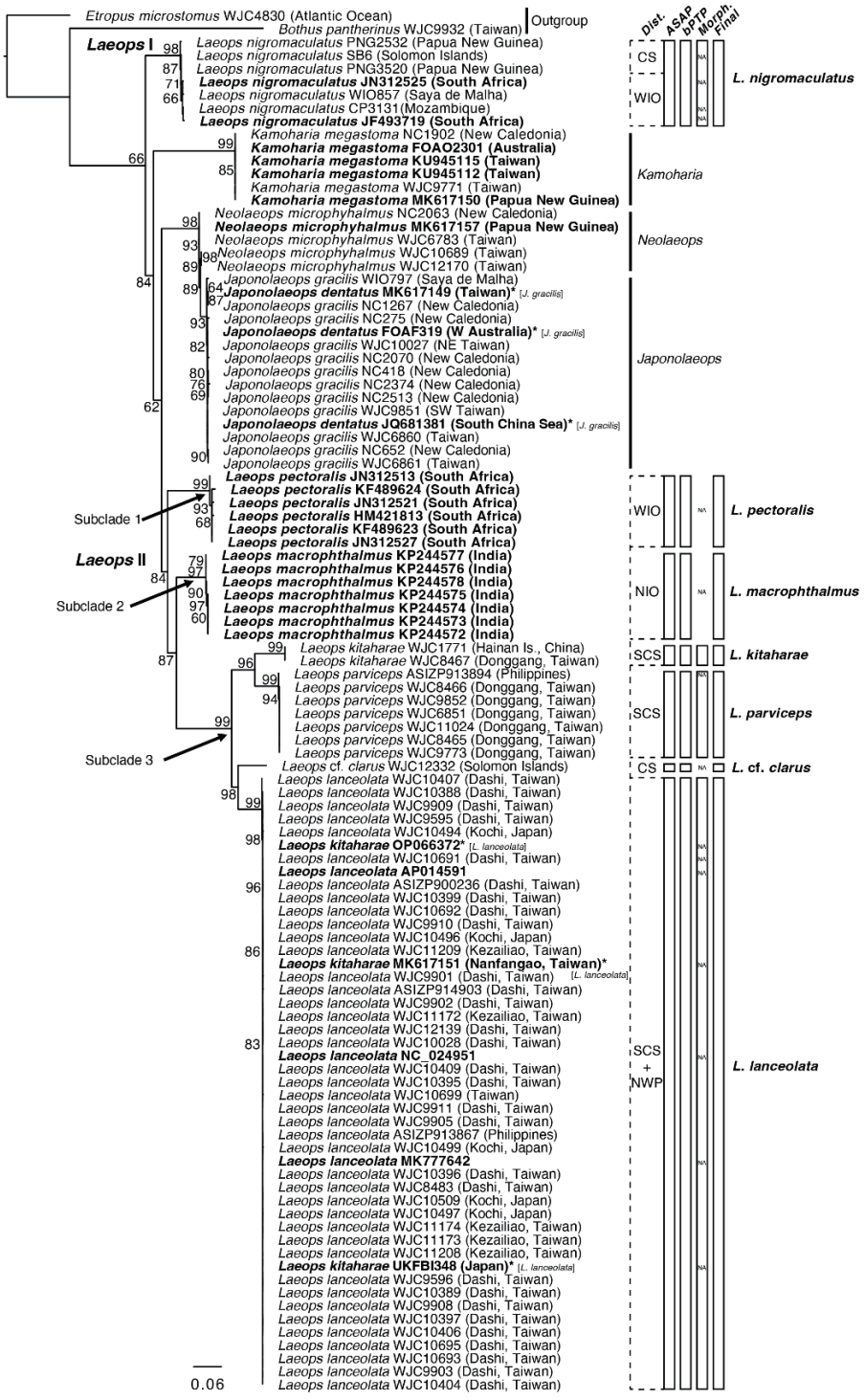

Figure 2. Maximum-likelihood (ML) phylogenetic tree based on *COI* gene sequences (636 bp. in length). Nodal supports are shown as ML bootstrap (BP) values from 1,000 BP replicates. Values below 60 are not shown. Branch lengths are proportional to the number of substitutions. Sequences retrieved from online databases are highlighted in bold. Erroneous sequences due to species misidentification are marked with an asterisk, followed by the proposed revised name in parentheses. Species delimitation results are represented by vertical bars on the right side of the tree. "NA" indicates that no voucher specimen was available for morphological examination. Abbreviations: CS, Coral Sea; NIO, North Indian Ocean; NWP, northwest Pacific; SCS, South China Sea; WIO, western Pacific.

In this study, two species delimitation methods (ASAP and bPTP) were used to test species validity among six out of nine currently recognized species and to explore *Laeops* species diversity in Taiwan. Results from both analyses are fully congruent, revealing seven Operational Taxonomic Units (OTUs) or putative species. Pairwise *K2P* distances at the *COI* locus show that genetic differences among the delimited OTUs range from 9.76 to 20.17%, while genetic differences within OTUs are less than 1% (*K2P* distance: 0.0000–0.0058) (Table 2). Further morphological examinations (see Taxonomy section below) confirm the validity of these delimited species based on *COI* sequences.

3.2 Taxonomy

***Laeops kitaharae* (Smith & Pope, 1906)**

English name: Kitahara's flounder; Taiwanese name: 北原氏左鮃
Figure 3; Tables 3–4
urn:lsid:zoobank.org:act:6DE1B0C2-4E9D-45EE-A97E-2067CE989220

Figure 3. Preserved specimen of *Laeops kitaharae* NTUM15820 (WJC8467), 116.8 mm SL, Taiwan. (A) ocular side; (B) blind side; (C) radiograph. Scale bar = 1 cm.

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Lambdopsetta kitaharae Smith and Pope, 1906: 496, Figure 12 (type locality: Kagoshima, Kyushu, Japan; holotype: USNM55612; original description with illustration of holotype).

Laeops kitaharae: Hubbs, 1915:460 (transferred to genus *Laeops* with brief description); Norman, 1934:258 (brief description with illustration); Amaoka, 1969:144 (in part) (detailed description with illustration); Amaoka, 1972:154 (description of larval stage); Shen, 1983:31 (in part) (detailed description with photograph); Amaoka in Masuda et al., 1984:350 (in part) (description with colored photo); Fukui and Ozawa, 1990:127 (description of larval stage); Shen, 1993:570 (in part) (brief description with colored photo); Lindberg & Fedorov, 1993:60 (in part) (detailed description with illustration); Evseenko, 1996:694 (example of outward intestinal coil of juvenile); Nakabo, 2002:1370 (in part) (brief description in key with illustration); Nakabo, 2013:1674 (in part) (brief description in key with illustration); Choi et al., 2003:429, 680 (in part) (description with colored photo); Kim et al., 2005:471 (in part) (brief description with colored photo); Ho et al., 2009:11 (listed in catalogued specimens); Ohashi and Motomura, 2011:93 (in part) (detailed description with colored photos); Shen and Wu, 2011:752 (brief description, with photo of *P. glossa*); Amaoka, 2016:123 (in part) (detailed description with colored photos); Voronina et al., 2016:391 (brief description with colored photo); Kimura et al., 2018:294 (brief description with colored photo); Amaoka in Koeda and Ho, 2019b:1239 (brief description with colored photo); Amaoka and Ho, 2019:194 (description with colored photos); Kim et al., 2020:193 (in part) (brief description with colored photo); Amaoka in Psomadakis et al., 2019a:591 (in part) (brief description with illustration).

Laeops paviceps (not of Günther): Li and Wang, 1995:176 (in part) (detailed description with illustration); Voronina et al., 2020:819 (junior synonym of *L. parviceps*).

Specimens examined.

Taiwanese specimen. One specimen: NTUM15820 (WJC8467), 116.8 mm SL, Donggang, Taiwan, 5 Sep. 2018.

Comparative specimens. Two specimens: CAS53068, 89.0 mm SL, 15°41'N, 108°42'E, 46 m, Vietnam, 27 Feb. 1960; NTUM15794 (WJC1771), 124.4 mm SL, Hainan Island, China, 26 Dec. 2010.

Radiograph. 1 specimen: USNM55612, holotype, 115.00 mm SL, Kagoshima, Kyushu, Japan

Diagnosis. D 100–103; A 78–83; P 12–14; C III+11+III=17; LLs 88–100; GR 1–2+5–6; vert. 11+36–38=47–49.

