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A Review of the Taxonomic History of Taiwan's Fishes

Kwang-Tsao Shao [1,2] Hsuan-Ching Ho [3,4,5]

[1] *Biodiversity Research Center, Academia Sinica, Taipei, Taiwan*
[2] *Institute of Marine Biology, National Taiwan Ocean University, Keelung, Taiwan*
[3] *Department of Aquaculture, National Kaohsiung University of Science and Technology, Kaohsiung, Taiwan*
[4] *Taiwan Ocean Research Institute, National Applied Research Laboratories, Kaohsiung, Taiwan*
[5] *Australian Museum, Sydney, Australia*

ABSTRACT

The study of the taxonomy of Taiwanese fishes started as early as 1858. Europeans, Canadians, and Americans were the pioneers in studying the fish fauna of Taiwan. After the Sino-Japanese war (1894–1895), China ceded Taiwan to Japan, and Japanese zoologists started the taxonomic study of Taiwanese fishes. After the end of WWII, Japan ended its colonial rule (1895–1945), and ichthyologists in Taiwan started their own studies on fish classification.

Professor Johnson Ta-Fu Chen was the earliest pioneer of fish taxonomy research in Taiwan. In 1954, he published the first edition of *Fishes of Taiwan*, which included 140 families and 675 species of fishes, along with key to all species. His *A synopsis of the vertebrates of* Taiwan, published in 1956, recorded a total of 870 species of fish and was used as a textbook on fish taxonomy in universities for more than 40 years. Professors Ren-Sheng Liang and Shih-Chieh Shen are considered the second generation of ichthyologists. Prof. Shen has been teaching fish taxonomy at the Department of Zoology, National Taiwan University, for more than 40 years since 1967. The *Fishes of Taiwan* he edited in 1993 compiled a total of 2,028 species. Students who took Prof. Shen's classes are considered the third generation, including Hin-Kiu Mok and Kwang-Tsao Shao, who specialized in marine fishes, and Chyng-Shyan Tzeng, who specialized in freshwater fishes. Later, they expanded into different fields such as ecology, evolution, and conservation. Prof. Che-Tsung Chen of National Taiwan Ocean University, a graduate of the University of Tokyo, specialized in cartilaginous fishes and fishery biology.

* Corresponding author, e-mail: zoskt@gate.sinica.edu.tw

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The master's or doctoral students supervised by the third generation after 2000, including Yu-Yun Chen, Hurng-Yi Wang, Shoou-Jeng Joung, Jeng-Ping Chen, I-Shiung Chen, Hong-Ming Chen, Hsuan-Ching Ho, Yun-Chih Liao, and Mao-Ying Lee, are considered the fourth generation, while the students supervised by them represent the fifth generation. In addition to using traditional morphological study methods, they also integrated genetics or DNA barcoding to conduct taxonomic or phylogenetic studies across various taxa, including species classification and exploration of their phylogeny. More than 400 new species and 1,000 new records in Taiwan have been described or documented. The results have been fruitful.

In addition, several outstanding scholars returned to Taiwan directly after studying abroad, including Wei-Jen Chen, Te-Yu Liao, and Hsiu-Chin Lin, who focused on exploring molecular phylogenetic relationships. Meanwhile, Chien-Hsiang Lin studied the application of otoliths and their fossils in fish classification and the reconstruction of paleobiodiversity and biogeography.

Taiwan's strength in fish taxonomy research is directly related to its unique geographical location and rich fish diversity. Moreover, the classification of adult fishes and the use of DNA barcoding for species identification of fish eggs and larvae have developed considerably and achieved laudable results. The Taiwan Fish Database has a history of 35 years and is very popular and well-known both in Taiwan and abroad. Taiwan hosted the 7th and 12th Indo-Pacific Fish Conferences in Taipei, in 2005 and 2025, respectively, which attracted many ichthyologists and taxonomists from abroad to engage in intellectual exchanges with domestic scientists.

In addition to introducing the aforementioned major scholars engaged in Taiwanese fish taxonomy research and their contributions, this article also briefly summarizes the evolution of the fish classification system, the status of Taiwanese specimen collections, statistics on the number of fish species in the database, types of fish geographical distribution and mechanisms of their formation, the classification of fish eggs and larvae, cooperation and exchanges in fish research between Taiwan and China, and the difficulties and future prospects of fish taxonomy studies. The aim is to chronicle the historical development of fish taxonomy in Taiwan for future reference. However, because the article involves many different aspects, it is impossible to describe them all in detail, and some omissions are likely to occur. It is hoped that any unintentional omissions may be excused and that overlooked facts will be added in future documentation.

Keywords: fish taxonomy, Taiwan, ichthyologists, DNA barcoding, species classification.

1 THE HERITAGE OF FISH TAXONOMICAL STUDIES IN TAIWAN

1.1 Foreign Scholars (1858–1945)

The study of Taiwanese freshwater fishes can be dated back to 1858–1866, when British Consul Robert Swinhoe (1836–1877) arrived in Taiwan and collected birds along with many biological specimens. He sold the specimens he procured to the British Museum. Later, the ichthyologist Albert C. L. G. Günther (1830–1914), then the museum's curator, recorded 16 species of Taiwanese fishes in his famous volumes *British Museum Fish Catalogue*. The seventh volume, published in 1868, described seven new species of freshwater fish, marking the beginning of taxonomic research on Taiwanese fishes (Günther, 1868). Subsequently, Boulenger (1894) and Regan (1908) described some new species, respectively. A Canadian medical doctor, Dr. George L. Mackay (1844–1901), also collected fish while practicing medicine in Taiwan and recorded 18 species of fishes (Wu, 2001).

Between 1896 and 1899, Japanese technician Tsunasuke Tada collected fishes in Taiwan. The samples were sent to Stanford University in the United States. Jordan and Evermann (1902) published 186 species of Taiwanese fishes, including two new genera and 17 new species. This was the first systematic study of Taiwanese fishes in history, introducing them to the world. Around the same time, German entomologist Hans Sauter (1871–1943) came to Taiwan and collected many biological specimens starting in 1902. His fish specimens were sold to several European and American countries through a specimen dealer in Japan. Jordan and Richardson (1909) published a list of 286 species from Taiwan, including one new genus and nine new species, as well as the 186 species previously recorded by Jordan and Evermann (1902). In addition, Jordan and Snyder (1908) reported three new species of Carangidae from Taiwan.

Japanese ichthyologist Masamitsu Oshima (1884–1965) was the first to conduct in-depth studies on Taiwanese fishes during this period. In 1919, Oshima published *Studies on the Freshwater Fishes of Taiwan,* which described 76 species of Taiwanese fish (including 15 new species), laying the foundation for the study of freshwater fishes in Taiwan (Oshima, 1919, 1920a, 1920b, 1926, 1929). The Taiwan trout (*Oncorhynchus masou formosanus*) was first discovered by Oshima's assistant Takeo Aoki. Aoki described the fish but did not name it as a new species (Aoki, 1917). It was later formally published and named by Jordan and Oshima (1919). Oshima (1924, 1927) also studied marine fish species in Taiwan, including scad, sea breams, razorfishes, mullets, and flounders. He published several papers, recording at least 60 species of marine fish in Taiwan, including some new species (Oshima, 1922a, 1922b, 1924, 1925, 1927, 1929). The book *Index of Japanese Fishes,* co-authored by Yaichiro Okada and Kiyomatsu Matsubara (1907–1968) in 1938, included 283 species of Taiwanese fishes. Another work, *Catalog of Japanese Vertebrates* (Okada, 1938), listed 430 species, although most lacked vouchers or direct evidence. In short, all fish research carried out in Taiwan until the end of WWII was done by European, American, and Japanese scientists, who recorded nearly 500 species of fishes in Taiwan.

1.2 The First Generation (1945–1970)

After WWII, Prof. Johnson Ta-Fu Chen (1898–1988) came to Taiwan and served as the director of the Taiwan Museum, while also holding a professorship at National Taiwan University. The first edition of Fishes of Taiwan (Chen, 1954) was published, listing 140 families and 675 species of fishes. In 1955, he moved to Tunghai University in Taichung, where he established a comprehensive fish collection. His book *A synopsis of the vertebrates of Taiwan* (Chen, 1956) catalogued a total of 870 fish species and was used as a textbook for fish taxonomy in universities for more than four decades. During this period, he published a total of 14 new fish species (Chen, 1948, 1963; Chen & Liang, 1948, 1949), among which he and Ting-Chen Weng reviewed the

Marine Research of the National Academy of Marine Research
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flatfishes and eels of Taiwan (Chen & Weng, 1965, 1967). Chen (1963) also described two new sharks from Taiwan: *Paragaleus tengi* (Chen, 1963) and *Squatina tergocellatoides* (Chen, 1963). His enlightenment and contribution to Taiwanese fish community were enormous.

During the same period, Dr. Huo-Tu Teng (1911–1978), who studied under Kiyomatsu Matsubara in Japan, served as the seventh director of the Fisheries Research Institute of Taiwan, Keelung. Between 1959 and 1962, he published descriptions of 11 new sharks and rays, as well as the first new hagfish species in Taiwan (Teng, 1958, 1959a, 1959b, 1959c, 1959d), which had a profound impact on and contributed to the research on cartilaginous fishes in Taiwan. Mr. Hong-Chia Yang, who served as Teng's assistant, was skilled in hand-drawing fishes and collected many specimens for Teng's studies. He also published a number of new fish records for Taiwan, as well as survey reports on the fishes of Kinmen and the Nansha Islands.

