Zoological Studies **63**:37 (2024)
doi:10.6620/ZS.2024.63-37

Zoological Studies

Open Access

Checklist and DNA Barcoding of the Scorpaenidae (Teleostei: Scorpaeniformes) in Taiwan

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Received 19 January 2024 / Accepted 26 June 2024 / Published 25 December 2024
Communicated by Chien-Hsiang Lin

Species of the family Scorpaenidae are easily misidentified due to their similar appearances, a result of camouflaging to their surroundings. In recent years, many species from this family have been described, and generic placements of some species have been revised. Previously, there were 80 species belonging to 29 genera of the Scorpaenidae recorded in Taiwanese waters. However, their taxonomy has not been revised for decades. It is necessary to update the checklist of the Scorpaenidae occurring in Taiwanese waters based on updated morphological and molecular data. In the present study, we revised the Taiwanese scorpaenids based on 296 specimens and updated the checklist, amounting to a total of 85 species of 29 genera, of which *Sebastapistes mauritiana* (Cuvier) is a new record, and three species from the genera *Phenacoscorpius*, *Scorpaenopsis*, and *Sebastapistes* are unable to be identified to any species. Using molecular analysis, we conducted the first comprehensive DNA barcoding study of the Scorpaenidae from Taiwanese waters based on a partial cytochrome *c* oxidase I (*COI*) gene of 655 bps. A total of 118 *COI* sequences were generated from voucher specimens of 66 species (28 genera) identified based on morphological characters. The *COI* sequences of *Parascorpaena maculipinnis*, *Scorpaena pepo*, and *Scorpaenopsis orientalis* are new to online databases. According to the Kimura-2 Parameter (K2P) genetic distance, the mean interspecific variation (15.61%) was distinctly greater than the mean intraspecific variation (0.22%), suggesting a barcoding gap. The maximum likelihood tree showed that all lineages were supported by high bootstrap values.

Key words: Diversity, Ichthyofauna, Mitochondrion, Stonefish, Taxonomy

BACKGROUND

Members of the family Scorpaenidae are known for the venomous spines on their dorsal, pelvic, and anal fins (Allen and Eschmeyer 1973; Nelson 2006), and their ability to camouflage with their surroundings using variable color patterns, tentacles, flaps, and barbels (Poss 1999; Randall and Eschmeyer 2002; Krzyżak and Korzeniewski 2021). This family is distributed in a variety of habitats, such as intertidal and sublittoral zones, sandy substrates, coral reefs, rocky reefs, and continental shelves with a depth range from 0 to 1,600 m (Masuda et al. 1984; Fedorov et al. 2003; Poss and Eschmeyer 2003; Randall 2005a).

The Scorpaenidae are a species-rich family, composed of 36 genera and more than 350 valid species (Nelson et al. 2016; Fricke et al. 2024), but their definition has been contentious (Matsubara 1943; Washington et al. 1984; Ishida 1994; Poss 1999; Imamura 2004; Shinohara and Imamura 2005; Smith

Citation: Chou TK, Huang WC, Jhuang WC, Liao TY. 2024. Checklist and DNA barcoding of the Scorpaenidae (Teleostei: Scorpaeniformes) in Taiwan. Zool Stud **63:**37. doi:10.6620/ZS.2024.63-37. doi:10.6620/ZS.2024.63-37.