Description. Body elongated and strongly compressed, with greatest depth at anterior 1/4 part of body (BD: 34.0–36.2% SL). Head small, HL less than 1/2 of body depth (15.6–19.7% SL); upper profile pointed, with notch at the anterior part of upper eye. Eyes small: upper eye close to dorsal margin of head, its diameter greater than upper-jaw length (5.4–6.2% SL); lower eye 5.8–6.5% SL. Interorbital width narrow with bony ridge. Mouth small: UJL (O) 3.4–3.7% SL; UJL (B) 3.2–3.8% SL; LJL (O) 5.5–6.4% SL; and LJL (B) 5.4–7.0% SL. Teeth in narrow bands on blind side, absent on both jaws of ocular side. Gill rakers 1–4 on upper limb, very small; 5–8 on lower limb small and pointed. Snout short, snout length about 1/3 of eye diameter (1.6–2.1% SL).

Scales small and cycloid on both sides. Dorsal- and anal-fin rays unbranched, fin membranes without perforation; first dorsal-fin ray originates on blind side, above posterior nostril; first two dorsal-fin rays detached from remaining fin rays. Pectoral fin short on both sides; ocular-side pectoral fin shorter than HL, its length about 2/3 of HL (68.6–73.1% HL); blind-side pectoral fin very short, its length about half of HL (53.8–58.9% HL). Caudal fin round and slender; three unbranched soft rays on upper and lower lobes; 11 unbranched fin rays in the middle. Caudal peduncle narrow, its depth 6.0–6.6% SL.

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Table 2. Pairwise genetic distances based on the *K2P* method at the *COI* locus for *Laeops* species examined in this study. Values in the lower-left portion of the table represent interspecific distances, while values in the upper-right represent variances estimated by the bootstrap method (1,000 reps.).

	Species	1	2	3	4	5	6	7	Intraspecific
1	*L.* cf. *clarus*		0.0138	0.0167	0.0194	0.0205	0.0159	0.0193	N/A
2	*L. lanceolata*	0.0976		0.0169	0.0201	0.0219	0.0158	0.0187	0.0007
3	*L. kitaharae*	0.1401	0.1307		0.0193	0.0203	0.0141	0.0186	0.0000
4	*L. macrophthalmus*	0.1810	0.1824	0.1723		0.0167	0.0189	0.0152	0.0026
5	*L. nigromaculatus*	0.1936	0.2017	0.1920	0.1470		0.0206	0.0167	0.0045
6	*L. parviceps*	0.1293	0.1302	0.0962	0.1744	0.2012		0.0191	0.0005
7	*L. pectoralis*	0.1809	0.1749	0.1662	0.1233	0.1491	0.1754		0.0058

Table 3. Morphometric and meristic counts of *Laeops kitaharae* and *L. parviceps*. Abbreviations: V, data of type specimenstaken from Voronina et al. (2020); P, data from the present study; n, number of examined specimens.

Characters	*L. kitaharae*				*L. parviceps*				
	Japan V	Taiwan (Donggang) P	Hainan Is. P	Vietnam P	Japan V	Taiwan (Donggang) P	Philippines P	*L. tungkongensis* (Donggang) P	*L. tungkongensis* (Donggang) P
	Holotype	n=1	n=1	n=1	Lectotype	n=6	n=1	Lectotype	Paralectotype n=3
Standard length, mm	115.1	116.8	124.4	89.0	120.1	83.8–131.9	112.0	130.7	129.2–135.5
	As percentage of standard length								
Head length	17.1	15.6	15.8	19.7	19.8	15.6–16.6	19.4	15.3	13.9–15.0
Head depth	–	24.6	20.2	23.2	–	24.2–26.5	27.9	24.6	24.8–24.9
Body depth	34.6	36.2	34.9	34.0	36.6	35.6–39.0	30.1	31.5	31.3–32.2
Snout length	2.1	1.7	1.6	2.1	3.4	2.2–2.7	2.8	2.3	2.2–2.8
Upper-eye diameter	6.2	5.6	5.7	5.4	6.3	5.6–6.4	6	5.8	5.8–5.9
Lower-eye diameter	6.5	6.5	6.5	5.8	6.3	6.1–7.2	6.4	6.1	5.9–6.1
Upper jaw length (O)	3.7	3.4	3.5	3.7	4.3	3.5–4.0	4.2	4	3.7–4.3
Upper jaw length (B)	3.8	3.2	3.3	3.4	4.1	3.5–3.8	3.8	3.6	3.5–4.0
Lower jaw length (O)	6.4	5.5	5.7	6.4	7.2	6.0–7.4	7.1	6.1	6.3–6.4
Lower jaw length (B)	6.6	5.4	5.7	7.0	6.7	5.8–7.5	6.1	5.8	6.0–6.1
Caudal peduncle depth	6.0	6.5	6.5	6.6	6.4	5.7–6.8	5.1	6.5	6.6–6.7
Pectoral-fin length (O)	12.4	10.7	11.5	11.8	–	9.3–11.0	9.1	10.2	8.8–9.6
Pectoral-fin length (B)	5.4	8.4	9.3	7.6	8	6.6–7.7	–	7.8	7.2–7.9
Pelvic-fin length (O)	8.8	8.3	–	9.3	7.7	6.3–8.4	6.3	–	–
Pelvic-fin length (B)	7.4	8.1	–	7.9	7.8	5.6–8.0	6.4	–	–
Pelvic-fin base (O)	6.4	6.4	6.9	6.5	6.7	6.2–7.2	6.7	6.4	6.2–6.7
Pelvic-fin base (B)	2.3	2.8	3.0	2.6	2.6	3.2–3.8	3.0	2.9	2.9–3.2
Longest dorsal-fin ray	11.4	11.1	10.3	11.4	11.1	9.9–12.1	8.7	–	–
Longest anal-fin ray	11.8	10.5	9.2	9.1	10.2	9.4–11.8	8.3	–	–
Middle caudal-fin ray	13.4	–	–	16.8	18.4	14.2–17.8	16.7	–	–
	Counts								
Dorsal-fin rays	103	101	101	100	104	106–109	105	105	–
Anal-fin rays	82	79	80	78	86	85–90	85	85	–
Pectoral-fin rays (O)	12	13	14	13	13	12–14	13	12	12–13
Pectoral-fin rays (B)	10	11	12	11	12	10–12	12	10	10–11
Caudal-fin rays	III+11+III	III+11+III	III+11+III	(17)	(17)	III+10–12+III	(17)	III+11+III	III+9–10+III
Scales in lateral line	100	88	–	96	93	90–93	93	94	–
Gill rakers	1+5–6	2+6	1+6	4+8	5+9	1–2+6–7	7+8	4+8	1–4+7–8
Vertebrae	11+37	11+38	11+37	11+36	10+38	11+39–40	11+37	11+40	11+39

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Table 4. Frequency distribution of dorsal- and anal-fin rays, lateral-line scales, vertebrae, and caudal-fin rays in five *Laeops* species from western Pacific. Bolded values indicate data from type specimens. Abbreviation: n, number of examined specimens. Meristic counts of the type specimens presented in this table are based on re-examinations conducted in this study, except for the lateral-line scale counts.

	Dorsal-fin rays																						
	n	**100**	**101**	**102**	**103**	**104**	**105**	**106**	**107**	**108**	**109**	**110**	**111**	**112**	**113**	**114**							
L. clarus	3		1	1	**1**																		
L. kitaharae	4	1	2		**1**																		
L. lanceolata	24									5	9	**7**	2			1							
L. parviceps	8						2	2	**1**	2	1												
L. tungkongensis	1						**1**																
	Anal-fin rays																						
	n	**78**	**79**	**80**	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**	**91**	**92**	**93**						
L. clarus	3							**2**	1														
L. kitaharae	4	1	1	1			**1**																
L. lanceolata	24										8	9	**4**	2			1						
L. parviceps	8								2	**1**	3		1	1									
L. tungkongensis	1								**1**														
	Lateral-line scales																						
	n	**88**	**89**	**90**	**91**	**92**	**93**	**94**	**95**	**96**	**97**	**98**	**99**	**100**	**101**	**102**			**103**	**104**			
L. clarus	2										**2**												
L. kitaharae	3	1								1				1									
L. lanceolata	23										4	6	2	6	1	1			1	2			
L. parviceps	6			1	1	1	**3**																
L. tungkongensis	1							**1**															
	Vertebrae (precaudal+caudal)												**Caudal-fin rays**										
	n	**11**	**12**	**+**	**36**	**37**	**38**	**39**	**40**	**41**			**n**	**II**	**III**	**+**	**9**	**10**	**11**	**12**	**+**	**II**	**III**
L. clarus	3	**3**						1	**2**				2		2			2				2	
L. kitaharae	4	**4**			1	**2**	1						3		3				3				3
L. lanceolata	28	**25**	3					3	**12**	13			23		23			1	18	4			23
L. parviceps	6	**6**				1	**1**	3	1				5		5			2	1	2			5
L. tungkongensis	4	**4**						3	**1**				3		**3**		1	1	**1**				**3**

Distribution. Western Pacific: Japan (type locality), Hainan Island (present study), Taiwan (present study), and Vietnam (present study) (Figure 1).