Many reports and books published by these scholars can be found in the Taiwan Fish Database (http://fishdb.sinica.edu.tw), and thus are not listed in detail here.

1.3 The Second Generation (1971–1990)

After Johson Ta-Fu Chen retired and moved to the Shanghai Museum, he left all the reference materials he had collected to Ming-Tzeng Yu (1928–2011) of the Department of Biology, Tunghai University. Later, Yu compiled and published a revised and enlarged version of *A synopsis of the vertebrates of Taiwan* (Chen & Yu, 1986), which listed a total of 2,252 fish species. He also translated the fourth edition of the *International Code of Zoological Nomenclature* (ICZN, 1999) into Chinese (International Commission on Zoological Nomenclature, 2002). Prof. Run-Sheng Liang of the Department of Zoology, National Taiwan University, studied under the guidance of Prof. Chen and specialized in freshwater fishes. While teaching fish taxonomy at National Taiwan Normal University, one of his students was Dr. Sin-Che Lee, who is considered part of the second generation. After graduation, Lee initially taught at Beimen Junior High School. Because of his collection work and the publication of several reports, he was hired by Prof. Liang as a lecturer at National Taiwan Normal University for two years. Later, Dr. Lee pursued a doctoral degree at the University of Bristol in the United Kingdom, under the guidance of Dr. Peter Miller, a global authority on goby classification. Upon returning to Taiwan, he worked at the Institute of Zoology, Academia Sinica. Dr. Lee began collaborating with Dr. Kun-Hsiung Chang, a fishery biologist, to investigate and study Taiwanese fishes by obtaining specimens from fish markets and sampling intertidal zones. He published more than 30 new fish records collected from the intertidal zones of northern and southern Taiwan and the Penghu Islands (Chang et al., 1969, 1973; Chang & Lee, 1971). Chang et al. (1978) added 40 coral reef fishes to the Taiwan fauna through scuba diving surveys. Between 1980 and 1990, Sin-Che Lee published several taxonomic and ecological survey reports on the intertidal zones of Sansiantai and Lanyu, Taitung (Lee, 1980a, 1980b). He later worked on morphological taxonomy and molecular evolution until his retirement in 2017.

Prof. Shih-Chieh Shen (1926–2025) of the Department of Zoology, National Taiwan University (NTU), played a pivotal role in promoting fish taxonomy studies in Taiwan. In 1966, he earned his doctoral degree from the University of Tokyo, specializing in the flounders of Hong Kong. The following year, he returned to NTU and taught until his retirement in 1999, continuing to teach fish taxonomy for almost 40 years. In addition to teaching, he was highly dedicated to taxonomic research. He has described three new genera, over 40 new species, and documented hundreds of new records in Taiwan, based on specimens acquired from fish markets, aquariums, fishermen, and intertidal zones. In the 1970s, he demonstrated that the three different color phases of *Rhinomuraena quaesita,* previously thought to represent different species, were in fact the same species: black juveniles, blue males, and yellow females (Shen, 1974). He later confirmed that a similar phenomenon occurs in the family Pomacanthidae, where males and females differ in body coloration. However, unlike the protandrous ribbon eel, angelfishes are protogynous (Shen & Liu, 1978).

Marine Research of the National Academy of Marine Research
DOI: 10.29677/MR.202506_5(1).0001

Dr. Labbish Ning Chao, an ichthyologist who has lived in Brazil for many years, is an internationally recognized authority on croaker studies. He was supervised by Johnson Ta-Fu Chen during his undergraduate studies at Tunghai University and is therefore considered part of the second generation (Chen & Chao, 1971). In 2003, he hosted the 83rd International Meeting of the American Society of Herpetology and Ichthyology (ASIH) in Manaus. Later, he served as convener of the IUCN Red List assessment for the Sciaenidae and completed the global croaker assessment in 2020. After his retirement, he worked as a visiting research fellow and lecturer at the National Museum of Marine Biology and Aquarium. Together with colleagues at the museum, he established the Global Sciaenidae Conservation Network (GSCN) and published the new species *Johnius taiwanensis* (Chao, et al., 2019). In collaboration with Prof. Meng-Hsien Chen and Dr. Chih-Wei Chang at National Sun Yat-sen University, he supervised master's student You-Yu Liu and doctoral student Hafiz Hanafi, who together revised the Sciaenidae in Taiwan (Hanafi, 2023).

1.4 The Third Generation (2001–2010)

Among the students who took Prof. Shen's taxonomy class, Prof. Hin-Kiu Mok and Prof. Kwang-Tsao Shao specialized in marine fishes and expanded into various fields such as ecology, behavior, evolution, and conservation. Prof. Chyng-Shyan Tzeng, co-supervised by Shen and Prof. Pien-Chien Huang (1931–2020), specialized in the morphology and molecular evolution of freshwater fishes. He conducted extensive surveys and collections between 1978 and 1984 and published the book *Freshwater Fishes of Taiwan* (Tzeng, 1986b).

Kwang-Tsao Shao's master's thesis focused on the systematics of the family of Sillaginidae (Shao & Chang, 1978). After graduation, he worked as a research assistant in Kun-Hsiung Chang's laboratory. He began to investigating coral reef fishes using scuba diving, which greatly increased the number of listed coral reef fish species, including many new species such as *Gorgasia taiwanese* (Shao, 1990). By the end of 1983, Shao had majored in numerical taxonomy and earned his doctoral degree from the State University of New York at Stony Brook. After returning to Taiwan, he focused his work on fish taxonomy. He published eight new species with his student Dr. Jeng-Ping Chen (Shao & Chen, 1987; Chen et al., 1990, 2007b; Chen & Shao, 1993, 1995, 2000, 2002; Randall et al., 2003, 2007; Gill et al., 1995); and one new genus and several new species of moray eels in collaboration with Prof. Hong-Ming Chen (Chen & Shao, 1995; Chen et al., 1996, 2008a). Prof. Che-Tsung Chen (1943–2008) who graduated from the University of Tokyo in 1977, worked at the National Taiwan Ocean University for more than three decades. He specialized in the classification and fishery biology of cartilaginous fishes. One of his team's most important discoveries was the viviparous reproductive mode of the whale shark (Joung et al., 1996), which caused a sensation in the international marine biology community.

Since 1985, the National Science Council has supported a number of fish taxonomists in Taiwan, including Shih-Chieh Shen, Sin-Che Lee, Hin-Kiu Mok, Che-Tsung Chen, Kwang-Tsao Shao, Chun-Hui Chen (Figure 1), and Chyng-Shyan Tzeng, in collecting and investigating different fish groups over several years. These efforts documented around 2,010 species in museum collections, including 75 freshwater fishes and 1,953 marine fishes. The marine group comprises eight hagfishes, 146 cartilaginous fishes, and 1,799 bony fishes Shen et al., 1993). This research led to the removal of hundreds of previously recorded species—due to lack of voucher specimens, missing references, or misidentifications—from the list in Chen and Yu (1986). Moreover, it added hundreds of newly recorded fish species from Taiwan.

Another comprehensive compilation of fish species list was completed during the Taiwan Biological Resources Survey and Information Management Symposium, sponsored by Academia Sinica in 1992. In this survey, Shao et al. (1992) reported 151 species of freshwater fishes.

Marine Research of the National Academy of Marine Research
DOI: 10.29677/MR.202506_5(1).0001

Figure 1. Group photo of several authors of the *Fishes of Taiwan* (Shen, et al., 1993). From left to right: front row – Sin-Che Lee, Shih-Chieh Shen, Hin-Kiu Mok; back row – Kwang-Tsao Shao, Che-Tsung Chen, Chun-Hui Chen.

1.5 The Fourth Generation (2000–2010)

Prof. Shoou Jeng Joung, a student of Che-Tsung Chen; Dr. Yu-Yun Chen and Dr. Chien-Siang Kuo, students of Hin-Kiu Mok; Prof. Te-Yu Liao, a master's student of Chyng-Shyan Tzeng; and Jeng-Ping Chen, Hong-Ming Chen, Hsuan-Ching Ho, Yun-Chih Liao, Mao-Yin Lee, and Yung-Chieh Chiu, doctoral students of Kwang-Tsao Shao, are considered the fourth generation. Thanks to their great efforts, the total number of recorded Taiwanese fish species increased significantly to nearly 3,500 within 15 years.

In the 2000s, Hin-Kiu Mok and his student Dr. Yu-Yun Chen used eel traps to collect many new eel species (Mok et al., 1991; Chen & Mok, 1995, 2001). Dr. Chien-Siang Kuo, a student of Sin-Che Lee, also collaborated with Mok to study hagfishes and published eight new species, including the red-tailed hagfish, *Rubicundus rubicundus,* a very primitive species later elevated to its own subfamily (Kuo et al., 1994, 2010; Mok & Kuo, 2001; Mok & Chen, 2001).

Dr. Ta-Ming Wang, a student of Che-Tsung Chen, studied laternfishes (Myctophidae) collected by the R/V Fishery Researcher I, identifying 16 genera and 40 species (Wang & Chen, 2001). Prof. Shoou-Jeng Joung published nine new records of cartilaginous fishes in 2004 and 2013.