et al. 2018). In the present study, the definition of the Scorpaenidae follows the classification of Smith et al. (2018) which was based on morphological and molecular characteristics of a large number of Scorpaeniformes specimens. Poss (1999) and Smith et al. (2018) proposed that this family is characterized by the presence of a suborbital stay firmly connected to the preopercle, spines on head, gill membranes free from isthmus, compressed body, presence of scales, 24 to 30 vertebrae, venomous glands of the dorsal, anal, and pelvic fin spines, dorsal fin with XII to XIII spines (rarely VIII), anal fin with III spines (rarely II), pelvic fins with one spine and five rays, and a well-developed pectoral fin with lower rays unbranched. Morphological identification of scorpaenids has been considered difficult because of limited diagnostic characters and variable color patterns based on surroundings for most species (Poss 1999; Randall and Eschmeyer 2002; Randall 2005a b; Krzyżak and Korzeniewski 2021). In the last two decades, most taxonomic work on Scorpaenidae was conducted based on specimens from the western Pacific, including descriptions of new species and/or synonymizations of nominal species in the genera *Brachypterois*, *Dendrochirus*, *Pterois*, *Scorpaena*, *Scorpaenopsis*, *Sebastapistes*, *Sebastiscus*, *Parascorpaena*, *Lythrichthys*, *Neomerinthe*, *Phenacoscorpius*, *Pteroidichthys*, *Scorpaena*, and *Scorpaenodes* (Randall and Eschmeyer 2002; Allen and Erdmann 2008; Motomura 2008 2009; Motomura and Senou 2008; Motomura et al. 2010a b 2014 2015 2016; Matsunuma et al. 2013 2017; Motomura and Kanade 2015; Matsunuma and Motomura 2015 2019; Morishita et al. 2018; Wibowo and Motomura 2019a b; Hoshino and Motomura 2021; Wada et al. 2021; Chou and Liao 2022; Chou et al. 2023; Matsumoto et al. 2023; Matsumoto and Motomura 2024). Among these studies, only Matsunuma et al. (2017), Wada et al. (2021), Chou and Liao (2022), and Chou et al. (2023) provided molecular characters of scorpaenids.

In Taiwan, the first study on the diversity of the Scorpaenidae was Chen (1969)'s synopsis of the vertebrates of Taiwan, in which 13 species from nine genera were recorded. Later, Chen (1981) revised the taxonomy of the Scorpaenidae from Taiwan and recorded 42 species of 25 genera, and Shen et al. (1993) updated the list to 48 species of 26 genera. Recent taxonomic studies of the Scorpaenidae have greatly expanded the biodiversity of this fish group in Taiwan (Randall and Eschmeyer 2002; Chen 2003; Motomura et al. 2007 2009a b 2010a 2011; Shao et al. 2008; Motomura and Senou 2009; Chen et al. 2010; Shen and Wu 2011; Morishita et al. 2018; Koeda and Ho 2019; Koeda et al. 2019; Chou 2021; Chou and Tang 2021; Wada et al. 2021; Chou and Liao 2022), amounting to a total of 80 species placed in 29 genera. Despite the increased number of recorded species, there was no taxonomic revision of the Scorpaenidae made from Taiwanese waters after Chen (1981). Furthermore, generic placements of some species have changed (Randall and Poss 2002; Motomura et al. 2010b; Poss et al. 2010; Wada et al. 2021), and some species in the western Pacific were considered junior synonyms or misidentifications (Nakabo 2002; Motomura et al. 2009a b 2010b 2015; Wibowo and Motomura 2019a b; Hoshino and Motomura 2021; Wada et al. 2021). These recent taxonomic works imply that the checklist of scorpaenids in Taiwan needs revision based on museum collections and recent taxonomic literature. In addition, DNA barcoding is needed to provide molecular references for the scorpaenids of Taiwan.

In the present study, we aimed to: (a) provide a reliable DNA barcoding reference of the Scorpaenidae from Taiwanese waters based on morphological examination; and (b) update the checklist of the Scorpaenidae present in Taiwan.

MATERIALS AND METHODS

Sampling and morphological analyses

Fresh specimens were collected in Taiwanese waters from 2017 to 2022 using hand nets and angling, as well as purchasing from local fish markets. Several islands around Taiwan were also surveyed, including Penghu, Liuqiu, Lanyu (Orchid Island), and Green Islands (Fig. 1). Fresh specimens were fixed in 10% neutral buffered formalin and preserved in 70% ethanol thereafter. Some examined materials were loaned from museum collections of the Academia Sinica Institute of Zoology, Taipei (ASIZP), and the National Museum of Marine Biology and Aquarium (NMMB-P), Pingtung. At least five specimens per species were examined whenever possible. The definition of habitat types in Taiwan followed Shao et al. (2008). Terminology and definitions of morphometrics and meristics generally followed Motomura (2004a b), Motomura et al. (2005a–c), and Motomura and Johnson (2006). The terminology of head spines followed Randall and Eschmeyer (2002). The meristics were examined on the left side of fish. The last two rays of the dorsal and anal fins were counted as one. The vertebra count was determined by X-radiographs. Measurements were carried out using a digital caliper with 1 mm precision. At least two tissue samples per species (when possible) were taken from the fin clips or dorsal muscle and preserved in 95% ethanol. Some tissue samples were loaned from the cryobank of the Research Center for Biodiversity of Academia Sinica. Voucher specimens collected in this study were deposited in ASIZP, Department of Oceanography, National Sun Yat-sen University, Kaohsiung (DOS), and NMMB-P.