Remarks. *Laeops kitaharae* was synonymized with *Laeops parviceps* by Voronina et al. (2020) based on morphometric counts, measurements of the holotype, and dorsal head profile morphology. The head profiles of *L. kitaharae* and *L. parviceps* are similar, both being pointed with a notch present. However, morphological examinations in this study, as well as by Voronina et al. (2020) (on type specimens), reveal that *L. kitaharae* differs from *L. parviceps* in several key characters: shorter snout length (1.6–2.1 [2.1% SL in holotype] vs. 2.2–3.4% SL [3.4% SL in lectotype]); lower numbers of dorsal-fin rays (100–103 [103 in holotype] vs. 105–109 [107 in lectotype]); and fewer anal-fin rays (78–83 [83 in holotype] vs. 85–90 [87 in lectotype]). Given these distinct morphological differences and genetic distinction (Figure 2 and Tables 2, 3–4), we herein resurrect *L. kitaharae* as a valid species and confirm its presence in Taiwanese waters.

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***Laeops lanceolata* Franz, 1910**

New standard English name: Lancet flounder; Taiwanese name: 矛狀左鮃
Figure 4; Tables 4–5

Laeops lanceolata Franz, 1910:62 (type locality: Fukuura and Dzushi, Japan; syntype: BMNH1931.11.16.2; original description with illustration).

Laeops lanceolata: Jordan and Hubbs, 1925:295 (in part) (brief description); Norman, 1934:259 (in part) (brief description with an illustration); Kuroda, 1962:3 (provided morphometrics); Chen and Weng, 1965:68 (description with an illustration); Li and Wang, 1995:177 (detailed description with an illustration); Voronina et al., 2016:391 (in part) (diagnosis; provided morphometrics with colored photo); Voronina et al., 2020:810 (detailed description with colored photos).

Laeops kitaharae (not of Smith & Pope): Amaoka, 1969:144 (in part) (morphometrics overlapping with *L. lanceolata*); Shen, 1983:31 (in part) (morphometrics overlapping with *L. lanceolata*); Amaoka in Masuda et al., 1984: 350 (in part) (morphometrics overlapping with *L. lanceolata*); Matsuura in Okamura, 1985:617, 738 (detailed description with colored photo); Shen, 1993:570 (in part) (morphometrics overlapping with *L. lanceolata*); Nakabo, 2002:1370 (in part) (morphometrics overlapping with *L. lanceolata*); Nakabo, 2013:1674 (in part) (morphometrics overlapping with *L. lanceolata*); Choi et al., 2003:429, 680 (in part) (morphometrics overlapping with *L. lanceolata*); Kim et al., 2005:471 (in part) (morphometrics overlapping with *L. lanceolata*); Ohashi and Motomura, 2011:93 (in part) (morphometrics overlapping with *L. lanceolata*); Amaoka, 2016:123 (in part) (morphometrics overlapping with *L. lanceolata*); Voronina et al., 2016:391 (in part) (morphometrics overlapping with *L. lanceolata*).

Laeops parviceps (not of Günther): Chen and Weng, 1965:62 (morphometrics overlapping with *L. lanceolata*).

Laeops variegata Franz, 1910:63 (original description); Hubbs, 1915:460; Norman, 1934:260 (description with illustration); Chen and Weng, 1965:69 (description with illustration).

Laeoptichthys fragilis: Hubbs, 1915:460 (original description); Norman, 1934:259 (description with illustration).

Specimens examined.

Taiwanese specimens. 18 specimens: NTUM17660 [three specimens] (WJC9908, WJC9909, WJC9914), 110.2–123.3 mm SL, Dashi, Yilan, Taiwan, 26 Jun. 2020; NTUM17658 [three specimens] (WJC9902–9903, WJC9905), 101.6–119.2 mm SL, Dashi, Yilan, Taiwan, 25 Jul 2020; NTUM17663 [two specimens] (WJC10389, WJC10403), 110.0–120.5 mm SL, Dashi, Yilan, Taiwan, 13 Aug 2021; NTUM17669 [five specimens] (WJC11232, WJC11234–11237), 118.1–125.7 mm SL, Dashi, Yilan, Taiwan, 22 Dec 2021; NTUM17667 (WJC11208), 144.1 mm SL, Kezailiao, Kaohsiung, Taiwan, 4 Jan. 2022; NTUM17668 [four specimens] (WJC11171–11174), 114.7–134.1 mm SL, Kezailiao, Kaohsiung, Taiwan, 5 Jan. 2022.

Comparative specimens. Seven specimens: NTUM17664 (WJC10494–10500), 123.1–139.4 mm SL, Saga fishing port, Kochi, Japan, 21 Apr. 2021.

Photographs and radiograph. One specimen: BMNH1931.11.16.2, syntype, 73.13 mm SL, Japan.

Diagnosis. D 108–114; A 87–93; P 13–16; C III+10–12+III=16–18; LLs 97–104; GR 1–4+6–9; vert. 11–12+39–41=50–53.

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Table 5. Morphometric measurements and meristic counts of *Laeops clarus* and *L. lanceolata*. Abbreviations: V, data of type specimens taken from Voronina et al. (2020); P, data from the present study; n, number of examined specimens.

Characters	*L. clarus*		*L. lanceolata*			
	Philippines V	Philippines P	Japan V	Japan P	Taiwan (Dashi, Nanfangao) P	Taiwan (Kezailiao) P
	Holotype	n=2	Lectotype	n=7	n=13	n=5
Standard length, mm	126.6	114.0–116.0	73.8	123.1–139.4	110.17–125.71	127.70–144.11
	As percentage of standard length					
Head length	17.6	14.1–16.3	19.5	14.1–15.0	14.3–15.7	13.6–15.3
Head depth	–	20.6–21.8	–	28.0–30.1	24.5–31.0	23.7–26.3
Body depth	27.0	25.8–28.3	32.5	36.9–40.6	32.3–38.5	31.2–35.3
Snout length	2.0	2.1–2.3	3.4	1.1–1.4	1.2–1.6	1.1–1.3
Upper-eye diameter	5.4	4.0–5.9	6.5	4.7–5.4	5.1–6.3	4.9–5.4
Lower-eye diameter	5.8	4.0–5.8	6.5	5.2–5.5	5.5–6.6	5.2–6.1
Upper jaw length (O)	4.2	3.6–4.0	4.6	2.8–3.6	3.2–3.8	3.2–3.5
Upper jaw length (B)	4.2	3.9–4.2	4.9	2.6–3.3	2.9–3.5	2.9–3.4
Lower jaw length (O)	6.6	5.1–7.4	7.6	5.9–6.5	6.0–7.4	5.9–6.2
Lower jaw length (B)	6.6	5.5–8.1	7.6	5.7–6.4	5.8–7.2	5.5–6.1
Caudal peduncle depth	4.9	4.3–4.6	6.6	5.7–6.5	5.4–6.5	6.3–6.7
Pectoral-fin length (O)	10.5	6.7–9.4	9.6	9.6–10.2	9.1–11.5	–
Pectoral-fin length (B)	9.9	6.8–8.5	–	7.0–7.9	6.1–8.8	7.1–8.1
Pelvic-fin length (O)	6.1	–	9.2	7.3–8.4	7.1–8.0	6.2–7.2
Pelvic-fin length (B)	4.0	–	8	6.8–7.4	5.8–7.9	5.7–6.3
Pelvic-fin base (O)	6.5	6.0–6.6	6.8	6.3–7.0	6.3–7.7	6.3–7.6
Pelvic-fin base (B)	3.1	2.9–3.2	2.6	2.9–3.6	2.6–3.5	2.5–3.0
Longest dorsal-fin ray	10.4	7.9–8.9	12.1	9.9–10.4	8.7–10.8	9.1–9.9
Longest anal-fin ray	10.4	8.2–9.3	12.1	9.3–10.2	8.2–10.5	8.8–9.3
Middle caudal-fin ray	16.8	16.1–16.4	–	13.4–15.2	14.9–18.4	13.0–14.6
	Counts					
Dorsal-fin rays	103	101–102	108	108–110	108–114	108–110
Anal-fin rays	84	84–85	81	87–88	87–93	87–90
Pectoral-fin rays (O)	10	13–15	14	14–16	13–16	13–15
Pectoral-fin rays (B)	10	13–14	13	11–13	11–13	12–13
Caudal-fin rays	(15)	III+10+II	(17)	III+10–11+III	III+11–12+III	III+11–12+III
Scales in lateral line	97	113	–	97–101	97–104	97–104
Gill rakers	0+10	5–6+7	4+7	1–2+6–9	0–4+6–8	0–2+6–7
Vertebrae	11+40	11+39–40	11+40	11–12+39–41	11–12+39–41	11+40–41