From 2002 to 2012, Kwang-Tsao Shao collaborated with Prof. Tien-Jen Chen, a crustacean expert at National Taiwan Ocean University, and secured long-term support from the National Science Council. They introduced various deep-sea trawling techniques (e.g., dredge, beam trawl, and otter trawl) aboard R/V Ocean Researcher I, II, III and Fishery Researcher I, allowing collection of deep-sea organisms from depths of 3,000–4,000 meters. In addition, commercial trawlers reaching depths of 600 meters were used to collect specimens. These efforts significantly increased the number of documented deep-sea fishes. During this period, master's and doctoral students, as well as postdoctoral fellows supervised by Shao, focused on the following groups: Myctophiformes (Dr. Min-Chih Wang; Wang & Shao, 2006); Stomiiformes (Dr. Yun-Chih Liao; Liao et al., 2006a, 2006b, 2009, 2011); Lophiformes (Dr. Hsuan-Ching Ho; Ho & Shao, 2004, 2007, 2008, 2010a, 2010b,

Marine Research of the National Academy of Marine Research
DOI: 10.29677/MR.202506_5(1).0001

2010c; Ho et al., 2009, 2011); Macrouridae (Miss Mei-Lun Chiou; Chiou et al., 2004a, 2004b); Synoglossidae (Dr. Mao-Ying Lee; Lee et al., 2009a, 2009b, 2014); Ophiformes and Alepocephalidae (Dr. Hsin-Ming Yeh; Yeh et al., 2005, 2006a, 2006b); and Ophichthidae (Dr. Yung-Chieh Chiu; Chiu et al., 2013, 2018, 2022). Many new species and records were described. Due to the large number of new records found in Taiwan, many have not yet been formally documented and exist only in the Taiwan Fish Database. Shao et al. (2008) reported a list of 2,133 fish species collected from southern Taiwan and the northern South China Sea, including Dong-sha and Nan-sha Islands. These included 10 hagfishes, 80 cartilaginous fishes, and 2,043 bony fishes.

During his master's and doctoral studies, Dr. Hsuan-Ching Ho focused on the taxonomy of anglerfishes (order Lophiiformes), including Ogcocephalidae, Lophiidae, and Chaunacidae. He has published 54 new anglerfish species (Ho et al., 2011, 2013). In 2010, he joined the National Museum of Marine Biology and Aquarium, where he began intensive specimen collection. Since then, he has added over 10,000 specimens to the museum's collection. Over the past 20 years, he has also studied many bony fish groups, including Pinguipedidae (Ho & Shao, 2010c, 2012), Synodontidae (Ho et al., 2016), Gadiformes (Iwamoto et al., 2009, 2011; Ho, 2019), and Paralepididae (Ho et al., 2019a, 2019b). In total, he has described two new genera and 154 new species—81 of them from Taiwan. Dr. Mao-Ying Lee, co-supervised by Hong-Ming Chen, Kwang-Tsao Shao, and Dr. Thomas Munroe of NOAA, mainly worked on the taxonomy of Cynoglossidae and other deep-sea fishes. He has published eight new species from Taiwan, including five Symphurus and two Chelidoperca (Lee & Munroe, 2021; Lee, 2022). Dr. Yung-Chieh Chiu focused on the taxonomy of snake eels (Ophichthidae) and used DNA barcoding to match adults with their eggs and larvae. He has also described several new species (Hibino et al., 2019; Chiu et al., 2022).

The researcher who has described the most new freshwater fish species from Taiwan is Prof. I-Shiung Chen of National Taiwan Ocean University. He was a master's student of Kwang-Tsao Shao (1992–1994), and later a doctoral student of Prof. Peter Miller of the University of Bristol in the United Kingdom (1996–1999). Specializing in gobies and freshwater fishes, he has collaborated with Prof. Lee-Shing Fang and Dr. Qiao-Quan Han since 1994 and published *The freshwater and estuarine fishes of Taiwan* (Chen & Fang, 1999), as well as reports on several new species (Chen & Shao, 1996). Together with Chyng-ShyanTzeng and Kwang-Tsao Shao, he was commissioned by the Forestry Bureau of Taiwan to compile the *Red Data Book of Freshwater Fishes in Taiwan* (Chen et al., 2012, p.242), assessing the conservation status of freshwater fishes in Taiwan. They conducted detailed sampling and classification research over three years, covering rivers and streams across the island, and discovered many potentially new species. Recently, he and his colleagues also edited a special issue of the *International Symposium on Tropical Fish Diversity* (Chang et al., 2024), which included 28 newly described fishes. In total, he has published four new genera and 105 new fish species across families such as Gobiidae, Cyprinidae, Balitoridae, Adrianichthyidae, Bagridae, and Tripterygiidae, making important contributions to the classification of fish species in East Asia. Among these, two new genera and 48 new species were described from Taiwan (46% of the total), including 31 freshwater and estuarine species and 17 marine species (Chen et al., 1995, 1996, 1998, 2002, 2006a, 2006b, 2008b, 2009; Chen & Fang, 2003, 2009; Chen & Chang, 2007). Notably, the genus *Formosaneleotris,* described from eastern Taiwan (Chen, 2024), is among the most distinctive.

1.6 The Fifth Generation (2010–)

The master's and doctoral students trained by the fourth-generation taxonomists mentioned above are considered the fifth generation. For example, Shoou-Jeng Joung's student, Shing-Lai Ng, has published a number of new species and new records from Taiwan (Ng et al., 2023, 2024a, 2024b).

Marine Research of the National Academy of Marine Research
DOI: 10.29677/MR.202506_5(1).0001

Prof. Hong-Ming Chen of National Taiwan Ocean University and his student, Dr. Kar-Hoe Loh, who is currently teaching at the University of Malaya, have worked on the molecular phylogeny and reproduction of moray eels, and have published several new species (Loh et al., 2012, 2015).

Prof. Te-Yu Liao of National Sun Yat-sen University, who graduated from Stockholm University, and his student, Dr. Wen-Chien Huang, studied the systematics and phylogeography of the family Muraenidae. They have described seven new species (Huang et al., 2020, 2021, 2024), and also documented the first known case of hybridization between moray species in nature (Huang et al., 2022). Dr. Tak-Kei Chou revised the stonefish family (Scorpaenidae), listing a total of 29 genera and 85 species, including one new genus, one new species, and three new records (Chou & Liao, 2022; Chou et al., 2023, 2024). Liao's student Wei-Cheng Jhuang studied the systematics and phylogeography of freshwater gobies in the subfamily Sicydiinae, recently describing a new species (Jhuang et al., 2024).

Hsuan-Ching Ho worked with his master's student, Ms. Wen-Chun Ma of National Dong Hwa University, to publish several new *Chaunax* (Ho & Ma, 2022); with Mr. Chii-Ngai Tang of National Taiwan Ocean University, he described several perchlets (Tang et al., 2020; Tang & Ho, 2021); and with Shing-Lai. Ng of National Taiwan Ocean University, he described a new snake eel and a new skate (Ho et al., 2022; Ng et al., 2023). After graduating from National Sun Yat-sen University, Yo Su collaborated with Ho to expand research into the order Beryciformes, publishing several new species and records in recent years (Su et al., 2023a, 2023b, 2024; Su & Ho, 2024). Altogether, Ho and his coauthors have reported several hundred new species and new records, significantly contributing to the understanding of marine fish diversity in Taiwan.

I-Shiung Chen and his students, Drs. Shih-Pin Huang and Shen-Chi Wang, published several studies on freshwater and migratory gobies found in streams, estuaries, and coastal areas of Taiwan (Chen et al., 2022; Wang et al., 1996). Shih-Pin Huang has published one new genus, four new gobies, and one new snake eel (Chen et al., 2013; Huang et al., 2013; Huang et al., 2016a, 2016b; Chiu et al., 2018; Chen et al., 2024b). I-Shiung Chen also supervised Dr. Min-Chia Chiang, who studied the taxonomy of triplefins (Tripterygidae) and described three new species (Chiang & Chen, 2008, 2012). Moreover, his Indonesian student, Mr. Tonisman Harefa, focused on sea gobies, especially *Trimma and Priolepis,* and has published one new species from each genus (Chen & Harefa, 2024; Chen et al., 2024a). Another student, Mr. Xian-En Lee, published two new goby species (Chen & Li, 2024; Li & Chen, 2024) and resurrected *Formosania gilberti* (Yeh et al., 2024).

1.7 Foreign Scholars Who Studied Taiwanese Fishes Over The Past 20 Years

In earlier years, researchers working on the taxonomy of Taiwanese fishes mainly relied on borrowing specimens, mostly from National Taiwan University and Academia Sinica. Due to unfamiliarity with Taiwanese fishes, most new species were described based on specimens from Japan or the Philippines, rather than from Taiwan itself. This trend began to shift markedly in 2005. During the 7th Indo-Pacific Fish Conference held in Taiwan, researchers from around the world visited the country, not only examining museum collections but also collecting numerous samples from fishing ports or fish markets. Since then, several new species have been published based on these specimens, such as *Acanthopagrus taiwanensis* (Iwatsuki & Carpenter, 2006), *Torpedo formosa* (Haas & Ebert, 2006), *Nuchequula mannusella* (Chakrabarty & Sparks, 2007), and *Scorpaena pepo* (Motomura et al., 2007). In addition, many collaborative relationships were forged with Taiwanese scientists. Over the following 20 years, foreign scholars continued to visit Taiwan and conduct various research projects in collaboration with Taiwanese colleagues.