DNA extraction, amplification, and sequencing

DNA was extracted from tissue samples using GeneMark Easy Tissue & Cell Genomic DNA Purification Kit following the manufacturer's protocol. The polymerase chain reaction (PCR) was used to amplify the cytochrome *c* oxidase subunit I (*COI*) gene. PCR products were amplified in a 25 µL volume containing 3 µL of 10X Taq Buffer, 2 µL of dNTP mixture at 10 mM, 1 µL of forward and reverse primers at 5 µM, 0.13 µL of Pro Taq Plus DNA polymerase (Protech Technology Enterprise, Taiwan), 1 µL of template DNA, and 16.87 µL of ultrapure water. The *COI* fragment was amplified using Ward et al.'s (2005) universal *COI* primers, and ScorF (5'-CTCAGCCATCCTACCTGTGG-3') and ScorR (5'-ACTTCTGGGTGRCCGAAGAA-3') designated by the present study. The thermal PCR condition of *COI* was composed of an initial denaturation step at 95°C for 4 min, then 35 cycles of 94°C for 30 s, 48°C for 30 s and 72°C for 1 min, and a final extension at 72°C for 10 min. PCR products were visualized on 2% agarose gels and subsequently purified using SAP-Exo Kit (Jena Bioscience). PCR products were sequenced in both forward and reverse directions by a biotechnology company (Genomics, Taiwan). The forward and reverse sequences were edited and assembled using BioEdit ver. 7.2.5 (Hall 1999). All sequences were deposited in Genbank (Table S1).

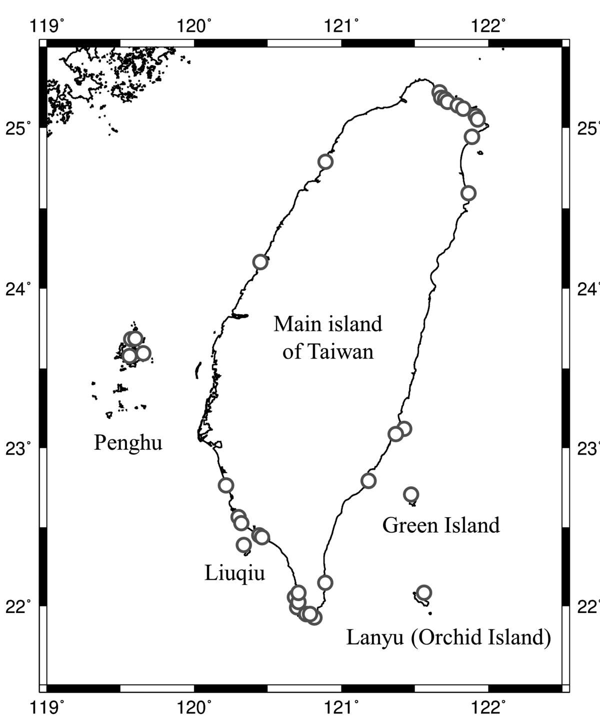

Fig. 1. Map of sampling sites in this study.

Sequence analysis

DNA sequences were aligned using ClustalW (Thompson et al. 1994) in BioEdit ver. 7.2.5 (Hall 1999). The substitution saturation of *COI* mutation was tested using DAMBE ver. 7.0.10 (Xia 2018). The Kimura-two parameter (K2P) model was implemented for *COI* gene in phylogenetic reconstruction and distance metrics among species. Phylogenetic analysis of *COI* sequences was conducted with the Maximum likelihood (ML) method using MEGA ver. 10.1.1 (Kumar et al. 2018). Branch support value was assessed using the bootstrapping criterion with 1,000 replicates. *Synanceia verrucosa* (accession number: JQ432179) of the Synanceiidae was chosen as outgroup for phylogenetic analysis. Genetic divergences at different taxonomic levels (inter-generic, inter-specific, intra-specific) were calculated using MEGA ver. 10.1.1 (Kumar et al. 2018). All *COI* sequences were compared with those from public databases using Basic Local Alignment Search Tool (BLAST) on GenBank and the BOLD Identification System (IDS) (Ratnasingham and Hebert 2007; Johnson et al. 2008). Sequences with similarity values greater than 98% were considered to be conspecific (Huang et al. 2023).