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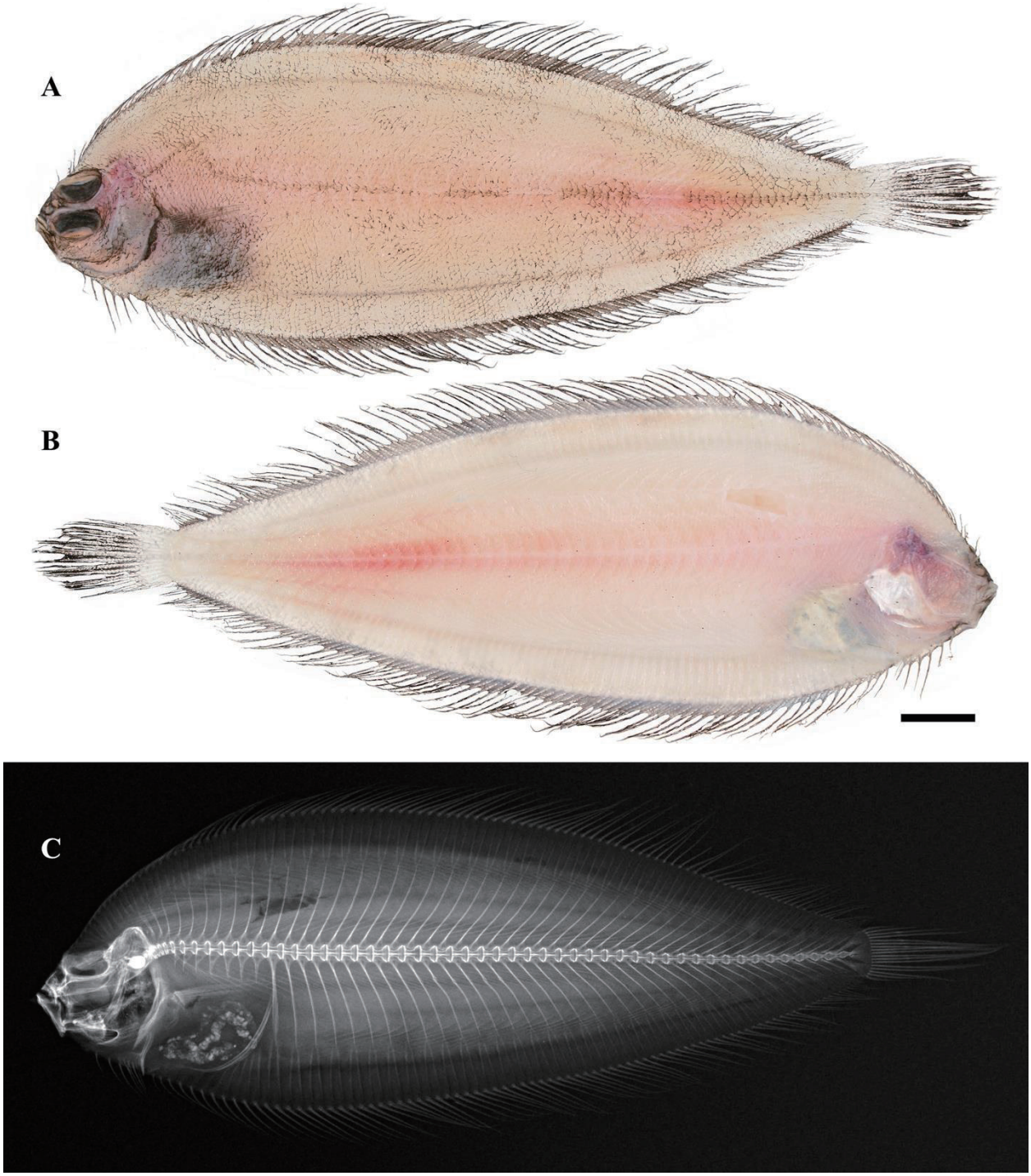

Figure 4. Fresh specimen of *Laeops lanceolata* NTUM17663 (WJC10389), 110.0 mm SL, Taiwan. (A) ocular side; (B) blind side; (C) radiograph. Scale bar = 1 cm.

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Description. Body ovate and strongly compressed, with greatest depth at anterior 1/4 of body (BD: 31.2–40.6% SL). Head small, HL less than 1/2 of body depth (13.6–19.5% SL); upper profile rounded without notch at anterior of upper eye. Eyes small: upper eye close to dorsal margin of head, its diameter greater than upper-jaw length (4.7–6.5% SL); lower eye 5.2–6.6% SL. Interorbital width narrow with bony ridge. Mouth small: UJL (O) 2.8–3.8% SL; UJL (B) 2.6–3.5% SL; LJL (O) 5.9–7.4% SL; and LJL (B) 5.5–7.2% SL. Teeth in one to two rows on blind side, absence on both jaws of ocular side. Gill rakers 0–4 on upper limb, very small; 6–9 on lower limb small and pointed. Snout very short, with length about 1/4 of upper eye diameter (1.1–1.6% SL).

Scales small and cycloid on both sides. Dorsal- and anal-fin rays unbranched, fin membranes without perforation; first dorsal-fin ray originates on blind side above posterior of nostril; first two dorsal-fin rays detached from remaining fin rays. Pectoral fin short on both sides; ocular-side pectoral fin shorter than HL, its length about 2/3 of HL (59.8–75.9% HL); blind-side pectoral fin very short, its length about half of HL (45.2–59.2% HL). Caudal fin round and slender, its length about equal to HL (93.1–105.3% HL); three unbranched soft rays on upper and lower lobes; 10–12 unbranched fin rays in the middle.

Distribution. Western Pacific Ocean: Japan (type locality and present study), Philippines (present study), Taiwan (present study), Vietnam (Voronina et al., 2016) (Figure 1).

Remarks. *Laeops lanceolata* resembles *L. clarus* in having a rounded snout and a head profile without a notch, but differs in several meristic counts: dorsal-fin rays (108–114 vs. 101–103 in *L. clarus*); anal-fin rays (87–93 vs. 84–85 in *L. clarus*); and caudal-fin formula (III+10–12+III=16–18 vs. III+10+II=15 in *L. clarus*). However, re-examination of the lectotype using a radiograph reveals a different number of anal-fin rays compared to Voronina et al. (2020) (89 in the present study vs. 81 in Voronina et al., 2020). Besides, *L. lanceolata* differs from other western Pacific congeners in having a shorter snout length (1.1–1.6% vs. 1.6–2.8 in other WP congeners); dorsal-fin rays (108–114 vs. 100–109 in other WP congeners); and lateral line scales (97–104 vs. 88–97 in other WP congeners).

***Laeops parviceps* Günther, 1880**

English name: Smallhead flounder; Taiwanese name: 小頭左鮃
Figures 5–6; Tables 3–4

Laeops parviceps Günther, 1880:29 (type locality: Arafura Sea, Australia; lectotype: BMNH1879.5.14.98; original description with illustration).

Laeops parviceps: Norman, 1934:256 (description based on type with illustration); Chen and Weng, 1965:62 (description with illustration; not this species); Shen, 1993:571 (in part) (description with color photo); Hensley and Amaoka in Carpenter and Niem, 2001:3814 (brief description with illustration and distribution map); Hoese and Bray, 2006:1821 (brief description); Shen and Wu, 2011:753 (brief description with illustration); Voronina et al., 2016:391 (diagnosis; morphometrics with color photo); Voronina et al., 2020:817 (detailed description with color photos); Ragul et al., 2024:291 (description with color photo).