Marine Research of the National Academy of Marine Research
DOI: 10.29677/MR.202506_5(1).0001

With financial support from various sources, Kwang-Tsao Shao has invited many fish taxonomists to Taiwan to guide students since 2000. Notable visitors include Drs. Tomio Iwamoto (Macrouridae) and John E. McCosker (snake eels) of the California Academy of Sciences, Prof. Ted W. Pietsch (deep-sea anglerfishes) of the University of Washington, Dr. Tom A. Munroe (Cynoglossidae) of NOAA, and Dr. David G. Smith (Anguilliformes) of the Smithsonian Institution. In addition to guiding and training students, these experts also produced numerous research papers (Ho & Shao, 2004; Chiou et al., 2004a, 2004b; Iwamoto et al., 2009, 2015; Lee et al., 2009b, 2014; Lee & Munroe, 2021).

After 2010, Hsuan-Ching Ho invited cartilaginous fish experts to participate in workshops in Taiwan and subsequently published a special issue titled *Systematics and biodiversity of sharks, rays, and chimaeras (Chondrichthyes) of Taiwan.* This publication documented 181 species of cartilaginous fishes, placing Taiwan among the top five countries in the world for Chondrichthyan diversity. Later, Ho invited eel experts Drs. J. E. McCosker and Yusuke Hibino to Taiwan and also visited the USNM to study with D. G. Smith. Together, they formed a team dedicated to studying Taiwanese eels and published two special issues on eel taxonomy, which comprised more than 30 new species and 40 new records. Combined with the results of recent studies, Taiwan now boasts nearly 250 eel species, more than any other country in the world (Ho et. al., 2015, 2018). In addition, Ho and Dr. Keita Koeda (University of the Ryukyus) co-edited the book *Fishes of Southern Taiwan* (Koeda & Ho, 2019), covering 60 newly described species, 116 new records, and several unnamed species. The book contains a total of 1,406 fish species, many of which are deep-sea fishes recorded from Taiwanese waters.

2 EVOLUTION OF FISH CLASSIFICATION SYSTEMS AND RESEARCH TOOLS

In the 1930s, the classification system developed by David S. Jordan (1923) was widely used in ichthyological research across many countries. In 1955, Soviet scientist Lev S. Berg (1876–1950) proposed a new fish classification system (Berg, 1947), combining both modern and fossil materials. This system was later adopted by Chinese ichthyologist Yi-Kang Wang (1958) in his book *Fish Taxonomy.* Greenwood et al. (1965) made significant changes to a new classification system due to the influence of cladistics, which led him to propose that a system established by exploring evolutionary or kinship relationships is a natural system. Later, most European and American ichthyologists also accepted the system proposed by Greenwood et al.

Joseph S. Nelson (1976, 1984, 1994, 2006) published four versions of the book *Fishes of the World*. The classification system in this book is currently the most commonly used around the world, following the system of Greenwood et al. (1965). It is notable that Nelson included all known living and fossil fishes, described the characteristics of higher-level taxa, and provided the latest information on the number of species in each group.

However, the fish classification system has become increasingly complex with time, greater understanding of fish species, more available specimens, and the development of tools and methods (Shao, 2009). After Nelson passed away in 2011, the fifth edition was revised and published with co-authors with Terry C. Grande and Mark V. H. Wilson (Nelson et al., 2016). This edition adopted many findings from molecular evolution, among which the higher levels of many taxa changed significantly. These changes were not readily recognized by some taxonomists and caused controversy. In addition, with an increasing number of reports on molecular systematics, modifications to the structure and names of each taxonomic level are still being debated. Therefore, there is no consensus on fish classification systems to date, and these systems and the taxon names of some fishes differ somewhat among different authoritative databases, such as FishBase (Froese & Pauly, 2024), the Eschmeyer's Catalog of Fishes of the California Academy of Sciences (CAS), the World Register of Marine Species (WoRMS), and the Ocean Biodiversity Information System (OBIS). In general, they mainly follow Nelson (2006) and partially adopt the names from the new system proposed in the 2016 version.

Marine Research of the National Academy of Marine Research
DOI: 10.29677/MR.202506_5(1).0001

The classification system in China traditionally followed Rass and Lindberg (1971), and then shifted to the fourth version of Nelson (2006) in the *Latin-Chinese Dictionary of Fishes Names* and *Latin-Chinese Dictionary of Fish Names by Classification System* compiled by Wu et al. (1999, 2012) and the *Species Catalogue of China* published by Zhang et al. (2021). For cartilaginous fishes, future revisions could be made based on Compagno et al. (2005). Since the inception of Taiwan Fish Database in 1997, the classification system has followed the latest edition of Nelson's book. However, after 2004, the classification system adopted by the database is mainly based on Eschmeyer's *Catalog of Fishes,* which has partly followed Nelson's sixth edition.

After completing systematic classification research on the Taiwan lancelet under the guidance of Kwang-Tsao Shao, Prof. Hsiu-Chin Lin went to the Scripps Institution of Oceanography at the University of California, San Diego to pursue a doctoral degree, engaging in the systematic classification of Blennioidei fishes using molecular markers to study their evolution. After returning to Sun Yat-sen University, Mr. Yo Su, a student co-supervised by Hsiu-Chin Lin and Hsuan-Ching Ho, published two new records and four new species of Trachichthyifomes (Su et al., 2022a, 2022b, 2023a, 2023b, 2024). In addition, she supervised Ms. You-Ci Fan in reviewing the systematic classification of the family Polymixiidae and published one new species (Fan et al., 2024).

Dr. Marites Ramos-Castro, who was supervised by Hong-Ming Chen and is currently teaching at Isabela State University in the Philippines, focuses on the comparative study of the cranial skeletons of anguilliform fishes and has published articles on the comparative anatomy of the cranial morphology of Anguilliformes and Muraenidae (Ramos-Castro et al., 2020, 2021).

The morphology of fish otoliths is highly taxonomically specific and has therefore been used in taxonomy (Mediodia et al., 2024) and systematics (Nolf, 1985, 1993, 2013; Schwarzhans, 2014). In addition, otoliths are crystals of calcium carbonate and are easily preserved in sediments. Therefore, otolith remains are a powerful tool for reconstructing fish communities in early history (Lin et al., 2019, 2023). Dr. Chien-Hsiang Lin of the Biodiversity Research Center, Academia Sinica, who was supervised by Dr. Hsi-Jen Tao for his master's degree research, specialized in comparative anatomy and fossil research in the Department of Zoology, National Taiwan University. He later went abroad and graduated from the University of Bari in Italy, specializing in paleobiogeography. He has published several reports on the use of otoliths in fish taxonomy (Ho & Lin, 2022; Ng et al., 2024b), as well as on the reconstruction of paleobiodiversity and paleobiogeography from various fossil sites (Lin et al., 2018, 2021, 2023; Lin & Chien, 2022).

Prof. Wei-Jen Chen of the Institute of Oceanography, National Taiwan University, earned his doctoral degree from the University of Paris VI in 2001. His research focuses on the relationships among higher-order bony fishes and the marine biogeography of the Indo-West Pacific region. In recent years, environmental DNA has been used to assist the Ocean Conservation Administration in investigating the distribution of marine fish in the waters surrounding Taiwan. Since returning to Taiwan in 2009, he has published 81 research reports, mainly presenting evidence that the early evolution of Ostariophysi is related to paleocontinental separation and continental drift. He investigates the breeding and dispersal mechanisms of large-eye seabreams (Lethrinidae), Sciaenidae, and Nemipteridae, and the data support the origin center hypothesis of the uneven distribution pattern of marine biodiversity. He has supervised graduate students, including Drs. Pei-Chun Lo, Jhen-Nien Chen, Man-Kwan Wong, and Lin-Lan Hsu, to explore ray-finned fish systematics by integrating molecular, morphological, fossil, and biogeographic evidence to study Actinopteri (Chen & Mayden, 2010), Acanthomorpha (Chen et al., 2014b), Elopomorpha (Chen et al., 2014a), Sciaenidae (Lo et al., 2015), Pleuronectoidei (Campbell et al., 2019), Actinopterygii (Chanet et al., 2023), and Ophidioidei (Wong & Chen, 2024).

Marine Research of the National Academy of Marine Research
DOI: 10.29677/MR.202506_5(1).0001

3 TAIWAN'S FISH SPECIMEN COLLECTION AND FISH SPECIES STATISTICS

Most early Taiwanese fish specimens were deposited at the Taiwan Fisheries Research Institute in Keelung (established by Huo-Tu Teng) and at Tunghai University (established by Johnson-Ta-Fu Chen). The Provincial Taiwan Museum, now the National Taiwan Museum, also holds a small collection with only one type specimen. The Department of Zoology at National Taiwan University has the largest fish collection, established by Shih-Chieh Shen before 1990. Since the 2000s, the Institute of Zoology at Academia Sinica has held the most abundant fish collection in Taiwan. In 2004, the collection was transferred from the Institute of Zoology to the newly established Biodiversity Research Center on the same campus. Additional specimens have been collected by the National Museum of Marine Biology and Aquarium (by Chih-Wei Chang and Hsuan-Ching Ho), National Taiwan Ocean University (I-Shiung Chen), National Tsing Hua University (Chyng-Shyan Tzeng), National Museum of Natural Science (Nian-Hong Chang-Liao), and National Sun Yat-sen University (Hin-Kiu Mok, Te-Yu Liao). The Taiwan Endemic Species Research Institute, now the Taiwan Biodiversity Research Institute, also holds many freshwater fish specimens. As for fish larvae and juvenile collections, National Taiwan University (Tai-Sheng Chiu) maintains the largest.