Ethics statement

The study was conducted in strict accordance with the Wildlife Conservation Act in Taiwan. No ethical approval was required for this study since all species in this study were not protected species and not listed in CITES. Some specimens were collected from Liuqiu and Kenting with the approvals of the Dapeng Bay National Scenic Area Administration, Tourism Bureau (Project #NAMR110029; Collection Permit #11005508700) and the Kenting National Park Headquarters (Project #NAMR110029; Collection Permit #1091002868), respectively. All individuals were not involved in animal experiments.

RESULTS

A total of 296 scorpaenid specimens belonging to 85 species from 29 genera (Table 1) were examined and literature reviewed in the present study (Table S1, Fig. S1), of which one species, *Sebastapistes mauritiana*

Table 1. Checklist of the Scorpaenidae from Taiwanese waters

Brachypterois
Brachypterois serrulata (Richardson, 1846)/ CS; m1: *Brachypterois serrulatus*
Brachypterois serrulifer Fowler, 1938/ CS
Caracanthus
Caracanthus maculatus (Gray, 1831)/ SR
Caracanthus unipinna (Gray, 1831)/ SR
Dendrochirus
Dendrochirus zebra (Cuvier, 1829)/ SR
Ebosia
Ebosia bleekeri (Döderlein, 1884)/ CS
Ectreposebastes
Ectreposebastes imus Garman, 1899/ DCS
Helicolenus
Helicolenus hilgendorfii (Döderlein, 1884)/ DCS; m1: *Helicolenus hilgendorfi*
Hoplosebastes
Hoplosebastes armatus Schmidt, 1929/ DCS
Iracundus
Iracundus signifer Jordan & Evermann, 1903/ SR
Lythrichthys
Lythrichthys cypho (Fowler, 1938)/ DCS
Lythrichthys eulabes Jordan & Starks, 1904/ DCS
Lythrichthys longimanus (Alcock, 1894)/ DCS; c: *Setarches longimanus*
Nemapterois
Nemapterois biocellatus Fowler, 1938/ SR; c: *Dendrochirus biocellatus*
Neochirus
Neochirus bella (Jordan & Hubbs, 1925)/ CS; c: *Brachirus bellus*, *Dendrochirus bellus*
Neochirus brachyptera (Cuvier, 1829)/ SR; c: *Dendrochirus brachypterus*
Neomerinthe
Neomerinthe erostris (Alcock, 1896)/ DCS; s: *Neomerinthe rotunda*
Neomerinthe ignea Matsumoto, Muto & Motomura, 2023/ DCS
Neomerinthe kaufmani (Herre, 1952)/ DCS
Neomerinthe megalepis (Fowler, 1938)/ DCS
Neomerinthe procurva Chen, 1981/ DCS
Parapterois
Parapterois heterurus (Bleeker, 1856)/ SR; m1: *Parapterois heterura*
Parascorpaena
Parascorpaena aurita (Rüppell, 1838)/ SR; m2: *Parascorpaena picta*, s: *Scorpaena bynoensis*
Parascorpaena maculipinnis Smith, 1957/ SR
Parascorpaena mcadamsi (Fowler, 1938)/ SR
Parascorpaena mossambica (Peters, 1855)/ SR
Parascorpaena poseidon Chou & Liao, 2022/ SR
Phenacoscorpius
Phenacoscorpius megalops Fowler, 1938/ DCS
Phenacoscorpius sp./ DCS
Pontinus
Pontinus macrocephalus (Sauvage, 1882)/ DCS
Pontinus tentacularis (Fowler, 1938)/ DCS
Pteroidichthys
Pteroidichthys acutus Motomura & Kanade, 2015/ CS
Pteroidichthys amboinensis Bleeker, 1856/ CS
Pteroidichthys noronhai (Fowler, 1938)/ CS; c: *Pteropelor noronhai*
Pterois
Pterois lunulata Temminck & Schlegel, 1843/ SR
Pterois russelii Bennett, 1831/ SR; m1: *Pterois russelli*, *Pterois russellii*
Pterois volitans (Linnaeus, 1758)/ SR
Pteropterus
Pteropterus antennatus (Bloch, 1787)/ SR; c: *Pterois antennata*
Pteropterus paucispinula (Matsunuma & Motomura, 2014)/ SR; c: *Pterois paucispinula*
Pteropterus radiatus (Cuvier, 1829)/ SR; c: *Pterois radiata*