Laeops tungkongensis Chen and Weng, 1965:63 (type locality: Taiwan; original description with illustration).

Laeops kitaharae (not of Smith & Pope): Chen and Weng, 1965:67 (description with illustration, not this species); Shen 1993:570 (in part) (morphometrics overlapping with *L. parviceps*); Voronina et al., 2016:391 (in part) (morphometrics overlapping with *L. parviceps*).

Laeops nigrescens (not of Lloyd): Chen and Weng, 1965:64 (description with illustration).

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Specimens examined.

Taiwanese specimens. *Laeops parviceps* (Six specimens): NTUM15809 (WJC6851), 83.8 mm SL, Donggang, Taiwan, 27 Dec. 2017; NTUM15820 [two specimens] (WJC8465–8466), 104.75–107.13 mm SL, Donggang, Taiwan, 5 Sep. 2018; NTUM17655 [two specimens] (WJC9773, WJC9852), 109.6–119.3 mm SL, Donggang, Taiwan, 24 May. 2020; NTUM17656 (WJC11024), 131.9 mm SL, Donggang, Taiwan, 7 Jan. 2022. *Laeops tungkongensis* (four specimens): NMMB–P5170 (formerly THUP 2301), lectotype, 130.7 mm SL, Donggang, Taiwan, 29 Mar. 1964; NMMB–P5170 (formerly THUP 2301), [three specimens], paralectotype, 129.2–135.5 mm SL, Donggang, Taiwan, 29 Mar. 1964.

Comparative specimens. One specimen: CAS33371, 112.0 mm SL, 13°34'N, 122°15'E, 128–143 m, Sandoval Point at Catanauan, Quezon, Philippines, 3 Nov. 1966.

Photographs and radiographs. Two specimens: BMNH1879.5.14.98, lectotype, 120.30 mm SL, Arafura Sea, Australia; ASIZP0068133 (ASIZP0913894), sta. CP2720, 14°27'N, 121°47'E, 300–301 m, Aurora, Philippines, 29 May 2007, AURORA 2007.

Diagnosis. D 105–109; A 85–90; P 12–14; C III+10–12+III=16–18; LLs 90–93; GR 1–7+6–8; Vert. 10–11+37–40=47–51.

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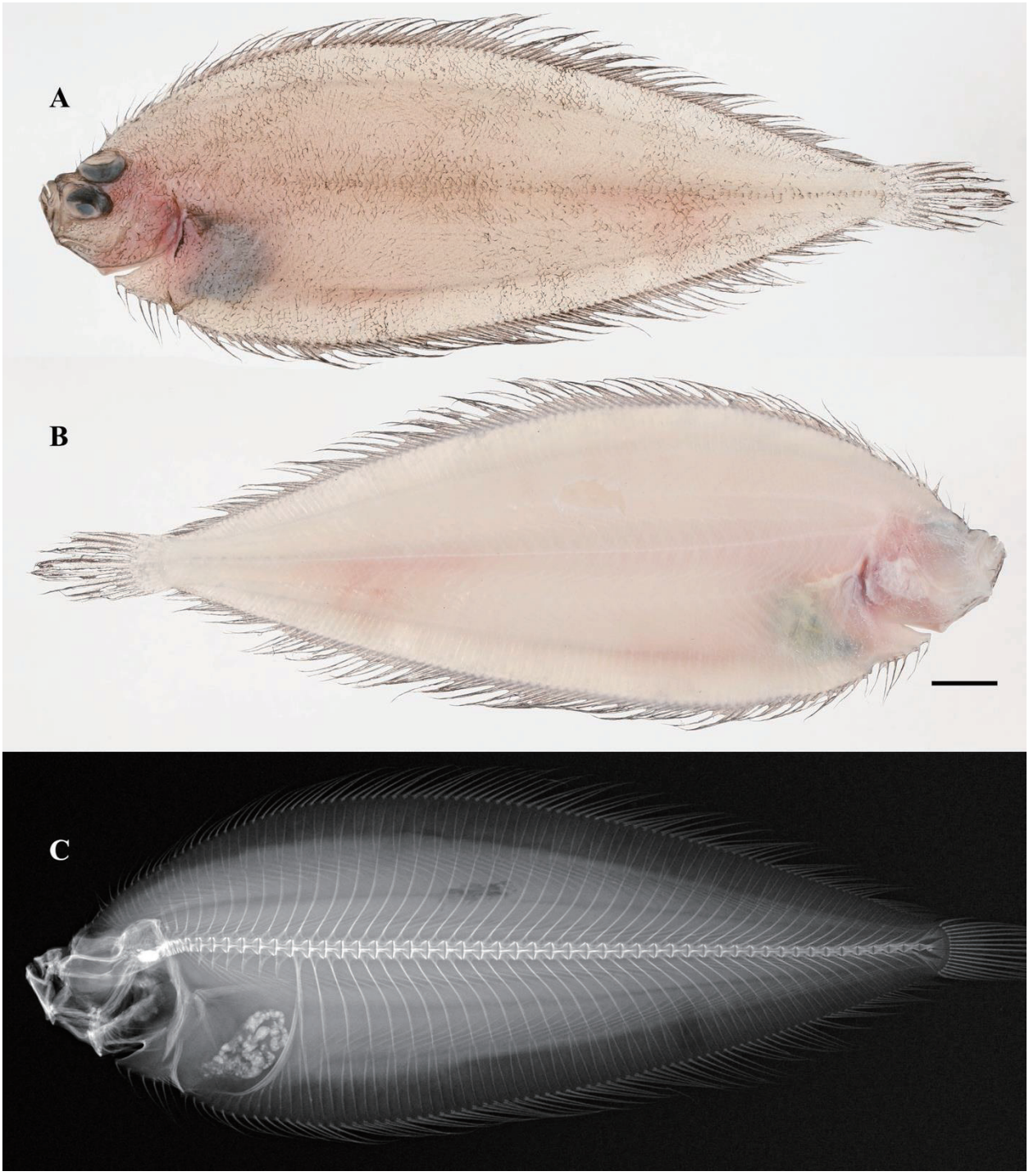

Figure 5. Fresh specimen photos of *Laeops parviceps* NTUM17656 (WJC11024), 131.9 mm SL, Taiwan. (A) ocular side; (B) blind side; (C) radiograph. Scale bar = 1 cm.

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Description. Body ovate and strongly compressed, with greatest depth at anterior 1/4 of body (BD: 30.1–39.0% SL). Head small, HL less than 1/2 of body depth (15.3–19.4% SL); upper profile pointed without notch at the anterior part of upper eye. Eyes small: upper eye close to dorsal margin of head, its diameter greater than upper-jaw length (5.6–6.4% SL); lower eye 6.1–7.2% SL. Interorbital width narrow with bony ridge. Mouth small: UJL (O) (4.3) 3.5–4.2% SL; UJL (B) (4.1) 3.5–3.8% SL; LJL (O) (7.2) 6.0–7.4% SL; and LJL (B) (6.7) 5.8–7.5% SL. Teeth in narrow band on blind side, absent on both jaws on ocular side. Gill rakers 1–7 on upper limb, very small; 6–8 on lower limb, small and pointed. Snout moderately long, snout length slightly less than half of upper eye diameter (2.2–2.8% SL).

Scales small, cycloid on both sides. Dorsal- and anal-fin rays unbranched, fin membranes without perforation; first dorsal-fin ray originates on blind side, above nostril posterior; first two dorsal-fin rays detached from remaining fin rays. Pectoral fin short on both sides; ocular-side pectoral fin shorter than HL, its length about 2/3 of HL (57.9–66.2% HL); blind-side pectoral fin very short, its length shorter than half of HL (41.2–46.6% HL). Caudal fin round and slender, its length about equal to HL (93.1–105.3% HL); three unbranched soft rays on upper and lower lobes; 10–12 unbranched fin rays in the middle.

Distribution. Western Pacific: Australia (type locality), Philippines (present study), South China Sea (Voronina et al., 2016), southwestern Taiwan (Donggang, present study) (Figure 1).

Remarks. *Laeops parviceps* was originally described on the basis of four specimens collected from the Arafura Sea, Australia. The morphometric data of the lectotype, as reported by Voronina et al. (2020), are consistent with those of the specimens from Taiwan and the Philippines examined in this study (Table 3). *Laeops parviceps* resembles *L. kitaharae*, but the two species can be differentiated by snout length and differences in the number of dorsal- and anal-fin rays (see Remarks of *L. kitaharae*).