Before 2001, only a few of the aforementioned specimens were digitized and managed separately. Fortunately, with financial support from the NDAP Phase I and TELDAP Phase II, most specimens in various institutions across Taiwan have been digitized, and a unified metadata-based database has been established and made publicly available online. The number of currently digitized fish specimens is as follows: Academia Sinica (25,211), National Taiwan University (8,652), National Museum of Marine Biology and Aquarium (6,298), Fisheries Research Institute (2,470), National Museum of Natural Science (1,680), National Taiwan Museum (1,470), National Museum of Marine Science and Technology (1,230), National Taiwan Ocean University (500), and National Tsing Hua University (500). The total number of type specimens collected in Taiwan is about 1,300, of which about 300 specimens are currently scattered abroad; however, their data and photographs have been repatriated and added to the Taiwan Fish Database through TELDAP. Unfortunately, after the completion of the digital archive project, it is unclear whether museums will continue to digitize specimens and update their collections online. At the very least, horizontal integration through the Taiwan Fish Database or TaiBIF's website has not yet occurred.

The number of fish species in Taiwan has also increased rapidly over the past 20 years due to the efforts of taxonomists—from 43 orders, 237 families, and 2,028 species recorded in the *Fishes of Taiwan* at the end of 1993, to 47 orders, 290 families, and 3,008 species registered in the Taiwan Fish Database by mid-2008. The book *2010 Taiwan Species List* (Shao, 2010) recorded a total of 51,218 native species in Taiwan. Among them, 34,154 species belong to the animal kingdom, including 2,897 species of fish. Excluding 111 species of freshwater fish, there are 2,786 marine fish species. These include: 11 species of hagfish, 168 species of cartilaginous fish, and 2,607 species of bony fish. In the same year, Chen et al. (2010) reported 1,154 species of fish found in the waters around Kenting. By 2018, there were 48 orders, 298 families, and 3,121 species; by 2024, the number had increased to 304 families and 3,480 species. On average, about 15 species are added each year.

Marine Research of the National Academy of Marine Research
DOI: 10.29677/MR.202506_5(1).0001

As of the end of 2024, type specimens include 495 new species originating from Taiwan. After deducting 114 invalid or questionable species, there are 381 valid species. Among them, nearly 80 species are primary freshwater fish, and about 400 species are marine or brackish-water species (Ho, pers. data). If divided by time periods: 41 new species were added from 1960 to the 1990s; 60 species were added from 1990 to the 2000s; and from 2000 to 2024, 232 new species were added. In other words, most of the new species have been added since 2000, which shows that fish taxonomy research in Taiwan not only has successors but is also continuously developing (Figure 2).

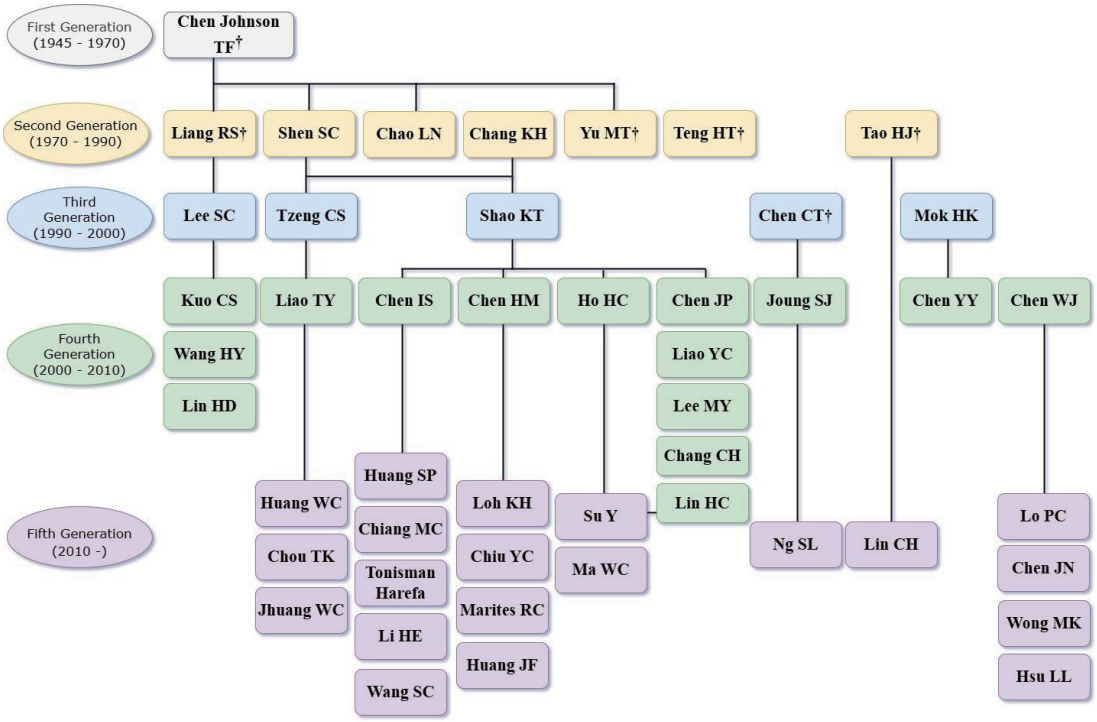

Figure 2. Since Taiwan's restoration in 1945, Taiwanese fish taxonomists can be roughly divided into five generations based on teacher-student relationships, with a total number of at least 50 individuals. Priority is given to scholars who hold a doctoral degree or academic position, have published new species, and are currently or expected to remain actively engaged in fish systematics research.

Over the past 20 years, the fish collections of the National Museum of Marine Biology and Aquarium, the Biodiversity Research Center of Academia Sinica, and National Taiwan University have grown significantly, attracting many international scholars to conduct research. Barry Russell (Nemipteridae, Synodontidae) from the Northern Territory Museum in Australia has visited Taiwan many times for research. Martin Gomon of Museum Victoria in Australia (*Cherodon, Hoplostethus, Chlorophthalmus*), John Sparks' team of the American Museum of Natural History (Leiognathidae), Hiroyuki Motomura's laboratory at Kagoshima University, Japan, Kunio Amoka (Bothidae), Kazuhiro Nakaya (cartilaginous fishes), and Toshio Kawai (Peristidiidae) of Hokkaido University have all made frequent visits in recent years. These scholars have collected a large number of samples, which has directly led to the publication of many collaborative studies (Chakrabarty et al., 2010; Nakaya et al., 2013, 2020; Russel & Ho, 2017; Amaoka & Ho, 2018, 2019, 2022).

Marine Research of the National Academy of Marine Research
DOI: 10.29677/MR.202506_5(1).0001

In addition, the frozen (cryobank) genetic tissue specimens of fish, supported by the Forestry and Conservation Administration of the Ministry of Agriculture, are stored in the Biodiversity Research Center of Academia Sinica. These include approximately 2,020 species, 5,689 liquid nitrogen specimens, and 14,345 alcohol-preserved specimens; backup specimens are housed at the Animal Research Institute's Seed Preservation Center at Hsinhua District, Tainan City. All specimen information, including access rules and sampling procedures, can be viewed on the website (https://taibol.biodiv.tw/). The main purpose of both the liquid nitrogen and alcohol-preserved specimens is to support research on molecular identification or molecular evolution. The COI database is also being actively built in conjunction with the international Fish-BOL project. This resource is believed to be highly helpful for future research on the identification of fish eggs, larvae, adult fish, and stomach contents, as well as for phylogenetic identification, phylogeography, and marine conservation. For example, Dr. Chia-Hao Chang, who graduated from the Department of Biotechnology at National Chiao Tung University in 2015, specializes in evolutionary biology and phylogenetic genomics. A study on the phylogenetic relationships of fishes in the subfamily Acheilognathinae showed that there are approximately 72 species and six valid genera in this group (Chang et al., 2014). A cryptic new species of the genus *Synagrops* was also recently published (Mediodia et al., 2024). Dr. Chang has compiled and published a list of barcodes of Taiwan's ray-finned fishes (Chang et al., 2017), and has used barcodes to test whether commercially available aquatic products mislead consumers (Chang et al., 2016a).

With the support of the National Digital Archive Program (TELDAP), Chien-Hsiang Lin assisted Chih-Wei Chang of the National Museum of Marine Biology and Aquarium in collecting thousands of fish otolith specimens, which have been archived at the Biodiversity Research Center of Academia Sinica. Together, they also published the *Otoliths Atlas of Taiwan Fishes* (Lin & Chang, 2012). In addition to adult fish specimens, the Biodiversity Research Museum of Academia Sinica also houses X-ray photos of bones, as well as specimens of fish eggs and larval fishes, all of which can be searched using the Taiwan Fish Database.