Table 1. (Continued)

Rhinopias
Rhinopias eschmeyeri Condé, 1977/ SR
Rhinopias frondosa (Günther, 1892)/ SR; m2: *Rhinopias aphanes*
Scorpaena
Scorpaena miostoma Günther, 1877/ CS; m2: *Parascorpaena picta*
Scorpaena neglecta Temminck & Schlegel, 1843/ CS; s: *Scorpaena izensis*
Scorpaena onaria Jordan & Snyder, 1900/ CS
Scorpaena pepo Motomura, Poss & Shao, 2007/ CS; m2: *Parascorpaena picta*
Scorpaenodes
Scorpaenodes albaiensis (Evermann & Seale, 1907)/ SR
Scorpaenodes evides (Jordan & Thompson, 1914)/ SR; s: *Scorpaenodes littoralis*
Scorpaenodes guamensis (Quoy & Gaimard, 1824)/ SR
Scorpaenodes hirsutus (Smith, 1957)/ SR
Scorpaenodes kelloggi (Jenkins, 1903)/ SR
Scorpaenodes minor (Smith, 1958)/ SR
Scorpaenodes parvipinnis (Garrett, 1864)/ SR
Scorpaenodes quadrispinosus Greenfield & Matsuura, 2002/ SR
Scorpaenodes scaber (Ramsay & Ogilby, 1886)/ SR
Scorpaenodes varipinnis Smith, 1957/ SR
Scorpaenopsis
Scorpaenopsis cirrosa (Thunberg, 1793)/ SR; m1: *Scorpaenopsis cirrhosa*
Scorpaenopsis cotticeps Fowler, 1938/ SR
Scorpaenopsis diabolus (Cuvier, 1829)/ SR; m1: *Scorpaenopsis diabolis*
Scorpaenopsis macrochir Ogilby, 1910/ SR
Scorpaenopsis neglecta Heckel, 1837/ SR; m2: *Scorpaenopsis gibbosa*
Scorpaenopsis obtusa Randall & Eschmeyer, 2002/ SR
Scorpaenopsis orientalis Randall & Eschmeyer, 2002/ SR
Scorpaenopsis oxycephala (Bleeker, 1849)/ SR
Scorpaenopsis papuensis (Cuvier, 1829)/ SR
Scorpaenopsis possi Randall & Eschmeyer, 2002/ SR
Scorpaenopsis ramaraoi Randall & Eschmeyer, 2002/ SR
Scorpaenopsis sp./ SR
Scorpaenopsis venosa (Cuvier, 1829)/ SR
Scorpaenopsis vittapinna Randall & Eschmeyer, 2002/ SR
Sebastapistes
Sebastapistes cyanostigma (Bleeker, 1856)/ SR; s: *Scorpaena albobrunnea*
Sebastapistes fowleri (Pietschmann, 1934)/ SR
Sebastapistes mauritiana (Cuvier, 1829)*/ SR
Sebastapistes sp./ SR
Sebastapistes strongia (Cuvier, 1829)/ SR; s: *Sebastapistes kowiensis*
Sebastapistes tinkhami (Fowler, 1946)/ SR
Sebastes
Sebastes joyneri Günther, 1878/ CS
Sebastes thompsoni Jordan & Hubbs, 1925/ CS
Sebastiscus
Sebastiscus albofasciatus (Lacepède, 1802)/ DCS; c: *Sebastes albofasciatus*
Sebastiscus marmoratus (Cuvier, 1829)/ DCS; c: *Sebastes marmoratus*
Sebastiscus tertius (Barsukov & Chen, 1978)/ DCS; c: *Sebastes tertius*
Sebastiscus vibrantus Morishita, Kawai & Motomura, 2018/ DCS
Setarches
Setarches guentheri Johnson, 1862/ DCS
Taenianotus
Taenianotus triacanthus Lacepède, 1802/ SR
Thysanichthys
Thysanichthys crossotus Jordan & Starks, 1904/ DCS

Asterisks (*) represent new records. Abbreviations: Habitat type— CS (coastal shore); SR (shallow reef, less than 60 m); DCS (deep continental shelf, deeper than 100 m depth). s - synonym; c - formerly used combination; m1 - misspelling; m2 - misidentification.