3.3 Taxonomy and Species Diversity of *Laeops* in Taiwan

Previous taxonomic studies on the genus *Laeops* from Taiwan were primarily based on morphology, with few diagnostic characters available to distinguish among species. Members of the genus *Laeops* often exhibit overlapping meristic and morphometric traits, such as the number of dorsal- and anal-fin rays, body depth, tooth arrangement, and head shape. Voronina et al. (2020) introduced new diagnostic characters, including vertebrae counts and dorsal-fin pterygiophore length; however, these osteological characters can only be observed in radiographs or cleared and stained specimens, making them impractical for examination under certain circumstances. This study is the first to integrate both morphological and molecular evidence to clarify the taxonomic status of *Laeops* species in Taiwan. Our revision confirms the presence of three valid species—*L. kitaharae*, *L. lanceolata*, and *L. parviceps*—in Taiwan and updates their distribution records (Figure 1). Despite extensive sampling efforts, no specimens identified as *L. clarus* were found. Voronina et al. (2020) recorded *L. clarus* from Taiwan based on the type series of *L. tungkongensis*, which they synonymized with *L. clarus*. However, our study reveals that *L. tungkongensis* is not valid and should instead be considered a junior synonym of *L. parviceps*, which is the predominant *Laeops* species landed at Donggang fishing port in southwestern Taiwan.

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Chen and Weng (1965) described *Laeops tungkongensis* (Figure 6; Tables 3–4) as a new species from Donggang, based on four type specimens. Later, Amaoka and Ho (2019) proposed it as a junior synonym of *L. kitaharae*, noting that the diagnostic characters (body depth, head length, and other meristic and morphometric traits) used by Chen and Weng (1965) could not distinguish the two species. Voronina et al. (2020) later suggested that *L. tungkongensis* was a junior synonym of *L. clarus*, based on congruent meristic and morphometric characters. Our re-examination, however, shows that the type specimens of *L. tungkongensis* differ from those measured in *L. clarus* in having a deeper body depth (31.3–32.2 vs. 25.8–28.3% SL), more dorsal-fin rays (105 vs. 101–103), and a different caudal-fin formula (II+9–11+III=15–17 vs. III+10+II=15) (Tables 3–5). Additionally, *L. tungkongensis* shares morphological characteristics with *L. parviceps* (body depth and snout length) but differs from *L. kitaharae* in snout length and the number of dorsal- and anal-fin rays. Therefore, based on both morphological and molecular evidence (*COI* sequences from *Laeops* individuals sampled at the type locality of *L. tungkongensis*), *L. tungkongensis* is considered a synonym of *L. parviceps* in this study.

Laeops kitaharae was previously proposed as a junior synonym of *L. parviceps* by Voronina et al. (2020), and a single specimen was collected from Donggang in this study. However, both genetic and morphological evidence in this study reject this suggestion, confirming them as distinct species. Additionally, their sympatric distribution in southwestern Taiwan or across the northern South China Sea (Figure 1) supports their species delimitation, with potential evidence for reproductive isolation (Kekkonen & Hebert, 2014).

Laeops lanceolata was described by Franz (1910) based on syntypes collected from Fukuura and "Dzushi" (likely a misspelling of Zushi in several references), Japan. Nine of the ten syntypes were subsequently lost, and the lectotype was designated by Voronina et al. (2020) based on the sole remaining type specimen (BMNH1931.11.16.2). In this study, specimens from Tosa Bay, Japan (n=7), and Taiwan (n=18) were examined, their morphometric and meristic counts matching the lectotype. Moreover, geographic variation in morphology within *L. lanceolata* was observed, in which the body depth tended to increase with increasing latitude: southwestern Taiwan (n=5, BD: 31.2–35.3% SL); northeastern Taiwan (n=13, BD: 32.3–38.5% SL); and Japan (n=7, BD: 36.9–40.6% SL). Average pairwise genetic differences within WP *L. lanceolata* were less than 1% (*K2P* distance = 0.0007), which means there is high genetic homogeneity among individuals of *L. lanceolata* in the western Pacific Ocean (Japan, Taiwan, and the Philippines). Additionally, potentially misidentified sequences were found in online databases. Three *COI* sequences identified as *L. kitaharae* were nested within the *L. lanceolata* lineage and should be reclassified as *L. lanceolata* based on their phylogenetic position and the absence of significant genetic differentiation observed in this study: *L. kitaharae* (UKFBI348, Japan); *L. kitaharae* (OP066372); and *L. kitaharae* (MK617151, Taiwan).

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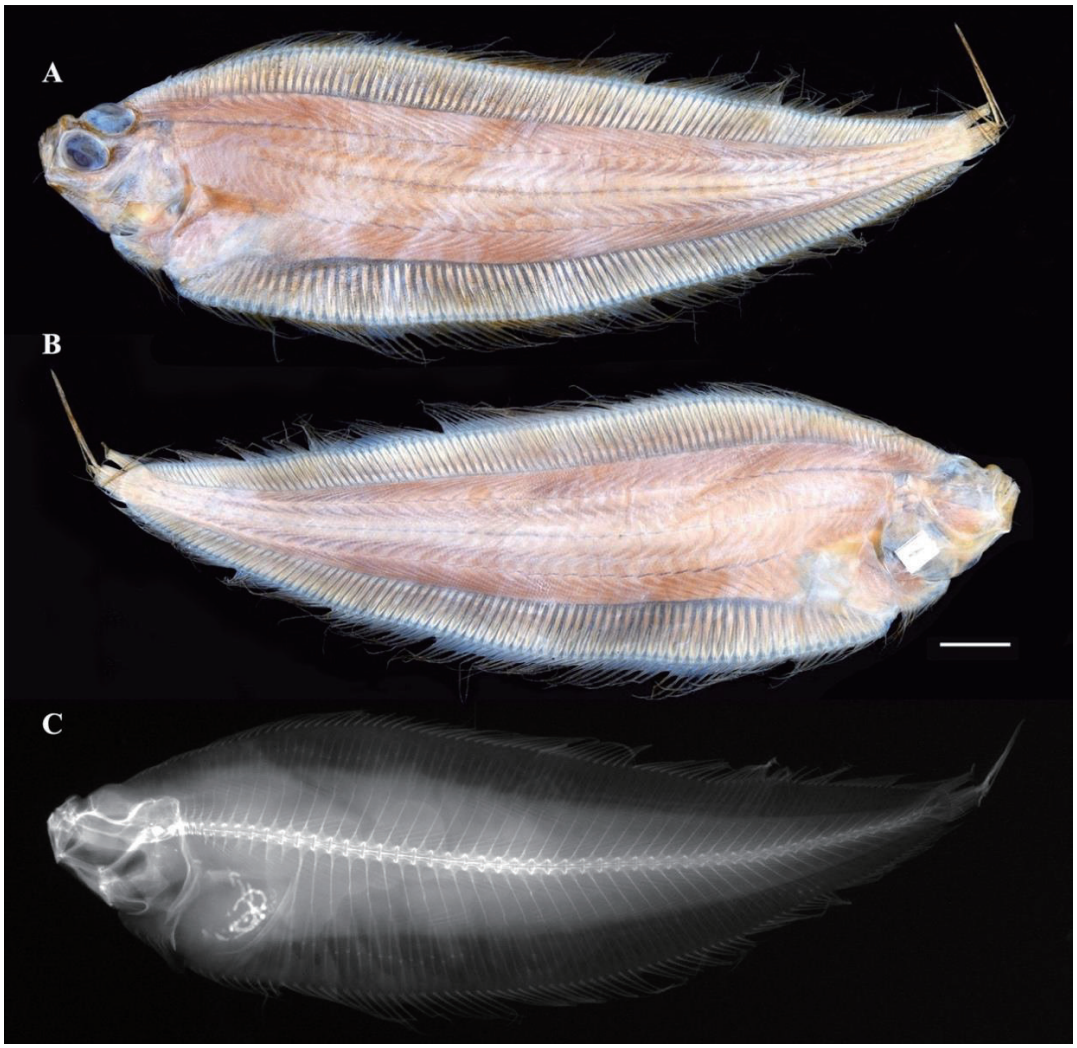

Figure 6. Preserved specimen photos of *Laeops tungkongensis* NMMB–P5170, lectotype, 130.7 mm SL, Taiwan. (A) ocular side; (B) blind side; (C) radiograph. Scale bar = 1 cm.