4 GEOGRAPHICAL DISTRIBUTION, GEOGRAPHICAL AFFINITY, AND FORMATION MECHANISMS OF TAIWAN'S FISHES

In the 1990s, with the support of the National Science Council and the Council of Agriculture, Kwang-Tsao Shao began conducting annual systematic and regional surveys of fish community structures on coral reefs (via diving) and in muddy and sandy areas (via bottom trawling) in Taiwan and its adjacent islands. These efforts also included research on geographical distribution and the establishment of a fish database. In addition to adding many new species and newly recorded species, the research results allowed scientists to infer distribution patterns of Taiwan's marine fishes. Several factors likely contribute to the high biodiversity of Taiwan's fish and marine life: (1) Taiwan's geographical location is unique: It lies on the edge of the world's largest landmass, the Eurasian continental plate, and the continental shelf region, encompassing both deep-sea and continental shelf marine environments; (2) it is situated on the northern edge of the East Indies Archipelago or Coral Triangle, where the world's richest marine biodiversity is found; (3) it is located at the intersection of three Large Marine Ecosystems (LMEs), the East China Sea, the South China Sea, and the Kuroshio Current, which creates an "ecotone" effect; (4) Taiwan's waters support high habitat diversity, including a wide range of ecological factors such as complex substrates, topography, water depths, ocean currents, and water temperature gradients. These contribute to the formation of various coastal marine ecosystems, such as coral reefs, estuaries, mangroves, seagrass, beaches, mudflats, algae reefs, sandy barrier lagoons, and rocky shores, all of which provide suitable habitats for the growth of various marine life.

Marine Research of the National Academy of Marine Research
DOI: 10.29677/MR.202506_5(1).0001

For example, the west coast consists mainly of sandy shallows, and the average depth of the Taiwan Strait is less than 50 meters. Apart from surface-dwelling migratory species, most fish here are bottom-dwelling or benthic species inhabiting sand and mud. In addition, the west coast hosts numerous estuaries and mangrove forests. On the contrary, the water depth off the east coast can reach thousands of meters, supporting many deep-sea fish. Coral reefs are distributed at the northern and southern ends of Taiwan, as well as several neighboring islands including Penghu, Hsiaoliuciu, Green Island, and Lanyu. (5) The eastern, southern, and neighboring islands such as Hsiaoliuchiu are mainly affected by the northward movement of the warm Kuroshio Current, while the northern part and Penghu are influenced by the southward movement of the cold current from the coast of Fujian and Zhejiang on the mainland. As a result, the temperature difference between the north and the south can reach four to five degrees Celsius in winter. Therefore, there are obvious differences in the marine species found in the northern and southern waters of Taiwan, with the dividing line near the northeast corner of Taiwan and Dongji Islet in Penghu (Shao et al., 1999; 2002b) (Figure 3). In addition, Taiwan also has many "geminate species" of Pacific and Indian Ocean origin, which are closely related sister species with very similar morphology due to speciation caused by the rise and fall of sea levels during the ice age. These species appear simultaneously on the southeast and northwest sides of Taiwan. It is truly rare for an island that is only 394 kilometers long to have two different underwater landscapes and marine species. This also provides scholars with an ideal research location and valuable materials for systematic classification, geographical distribution, ecological conservation, resource utilization, and more.

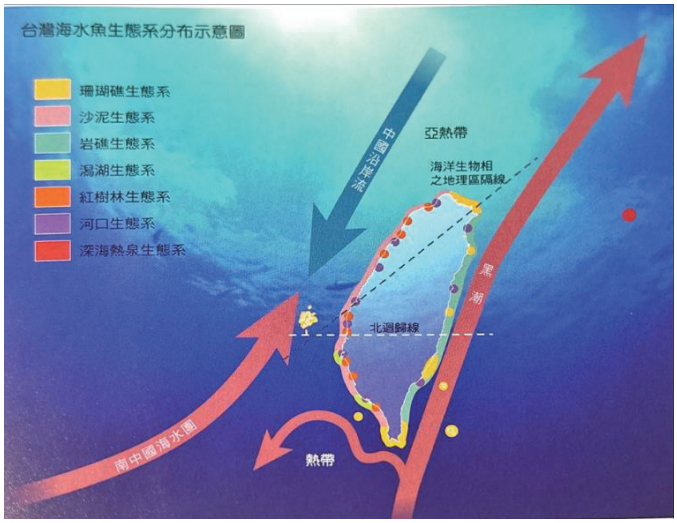

Figure 3. The distribution types of marine fish in Taiwan are mainly influenced by ocean currents and habitat (ecosystem) types. (Quoted from Shao et al., 2004)

As for the geographical distribution of freshwater fish and its formation mechanisms in Taiwan, there are three different views. The first zonation, proposed by Chyng-Shyan Tzeng, designates three geographical regions—East, South and North-Central—based on the distribution of representative fish species in each region (Tzeng, 1986a; Shao et al., 1992). The second zonation scheme, proposed by Chen and Fang (1999), contains six geographical regions—East, South, Northwest, Southwest, Hengchun, and Lanyu (Figure 4)—based on molecular phylogenetic analysis studies of certain species of Cyprinidae, Cobitidae, and Gobiidae.

Marine Research of the National Academy of Marine Research
DOI: 10.29677/MR.202506_5(1).0001

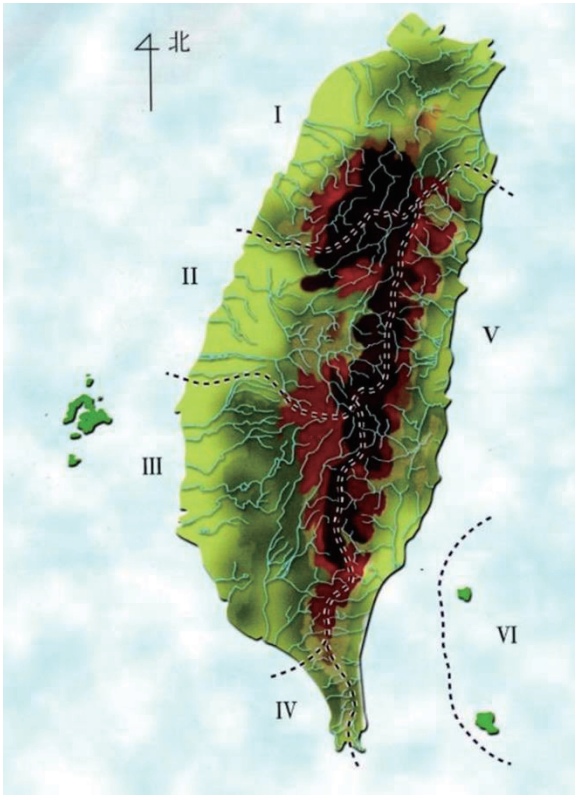

Figure 4. According to Chen and Fang (1999), the geographical distribution types of freshwater fish in Taiwan can be divided into six geographical regions: (I). Northern Taiwan Region; (II). Central Taiwan Region; (III). Southern Taiwan Region; (IV). Hengchun Peninsula Region; (V). Eastern Taiwan Region and (VI). Lanyu Green Island Region (which has no primary freshwater fish).

In the past 20 years, due to the influence of the so-called high impact factor of SCI journals publishing molecular systematic papers, many fourth-generation scientists have included molecular evolution or phylogeography studies alongside traditional morphological classification methods when guiding graduate students. For example, after his retirement, Sin-Che Lee continued working with his former student, Hurng-Yi Wang of the National Taiwan University Medical School, and Hong-Du Lin, who teaches at the Affiliated School of National Tainan First Senior High School. They have used DNA sequencing to study the geographical affinities of freshwater fishes. By comparing the genetic structure of similar species, closely related species, or populations in mainland China and Southeast and Northeast Asia, they have been able to identify species (new species, subspecies, valid species, or endemic species), as well as determine their origins, distribution paths, or mechanisms of speciation.

Based on their study results, the third zonation scheme for Taiwan's freshwater fish divides the island into four regions, corresponding to four major geographical formations: the Central Mountain Range, Taoyuan Plateau, Miaoli Plateau, and Taiwan Plateau. These are: (1) the Lanyang freshwater region, (2) the Touhou and Houlong regions, (3) the central region (Da'an, Dajia, Dadu, Zhuoshui), and (4) the southeastern region (Zengwen, Kaoping, Hualien, Xiuguluan, Beinan) (Wang et al., 2004; Lin et al., 2008; Liao et al., 2008; Jean et al., 2014; Chang et al., 2016b; Chiang et al., 2017).

Taiwan's primary freshwater fishes entered the island mainly via land connections during the last Ice Age. Three main routes can be inferred: (1) The northern origin route—from the Zhejiang River system into the northern freshwater river system of Taiwan, such as: *Squalidus* (Yang et al., 2012) and *Hemibarbus labeo* (Lin

DOI: 10.29677/MR.202506_5(1).0001

et al., 2010); (2) the middle origin route—from the Minjiang River in Fujian to the Miaoli platform water system in Taiwan, for example: Taiwan shovelhead fish (*Onychostoma barbatulum*) (Wang et al., 2004) and Taiwan stone barb (*Acrossocheilus paradoxus*) (Ju et al., 2018); and (3) the southern origin route—from the water system east of Lianhua Mountain in Guangdong to the southern Taiwan water system, for example: striped barb (*Barbodes semifasciolatus*) (Wang et al., 2023). Some species that migrate bilaterally or whose larvae and juveniles go to sea, such as the bignose goby (*Rhinogobius gigas*) (Liao et al., 2021) and the Japanese baldhead shark (*Sicyopterus japonicas*) (Ju et al., 2013), may have spread from the south via ocean currents such as the Kuroshio Current.

5 OVERVIEW OF THE CLASSIFICATION OF FISH EGGS AND LARVAE

The early life stage of fish is also referred to as ichthyoplankton, a type of zooplankton that includes fish eggs and the various developmental stages of larvae and juveniles. Helfman et al. (2009) further divided larvae and juveniles into two distinct periods: the larval period before metamorphosis and the juvenile period after metamorphosis. Fish taxonomists can generally be divided into three types: those who specialize in adult fish, fry, and eggs. The number of experts in adult fish classification is often more than ten times greater than the number of experts specializing in larval fishes and fish eggs. The main reason is that larval fishes are small in size, have few distinguishing characteristics, and are difficult to classify.