(Cuvier, 1829), was newly recorded, and three species of *Phenacoscorpius*, *Scorpaenopsis*, and *Sebastapistes* were not able to be identified to any known species. In total, 118 *COI* sequences belonging to 66 species of 28 genera were generated, in which sequences of *Parascorpaena maculipinnis*, *Scorpaena pepo*, and *Scorpaenopsis orientalis* were new to online databases (GenBank and BOLD systems). Eight species in four genera were only examined morphologically without molecular data (Table S1).

DNA barcoding

All data are available in GenBank with accession numbers and catalog numbers of voucher specimens listed in table S1. After alignment, the consensus length of all *COI* fragments was 655 bps. The saturation was tested for the entire fragment and each codon position of the *COI* sequences using DAMBE v. 7.0.10 (Xia 2018), and no signs of saturation were detected. No insertion, deletion, and stop codon were found.

The ML tree is shown in figure 2. All morphology-based species were monophyletic groups supported by high bootstrap values. Three genera of the Scorpaenidae were non-monophyletic, including *Pteroidichthys*, *Scorpaenodes*, and *Sebastapistes*. The pairwise genetic distances at different taxonomic levels are summarized in table 2. The intraspecific K2P distance was between 0 and 1.37%, with a mean of 0.22%. The maximum value was found in *Helicolenus hilgendorfii* (1.37%). The interspecific K2P distance was from 0.46 to 32.32% with a mean of 15.61%. Several species pairs had interspecific distances lower than 2%, including *Neochirus bella* vs. *Neochirus brachyptera* (0.69%), *Pterois lunulata* vs. *Pterois russelii* (0.62%), *Pterois lunulata* vs. *Pterois volitans* (0.85%), *Pterois russelii* vs. *Pterois volitans* (0.85%), and *Sebastiscus tertius* vs. *Sebastiscus vibrantus* (0.46%). Overall, the mean interspecific distances were over 70-fold higher than the mean intraspecific distances. Aside from the abovementioned five species pairs, the distribution of genetic distances (Fig. 3) also showed a barcoding gap between intraspecific and interspecific divergences. After blasting in GenBank and BOLD databases, sequences of 22 species of nine genera were found to have more than one species with similarities ≥ 98% (Table S2). Three specimens of three genera, *Phenacoscorpius*, *Scorpaenopsis* and *Sebastapistes*, were unsuccessfully identified to any species and their sequences do not match any species in the online database.

The Scorpaenidae fauna in Taiwanese waters

The updated checklist of the Scorpaenidae from Taiwanese waters is shown in table 1. The counts of dorsal, pectoral, and anal fins of all examined specimens are shown in table 3, while the standard length of all examined specimens is shown in table S1. In the present study, 11 species listed in the checklist have a lack of examined specimens and sequences, as their records are only based upon references. Remarks on the new records, species without examined specimens, taxonomically uncertain species, and species pairs with low genetic distance were provided as follows.

Iracundus signifer Jordan & Evermann, 1903

Remarks: No specimen was examined in this study. The record was based on a specimen (BPBMI23411) collected in Nanwan, Pingtung by J.E. Randall in 1978 (Chen 1981), in which some specimens were collected from Taiwanese waters.

Lythrichthys cypho (Fowler, 1938)

Remarks: No specimen was examined in this study. The record was based on Wada et al. (2021).

Lythrichthys longimanus (Alcock, 1894)

Remarks: No specimen was examined in this

Table 2. Summary of K2P genetic distances at different taxonomic levels

Taxonomic level	Distance (%)		
	Minimum	Maximum	Mean ± SE
Intra-specific (52 species)	0.00	1.40	0.22 ± 0.04
Inter-specific (41 species)	0.46	32.32	15.61 ± 0.58
Inter-generic (24 genera)	7.19	27.77	21.19 ± 0.19

SE, standard error. Species with only one sequence were excluded from intra-specific distance calculations; genera with only one species were excluded from inter-specific distance calculations within the same genus; families with only one genus were excluded from inter-genus distance calculations within the same family.