3.4 Notes on *Laeops clarus*, a Rare Species from the Western Pacific

The clear fin-base flounder, *Laeops clarus*, is a lesser-known species in the western Pacific, with few documented occurrences (Fowler, 1933; Hensley & Amaoka in Carpenter & Niem, 2001; Voronina et al., 2020). The record of *L. clarus* in Taiwan was made based on the type series of *L. tungkongensis*, which was a misidentification of *L. parviceps* (see above). *Laeops clarus* differs from its WP congeners by having a narrower body depth (25.8–28.3 vs. 30.1–40.6% SL in other WP congeners) and dorsal-fin pterigiophores longer than the neural spines of the first four caudal vertebrae (Figure 7 and Tables 4–5). The original description of *L. clarus* did not mention the number of soft caudal-fin rays in the holotype. In this study, a radiograph of the holotype (USNM93083) and two non-type specimens (CAS33792 and CAS34554) collected from the Philippines (type locality) were studied for comparison with Taiwanese congeners. The numbers of caudal-fin rays in the examined specimens were consistent with the total number of 15 caudal-fin rays: three unbranched fin rays on the upper lobe, 10 branched fin rays in the middle of the caudal-fin ray, and two unbranched fin rays on the lower lobe. Morphometric and meristic counts of the examined specimens are consistent with those of the holotype and non-type specimens in Voronina et al. (2020) (Tables 4–5). However, no tissue samples were available for molecular analysis from the voucher specimens.

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During the SALOMONBOA 3 expedition in the Solomon Islands, a single specimen of the genus *Laeops* was collected along with a tissue sample, WJC12332, sta. CP2828, 10°26'S, 161°58'E, 173–379 m, Solomon Islands, 20 Sep. 2009, SALOMONBOA 3 (Figure 1). Unfortunately, the voucher specimen was lost, and only a photograph was available for morphological examination. The body depth of the specimen measured from the photograph was 28.2% SL, and its transparent body matched the description of *L. clarus* (clear fin-base flounder). Therefore, the specimen collected from the Solomon Islands was primarily identified as *L. clarus*. However, to remain cautious, we tentatively assign it as cf. to its similar species. Despite this, molecular data show that *L.* cf. *clarus* (WJC12332) is a distinct species from the other three *Laeops* species in the West Pacific. The interspecific genetic diversity between *L.* cf. *clarus* and the other congeners ranges from 9.7–19.4% (Table 2).

Figure 7. Preserved specimen of *Laeops clarus* CAS33792, 114.0 mm SL, Philippines. (A) ocular side; (B) blind side; (C) Radiograph taken by J. Fong. Scale bar = 1 cm.

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3.5 Key to the Species of *Laeops* II

This identification key is modified from Voronina et al. (2020).

1A. Ocular-side pectoral fin long, its length > 21.5 % SL **2**

1B. Ocular-side pectoral fin short, its length < 13% SL **4**

2A. Ocular-side pectoral fin nearly twice as long as HL, upper jaw shorter than eye diameter ..... ***L. pectoralis***

2B. Pectoral fin of ocular side as long as or shorter than HL, upper jaw as long as eye diameter **3**

3A. HL 33.1–33.3% SL; ocular-side pectoral fin slightly shorter than HL; D 83–89; A 61–72; Vert. 10+30–32=40–42 ..... ***L. macrophthalmus***

3B. HL 22.6–23.3% SL; ocular-side pectoral fin as long as HL; dorsal-fin rays 93–101, anal-fin rays 72–81, vert. 10+35–37 ..... ***L. nigrescens***

4A. D ≤ 100; BD: 35.7–46.33% SL **5**

4B. D ≥ 100; BD: 25.8–36.23% SL **6**

5B. Upper profile without notch anterodorsal to upper margin of upper eye; D 92–100; A 73–81; LLs 79–93; vert. 11–12+34–36=45–48 ..... ***L. guentheri***

5B. Upper profile with notch anterodorsal to upper margin of upper eye; D 89–98; A 70–77; LLs 73–85; vert. 11+33–35=44–46 ..... ***L. natalensis***

6A. D 100–103; A 78–85 ..... **7**

6B. D 105–114; A 84–93 ..... **8**

7A. Body depth 25.8–28.3% SL; A 84–85; C 15 (III+10+II); dorsal-fin pterigiophores longer than neural spines of first four caudal vertebrae ..... ***L. clarus***

7B. Body depth 34.0–36.2% SL; A 78–82; C 17 (III+11+III); dorsal-fin pterigiophores shorter than neural spines of first four caudal vertebrae ..... ***L. kitaharae***

8A. D 108–114; LLs 97–104; snout length 1.1–1.6% SL ..... ***L. lanceolata***

8B. D 105–109; LLs 90–94; snout length 2.2–2.8% SL ..... ***L. parviceps***

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4 CONCLUSIONS

This is the first comprehensive study of *Laeops* species occurring in Taiwanese waters using an integrated taxonomic approach. By considering both morphological and molecular evidence, we confirm *L. kitaharae* as a valid and distinct species, separate from *L. parviceps.* We also synonymize *L. tungkongensis* with *L. parviceps*. Phylogenetic analysis reveals the paraphyletic status of the genus, with two distinct lineages. Three species of *Laeops*—*L. kitaharae, L. lanceolata,* and *L. parviceps*—are present in Taiwanese waters. This study highlights the effectiveness of integrative taxonomy in resolving complex taxonomic issues within the genera of Bothidae.

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Appendix

Supplementary Table 1. List of specimens used in molecular analyses, including sampling locations (with cruise station numbers if applicable) and GenBank or BOLD accession numbers. Sequences from the online database are highlighted in bold. Potential misidentifications are marked with asterisks. Cruise details can be referenced in BasExp, the TDSB expedition database (https://expeditions.mnhn.fr/).

Species name	Sample ID	Voucher ID	Sample location	GenBank/ Bold	Revised name
Laeops cf. clarus	WJC12332	N/A	Solomon Islands (CP2828)	PV131423	
Laeops kitaharae	WJC1771	NTUM15794	China (Hainan Island)	PV131424	
Laeops kitaharae	WJC8467	NTUM15820	Taiwan (Donggang)	PV131425	
*Laeops kitaharae**	KUIT 2506	KUI 27272	Japan	**UKFBI348**	*L.lanceolata*
*Laeops kitaharae**	WJC943	N/A	Taiwan (Nanfangao)	**MK617151**	*L.lanceolata*
*Laeops kitaharae**	N/A	N/A	N/A	**OP066372**	*L.lanceolata*
Laeops lanceolata	WJC8483	NTUM15826	Taiwan (Dashi)	PV131426	
Laeops lanceolata	WJC9595	NTUM17657	Taiwan (Dashi)	PV131427	
Laeops lanceolata	WJC9596	NTUM17657	Taiwan (Dashi)	PV131428	
Laeops lanceolata	WJC9901	NTUM17658	Taiwan (Dashi)	PV131429	
Laeops lanceolata	WJC9902	NTUM17658	Taiwan (Dashi)	PV131430	
Laeops lanceolata	WJC9903	NTUM17658	Taiwan (Dashi)	PV131431	
Laeops lanceolata	WJC9905	NTUM17658	Taiwan (Dashi)	PV131432	
Laeops lanceolata	WJC9908	NTUM17660	Taiwan (Dashi)	PV131433	
Laeops lanceolata	WJC9909	NTUM17660	Taiwan (Dashi)	PV131434	
Laeops lanceolata	WJC9910	NTUM17660	Taiwan (Dashi)	PV131435	
Laeops lanceolata	WJC9911	NTUM17660	Taiwan (Dashi)	PV131436	
Laeops lanceolata	WJC10028	NTUM17661	Taiwan (Dashi)	PV131437	
Laeops lanceolata	WJC10388	NTUM17662	Taiwan (Dashi)	PV131438	
Laeops lanceolata	WJC10389	NTUM17663	Taiwan (Dashi)	PV131439	
Laeops lanceolata	WJC10395	NTUM17663	Taiwan (Dashi)	PV131440	
Laeops lanceolata	WJC10396	NTUM17663	Taiwan (Dashi)	PV131441	
Laeops lanceolata	WJC10397	NTUM17663	Taiwan (Dashi)	PV131442	
Laeops lanceolata	WJC10399	NTUM17663	Taiwan (Dashi)	PV131443	
Laeops lanceolata	WJC10404	NTUM17663	Taiwan (Dashi)	PV131444	