The earliest attempts to identify fish eggs in Taiwan were made in Kwang-Tsao Shao's laboratory. In addition to examining the egg shape, egg diameter, and the size and number of oil globules, electron microscopy was also used to observe the morphology of the egg membrane and the ovum (Chen et al., 1999, 2007a). For example, Shao et al. (2001) used both optical and electron microscopy to identify about 150 species in the waters around the Yanliao Bay Nuclear Power Plant No. 4 from 1995 to 2000 and published the *Illustrated Guide to Fish Eggs in Taiwan's Waters.* Professor Tai-Sheng Chiu of the Department of Zoology at National Taiwan University collected numerous larval fish specimens while he was conducting the National Science Council's Kuroshio Edge Exchange Processes (KEEP) Project. He also published the *Illustrated Guide to Larval Fish in Taiwan* (Chiu, 1999). Dr. You-Tze Wang of the Taiwan Fisheries Research Institute, Hong-Yan Hsieh and Te-Yu Liao of Sun Yat-sen University, Ming-Yi Luo of the National Museum of Marine Biology and Aquarium, and Ming-An Lee of the National Taiwan Ocean University have also carried out identification work on larvae and juveniles when implementing various projects. However, relying solely on morphological characteristics often results in difficulties confirming species identity.

Fortunately, in 2003, a method using mitochondrial DNA fragments, such as CO1, a sequence of about 650 bp of mitochondrial cytochrome c oxidase 1, as a barcode for species identification was proposed and widely adopted (Herbert et al., 2003). This approach led to new breakthroughs in basic research and applications in the classification, ecology, evolution, and conservation of marine life. In particular, it addressed the problem that, in the past, the error rate of identifying fish eggs and larval fish based solely on morphology could reach as high as 70% to 80% (Ko et al., 2013). In addition, barcoding revealed that postflexion or settlement-stage larvae have the ability to swim and choose habitats (e.g., substratum type and proximity to the shore) (Ko, 2007). Yen-Wei Chang once attempted to use life barcode sequences to identify the species of late larvae, and then compiled a key table of 30 species of damselfish in nine genera based on their external morphology (Chang et al., 2019). Chiu (2023) explored the accuracy of the comparison results based on the barcode database established from the morphological classification of adult snake eels produced in Taiwan, which identified the eggs and leptocephali larvae of snake eels collected in the waters around Taiwan and integrated the species information of the pelagic and adult stages.

Marine Research of the National Academy of Marine Research
DOI: 10.29677/MR.202506_5(1).0001

The success rate of using DNA to identify species depends on whether the barcode database for the genes used is complete. Over the past 20 years, Academia Sinica has collected barcode data on 2,500 species of fish in the Taiwan Fish Database and the Taiwan Barcode of Life Database (TaiBOL). DNA has been used to identify tens of thousands of fish egg and larval fish specimens, along with their ecological distribution data in the waters around Taiwan. These data have been provided to the National Ocean Database And Sharing System (NODASS) for public online access (https://nodass.namr.gov.tw/edna/sequencesCO1/).

At the end of 2024, Kwang-Tsao Shao's team and the National Academy of Marine Sciences cooperated to publish the illustrated book *The Eighteen Transformations of Fish: Eggs and Larvae of 500 Taiwan Fishes.* This is the world's first illustrated book featuring a total of 505 Taiwanese fish eggs and fish larvae identified by DNA (Shao et al., 2024). This information can be used to understand the spawning periods and spawning grounds of various fish species and is important for marine ecological impact assessments, the management and sustainable use of fishery resources, marine spatial planning, and the planning of marine protected area networks. For example, it can be used to accurately estimate the economic losses caused by power plant entrainment and impingement (Figure 5), and to explore whether it can help reduce the impact of noise on fish during the construction of offshore wind turbines.

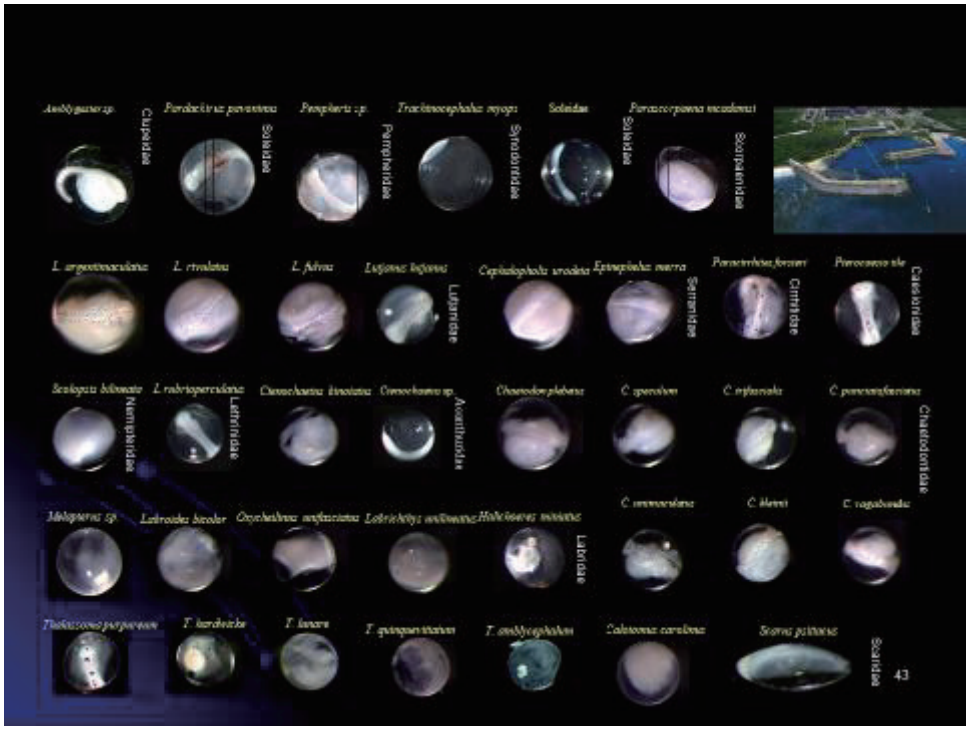

Figure 5. Assessment of economic losses to fisheries caused by entrainment and impingement at nuclear power plants - The use of DNA barcodes can accurately identify the species of fish eggs and larval fishes.

DOI: 10.29677/MR.202506_5(1).0001

6 COOPERATION AND EXCHANGE IN FISH RESEARCH BETWEEN TAIWAN AND CHINA

More formal and organized exchanges in ichthyological research between the two sides of the Taiwan Strait started after the "1992 Consensus" was reached in 1992, marking the start of increasingly active academic collaboration. The Chinese Society of Limnology and Ichthyology established an Ichthyology Society at South China Normal University in Guangdong in 1995 and invited several ichthyologists from Taiwan to attend its first meeting. In 1999, the Ichthyological Society of Taiwan was established with the aim of promoting basic research on the systematic classification, evolution, ecology, physiology, behavior, morphology, genetics, development, and conservation of fish, as well as the sustainable use of fishery resources. The first chairman of the board was Shih-Chieh Shen, professor in the Department of Zoology at National Taiwan University, while Dr. Chyng-Shyan Tzeng of the Department of Life Sciences at National Tsing Hua University served as the executive secretary. At that time, the International Symposium and Workshop on Fish Systematic Classification, Ecology and Physiology was held, and several pioneering ichthyologists from China, including Professors Si-Zhong Li, Han-Lin Wu, Yun-Fei Wu, Xiang-Lin Chen, and Shu-Yuan Qiu, were invited to Taiwan to attend the meeting. In 2005, in conjunction with the 7th Indo-Pacific Fish Conference, the first Cross-Strait Ichthyology Symposium was held at National Tsinghua University in Hsinchu City (Figure 6).

Figure 6. The first Cross-Strait Ichthyology Symposium was held at National Tsing Hua University in 2005. First row from left: Chyng-Shyan Tzeng, His-Jen Tao, I-Hsun Ni, Yun-Fei Wu, Kwang-Tsao Shao, Ning Chao, Shih-Chieh Shen, Xiang-Lin Chen, and Jian-Ping Wang.

Marine Research of the National Academy of Marine Research
DOI: 10.29677/MR.202506_5(1).0001

Afterward, with the strong support of Chinese Academician Yi-Yu Chen, a fish scholar who later became chairman of the National Natural Science Foundation of China, and another Chinese Academician Wen-Xuan Cao, chairman of the China Ichthyology Society and the Institute of Hydrobiology of the Chinese Academy of Sciences in Wuhan, Taiwan was invited to participate in the ichthyology seminars held every two to four years and to deliver keynote speeches at these conferences. A total of seven bilateral meetings have been held since 1999, including in Xiamen (1999; Figure 7), Chengdu (2001), Chongqing (2004), Shanghai (2006), Xinjiang (2010), Lanzhou (2012), and the most recent in Tianjin (2014). Each time, about a dozen to twenty faculty and graduate students from Taiwan were invited to participate, delivering oral research reports or presenting posters. Kwang-Tsao Shao was invited to give a keynote speech at each meeting. The topics ranged from taxonomy, geographical distribution, ecological conservation, fish database, research on fish eggs and larval fishes, marine protected areas, and the sustainability of fishery resources.