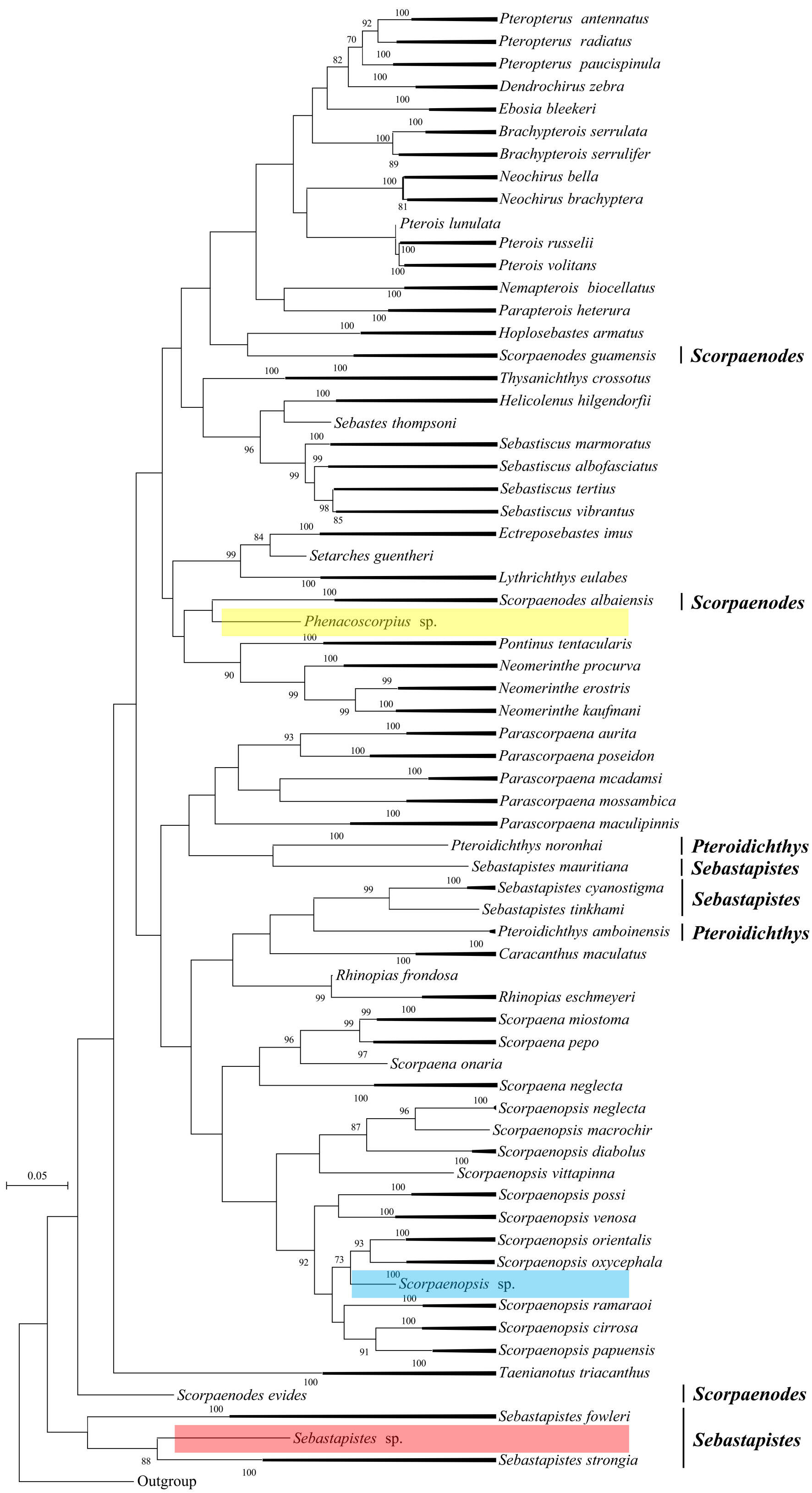

Fig. 2. The maximum likelihood tree based on 118 *COI* sequences of 66 species of the Scorpaenidae collected from Taiwanese waters. Numerals on nodes represent bootstrap values. Bootstrap values below 70 are not shown. Right hand side labels mark non-monophyletic genera. Color blocks on lineages denote the taxonomically uncertain taxa, including *Phenacoscorpius* sp. (yellow), *Scorpaenopsis* sp. (blue), and *Sebastapistes* sp. (red).

study. The record was based on Wada et al. (2021), in which some specimens were collected from Taiwanese waters.