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Species name	Sample ID	Voucher ID	Sample location	GenBank/ Bold	Revised name
Laeops lanceolata	WJC10406	NTUM17663	Taiwan (Dashi)	PV131445	
Laeops lanceolata	WJC10407	NTUM17663	Taiwan (Dashi)	PV131446	
Laeops lanceolata	WJC10409	NTUM17663	Taiwan (Dashi)	PV131447	
Laeops lanceolata	WJC10494	NTUM17664	Japan (Kochi)	PV131448	
Laeops lanceolata	WJC10496	NTUM17664	Japan (Kochi)	PV131449	
Laeops lanceolata	WJC10497	NTUM17664	Japan (Kochi)	PV131450	
Laeops lanceolata	WJC10499	NTUM17664	Japan (Kochi)	PV131451	
Laeops lanceolata	WJC10509	NTUM17664	Japan (Kochi)	PV131452	
Laeops lanceolata	WJC10691	NTUM17665	Taiwan (Dashi)	PV131453	
Laeops lanceolata	WJC10692	NTUM17665	Taiwan (Dashi)	PV131454	
Laeops lanceolata	WJC10693	NTUM17665	Taiwan (Dashi)	PV131455	
Laeops lanceolata	WJC10695	NTUM17663	Taiwan (Dashi)	PV131456	
Laeops lanceolata	WJC10699	NTUM17666	Taiwan (off Hsinchu)	PV131457	
Laeops lanceolata	WJC11172	NTUM17668	Taiwan (Kezailiao)	PV131458	
Laeops lanceolata	WJC11173	NTUM17668	Taiwan (Kezailiao)	PV131459	
Laeops lanceolata	WJC11174	NTUM17668	Taiwan (Kezailiao)	PV131460	
Laeops lanceolata	WJC11208	NTUM17667	Taiwan (Kezailiao)	PV131461	
Laeops lanceolata	WJC11209	NTUM17667	Taiwan (Kezailiao)	PV131462	
Laeops lanceolata	WJC12139	NTUM17849	Taiwan (Dashi)	PV131463	
Laeops lanceolata	ASIZP0900236	ASIZP0061852	Taiwan (off Hsinchu)	PV131464	
Laeops lanceolata	ASIZP0913867	ASIZP0068106	Philippines (CP2712)	PV131465	
Laeops lanceolata	ASIZP0914903	N/A	Taiwan (CC4903)	PV131466	
Laeops lanceolata	N/A	N/A	N/A	**AP014591**	
Laeops lanceolata	N/A	N/A	N/A	**NC_024951**	
Laeops lanceolata	N/A	N/A	N/A	**OP066372**	
Laeops macrophthalmus	PK52	NBFGR:CHN:PK52	India	**KP244572**	
Laeops macrophthalmus	KN22	NBFGR:CHN:KN22	India	**KP244573**	
Laeops macrophthalmus	KN23	NBFGR:CHN:KN23	India	**KP244574**	
Laeops macrophthalmus	KN24	NBFGR:CHN:KN24	India	**KP244575**	

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Species name	Sample ID	Voucher ID	Sample location	GenBank/ Bold	Revised name
Laeops macrophthalmus	PK63	NBFGR:CHN:PK63	India	**KP244576**	
Laeops macrophthalmus	KN28	NBFGR:CHN:KN28	India	**KP244577**	
Laeops macrophthalmus	PK52	NBFGR:CHN:PK52	India	**KP244578**	
Laeops nigromaculatus	CP3131	N/A	Mozambique (CP3131)	PV131467	
Laeops nigromaculatus	PNG2532	NTUM11064	Papua New Guinea (CP4418)	PV131468	
Laeops nigromaculatus	PNG3520	NTUM11342	Papua New Guinea (CP4496)	PV131469	
Laeops nigromaculatus	SB6	N/A	Solomon Islands (CP2830)	PV131470	
Laeops nigromaculatus	WIO857	NTUM17843	Saya de Malha (CP5433)	PV131471	
Laeops nigromaculatus	N/A	ADC09_259.12#1	South Africa	**JF493719**	
Laeops nigromaculatus	N/A	ADC11_259.12 #3	South Africa	**JN312525**	
Laeops parviceps	ASIZP0913894	ASIZP 68133	Philippines (CP2720)	PV131472	
Laeops parviceps	WJC6851	NTUM15809	Taiwan (Donggang)	PV131473	
Laeops parviceps	WJC8465	NTUM17654	Taiwan (Donggang)	PV131474	
Laeops parviceps	WJC8466	NTUM17654	Taiwan (Donggang)	PV131475	
Laeops parviceps	WJC9773	NTUM17655	Taiwan (Donggang)	PV131476	
Laeops parviceps	WJC9852	NTUM17655	Taiwan (Donggang)	PV131477	
Laeops parviceps	WJC11024	NTUM17656	Taiwan (Donggang)	PV131478	
Laeops pectoralis	N/A	ADC09_259.13 #1	South Africa (Tugela Banks)	**HM421813**	
Laeops pectoralis	N/A	ADC11_259.13 #5	South Africa	**JN312513**	
Laeops pectoralis	N/A	ADC11_259.13 #6	South Africa	**JN312521**	
Laeops pectoralis	N/A	ADC11_259.12 #6	South Africa	**JN312527**	
Laeops pectoralis	N/A	ADC11_259.13 #2	South Africa	**KF489623**	
Laeops pectoralis	N/A	ADC11_259.13 #3	South Africa	**KF489624**	
Japonolaeops gracilis	NC275	NTUM15776	New Caledonia (CP4674)	PV131479	
Japonolaeops gracilis	NC418	NTUM15782	New Caledonia (CP4694)	PV131480	
Japonolaeops gracilis	NC652	NTUM15788	New Caledonia (CP4739)	PV131481	
Japonolaeops gracilis	NC1267	NTUM13520	New Caledonia (CP4985)	PV131482	
Japonolaeops gracilis	NC2070	NTUM17853	New Caledonia (CP5131)	PV131483	

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Species name	Sample ID	Voucher ID	Sample location	GenBank/ Bold	Revised name
Japonolaeops gracilis	NC2374	NTUM17854	New Caledonia (CP5181)	PV131484	
Japonolaeops gracilis	NC2513	NTUM17855	New Caledonia (CP3087)	PV131485	
Japonolaeops gracilis	WIO797	NTUM17841	Saya de Malha (CP5421)	PV131486	
*Japonolaeops dentatus**	WJC6859	NTUM15811	Taiwan (Donggang)	**MK617149**	*J. gracilis*
Japonolaeops gracilis	WJC6860	NTUM15811	Taiwan (Donggang)	PV131487	
Japonolaeops gracilis	WJC6861	NTUM15811	Taiwan (Donggang)	PV131488	
Japonolaeops gracilis	WJC9851	NTUM17856	Taiwan (Donggang)	PV131489	
Japonolaeops gracilis	WJC10027	NTUM17857	Taiwan (Dashi)	PV131490	
*Japonolaeops dentatus**	N/A	FNSIC120–1	South China Sea	**JQ681381**	*J. gracilis*
*Japonolaeops dentatus**	N/A	CSIRO H 6418–11	Australia (N of Monte Bello Islands)	**FOAF319**	*J. gracilis*
Kamoharaia megastoma	NC1902	NTUM17842	New Caledonia (CP5120)	PV131491	
Kamoharaia megastoma	PNG2408	NTUM11381	Papua New Guinea (CP4337)	**MK617150**	
Kamoharaia megastoma	WJC9771	NTUM17858	Taiwan (Donggang)	PV131492	
Kamoharaia megastoma	ASIZP0915445	ASIZP072772	Taiwan (Su'ao)	**KU945112**	
Kamoharaia megastoma	ASIZP0915450	ASIZP072777	Taiwan (Donggang)	**KU945115**	
Kamoharaia megastoma	BW–A15369	NMVA29717–001	Australia (off Cape Leveque)	**FOAO2301**	
Neolaeops microphthalmus	ASIZP0916287	ASIZP0073785	Papua New Guinea (CP3636)	**MK617157**	
Neolaeops microphthalmus	NC2063	NTUM17850	New Caledonia (CP5131)	PV131493	
Neolaeops microphthalmus	WJC6783	NTUM15808	Taiwan (Dashi)	PV131494	
Neolaeops microphthalmus	WJC10689	KUMF 7743	Taiwan (Dashi)	PV131495	
Neolaeops microphthalmus	WJC12170	NTUM17851	Taiwan (Donggang)	PV131496	
Outgroup					
Bothus pantherinus	WJC9932	NTUM17852	Taiwan (Kezailiao)	PV131497	
Etropus microstomus	WJC4830	KUI 27165	Atlantic Ocean	PV131498	

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