Figure 7. Ichthyologists from both sides of the Taiwan Strait gathered at Academia Sinica. From left: Shun-Ping Ho, Chyng-Shyan Tzeng, Sin-Che Lee, Kwang-Tsao Shao, Yi-Yu Chen, Shih-Chieh Shen, Yi-Feng Chen, Jeng-Siang Liu. (Photo source: Taiwan Aquatic News, April 27, 1999)

However, these exchanges were interrupted after 2016 due to tensions in cross-strait relations. The largest cross-strait exchange was the 7th Indo-Pacific Fish Conference (IPFC7), held by Kwang-Tsao Shao in Taipei in 2005. More than 40 Chinese scholars were invited to participate in the Cross-Strait Fish Conference, which was held simultaneously with IPFC7 (Figure 8). The successive presidents of the Taiwan Ichthyological Society, following Shih-Chieh Shen and Kwang-Tsao Shao, were Chyng-Shyan Tzeng, Peng-Peng Huang (fish physiologist), Jen-Chieh Hsiao, and Te-Yu Liao. Each term lasts three years, with candidates eligible for one re-election. The general meeting of members, scheduled for June 2025, will oversee the next re-election.

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Figure 8. IPFC7 group photo, held at Howard Plaza Hotel, National Taiwan University, Taipei.

Although formal exchanges between scholars from China and Taiwan have been temporarily suspended, individual exchanges or invitations among scholars have continued. For example, Chyng-Shyan Tzeng was often invited to China to provide guidance on freshwater conservation and the construction of fish ladders. I-Shiung Chen and his students, including Shih-Pin Huang, often traveled to Fujian and Guangdong provinces along the coast of China to collect and conduct research on freshwater fish classification. Kwang-Tsao Shao also worked with the Institute of Zoology of the Chinese Academy of Sciences in Beijing and with Shanghai Ocean University to establish cross-strait fish species lists and to work on database exchange and collaboration. Notable achievements include joint publications with Professor Han-Lin Wu (1934–2022) of Shanghai Ocean University, such as *the Latin-Chinese Dictionary of Fishes Names* (Wu et al., 1999) and the *Latin-Chinese Dictionary of Fish Names by Classification System* (Wu et al., 2012), both published by the Taiwan Fisheries Publishing House. In addition, the collaboration with Chun-Guang Zhang resulted in the publication of the *Species catalogue of China: Volume 2. Animals. Vertebrates (V)* Fishes (Zhang et al., 2021) by the China Science Press. The collaboration with Professor Min Liu of Xiamen University resulted in the publication of the *Atlas of Marine Fishes of China* (Liu et al., 2024), which was published by the Strait Bookstore. There are also several academic journal papers jointly published by scholars from Taiwan and China, including taxonomic articles on freshwater fishes by I-Shiung Chen, Chyng-Shyan Tzeng, and Hung-Du Lin, as well as systematic classification article on marine fish by Kwang-Tsao Shao. The *Key to marine and estuarial Fishes of China,* compiled and published by Han-Lin Wu during his lifetime, invited some scholars from Taiwan to contribute to the writing of several families. A total of 3,711 species were included, some of which are fish species from Taiwan (Wu & Zhong, 2021).

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7 DIFFICULTIES AND PROSPECTS OF FISH TAXONOMY RESEARCH

Fish taxonomy in Taiwan has encountered the same conundrum as the classification of other biological groups, namely, the perception among many leaders that taxonomy is a traditional and outdated discipline. As a result, job vacancies and funding have been greatly reduced, resulting in a continuous loss of expertise in traditional morphological classification. Many taxonomists have had no choice but to conduct ecological and evolutionary research at the same time.

The current evaluation method using Impact Factor (IF), commonly adopted by the National Science Council and many scientific research institutions for assessing articles in the biological field, is extremely unfavorable to taxonomists. For example, when evaluating individual research output, only the ranking of SCI journals or the numerical value of the IF—reflecting the number of citations a report or journal receives within three years—is considered, without taking into account the length of time (half-life) that the article has been cited for. Therefore, when comparing the taxonomic community, which has a relatively small number of scholars, with the molecular evolution community, which includes a larger pool of researchers, taxonomists are at a clear disadvantage. This is because the likelihood of a taxonomic report being cited within three years is much lower than that of a report on molecular evolution. Moreover, many important taxonomic reports are published in the form of special issues, books, atlases, or databases, or appear in non-SCI journals. Although these works may be cited frequently, they are generally not included in annual performance evaluations. If this unfair evaluation method is not reformed, taxonomic research will inevitably decline due to a lack of competitiveness in recruitment, promotion, or the renewal of academic appointments. This is also the reason why fewer and fewer young students are willing to pursue traditional morphology and anatomical studies; instead, most prefer to engage in molecular-based evolutionary and phylogeographical research. A future response strategy is to encourage students to develop expertise in the traditional taxonomy of a specific group of organisms, and then to further apply additional tools, including molecular techniques, to explore evolution, ecology, physiology, conservation, and even bionics research, to avoid the conundrum of a lack of new recruits entering the field of fish taxonomy.

The rapid loss of Taiwan's fish diversity represents another major crisis. The causes are generally attributed to human factors such as: (1) overfishing and bycatch, (2) habitat destruction, (3) pollution, and (4) introduced and invasive species; as well as natural factors such as (5) global climate change, which is largely driven by human activity. The number of endangered species among Taiwan's stream freshwater fish has increased from 10 in the past to 18 now. For marine fish, overfishing is the most serious problem. According to recent long-term surveys of fish communities in rocky tidal pools and the impingement data from Nuclear Power Plants I & II in northern Taiwan (Chen et al., 2010; Ho, 2023), large, economically valuable species have disappeared in large numbers, while smaller species such as blennies and gobies have increased. If this trend continues, not only will future generations be unable to eat wild-caught fish from the sea or see beautiful coral reef fish while diving, but students wishing to conduct fish taxonomy research may also be unable to obtain research materials.

Marine Research of the National Academy of Marine Research
DOI: 10.29677/MR.202506_5(1).0001

Although the Conference of the Parties to the Convention on Biological Diversity required countries to pay attention to and strengthen taxonomic research, and proposed the Global Taxonomy Initiative from 2000 to 2010, its effectiveness is still unknown. At that time, the international community was also vigorously promoting the integration of biodiversity information, or biodiversity informatics. With the advancement of information technology, the establishment of literature, specimen distribution, and audio-visual databases, as well as DNA barcoding and even AI, enabled taxonomists to conduct research more quickly and conveniently. Taiwan has also followed the international trend. In 2001, the Executive Yuan issued a biodiversity promotion plan, which set out the need to strengthen taxonomic capacity building and to establish biodiversity databases and share them publicly. The plan includes work projects, deadlines, and indicators, such as supporting taxonomic research, compiling biodiversity atlases, and establishing databases. Therefore, more than ten Biota of different taxa were published in the decade from 2004 to 2014, but fishes were not included. During this period, although many fish illustrations or guidebooks were published, most of them were based on scientific education and commercial value. There are relatively few academic fish atlases that focus on classification, including the *Fishes of Taiwan* by Shih-Chieh Shen and Gao-Yi Wu (2011) and the *Fishes of Southern Taiwan I & II,* co-authored by Keita Koeda and Hsuan-Ching Ho (2019).

Taiwan's fish taxonomy research capabilities are already at the forefront internationally. As a result, in May 2005, Taiwan won the right to host the 7th Indo-Pacific Fish Conference; in September 2007, it was also invited to host the 2nd International Barcode of Life Conference; and in June 2025, it will host the 12th Indo-Pacific Fish Conference and the Asian Ichthyology Conference organized by Wei-Jen Chen. Therefore, we very much hope that the government will pay attention to and strengthen basic taxonomic research, and that it will value, make good use of, and protect Taiwan's unique biodiversity resources. Looking to the future, the most urgent task should be to cultivate young and outstanding taxonomic talents so that the torch can be passed on to them. We also hope that the government can support taxonomic scholars in conducting research and surveys, compiling and publishing biological annals, improving and expanding museum specimens, training and employing talents, and integrating and maintaining databases, etc.

8 ACKNOWLEDGEMENTS AND REMARKS

First of all, the authors would like to thank the guest editor of this special issue, Professor Hong-Young Yan, for inviting us to draft the manuscript of this article. If we count from Dr. Johnson Ta-Fu Chen as the first generation of fish taxonomists after WWII, it has been about 80 years since then, and now the sixth generation should start playing a major role. As basic taxonomy declines globally, brain drain has become another crisis for biodiversity conservation. However, Taiwan's fish taxonomy level and research results are still internationally renowned. The main reason for this, in addition to Taiwan's rich fish diversity, is the outstanding performance of some third- and fourth-generation fish taxonomists over the past 20 years, including Hsuan-Ching Ho, Wei-Jen Chen, I-Shiung Chen, Te-Yu Liao, and Hurng-Yi Wang. As part of the third or fourth generation, the author should also fulfill the responsibility of carrying on the past and ushering in the future. In addition, writing this article required collecting and verifying the accuracy of a large amount of information, which is definitely not something the author could accomplish alone. Therefore, we would like to thank more than a dozen senior and junior fish taxonomists for their great assistance and for providing information about their respective fish taxonomic achievements. We believe that with the efforts of the new generation, they will be able to surpass their predecessors.

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