Neochirus bella **(Jordan & Hubbs, 1925)**

Remarks: This species was proposed as a member of the *Dendrochirus* (= *Neochirus*) *brachypterus* complex due to the similarity in overall body appearance (Matsunuma et al. 2017). *Neochirus bella* could be distinguished from *N. brachyptera* by the lower count of longitudinal scale series (ca. 34 in *N. bella* vs. 45–54 in *N. brachyptera*). Based on our examined materials, the lower count of longitudinal scale series (29–33) matched the description of *N. bella*.

Neochirus brachyptera **(Cuvier, 1829)**

Remarks: The comparison between *Neochirus bella* and *N. brachyptera* was shown in the remark of *Neochirus bella*. Based on our examined materials, the higher count of longitudinal scale series (41–44) matched the description of *N. brachyptera*.

Neomerinthe ignea **Matsumoto, Muto & Motomura, 2023**

Remarks: No specimen was examined in this study. The record was based on Matsumoto et al. (2023), in which some specimens were collected from Taiwanese waters.

Neomerinthe megalepis **(Fowler, 1938)**

Remarks: No specimen was examined in this study. The first record was reported by Chen (1981) based on six specimens (CAS27744, SDSC73-37, SIO80-206, SIO80-207, SIO80-208, SIO80-221) from Tungkang, Pingtung. But these specimens showed more scales in longitudinal series (36–41), a discrepancy from the 25–30 scales in the original description (Fowler 1938; Herre 1952). These specimens are actually *N. kaufmani* based on the number of longitudinal series. We also examined a specimen (ASIZP0064297) originally identified as *N. megalepis* and found that it is a misidentification of *N. kaufmani*. However, some specimens of *N. megalepis* were collected from Taiwanese waters by Matsumoto and Motomura (2024).

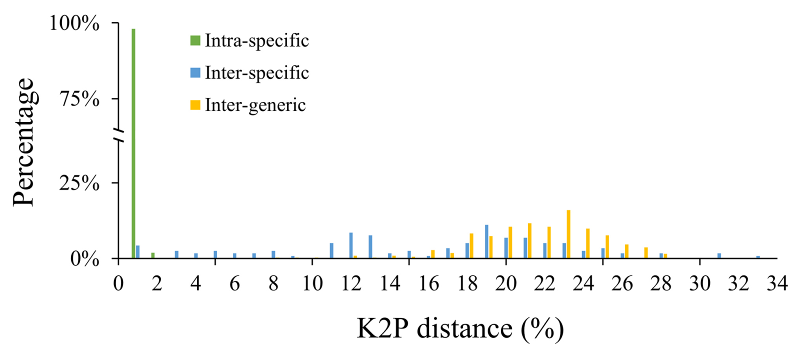

Fig. 3. Distribution frequency of K2P genetic distances (%) for *COI* of the Scorpaenidae at different taxonomic levels.

Table 3. Frequency distribution of spine and ray counts on dorsal, pectoral, and anal fins in Taiwanese species of the Scorpaenidae

	Dorsal-fin spines						Dorsal-fin rays								Pectoral-fin rays											Anal-fin spines		Anal-fin rays									
	7	8	/	11	12	13	7	8	9	10	11	12	13	14	12	13	14	15	16	17	18	19	20	21	22	2	3	4	5	6	7	/	11	12	13	14	15
Brachypterois serrulatus						5				4	1							1	4								5		5								
Brachypterois serrulifer						3				2	1								3								2		3								
Caracanthus maculatus	2	3										3	1	1	1	1	3									5							2	1	1		
Caracanthus unipinna		1								1					1											1											1
Dendrochirus biocellatus						5			5													2	3				5		5								
Dendrochirus zebra					1	4				5										4	1						5			5							
Ebosia bleekeri					2	3		1	3									1	4								5		1	3	1						
Ectreposebastes imus					5			1	1	3										1		2	1	1			5		1	4							
Helicolenus hilgendorfii					5						2	3										4	1				5		5								
Hoplosebastes armatus						5			3	2										1	2	2				5				5							
Lythrichthys eulabes					5				1	4															5		5		5								

Table 3. (Continued)

	Dorsal-fin spines						Dorsal-fin rays								Pectoral-fin rays											Anal-fin spines		Anal-fin rays									
	7	8	/	11	12	13	7	8	9	10	11	12	13	14	12	13	14	15	16	17	18	19	20	21	22	2	3	4	5	6	7	/	11	12	13	14	15
Neochirus bella						5		2	3											2	3						5		5								
Neochirus brachyptera						2			2												2						2		2								
Neomerinthe erostris				1	4				4	1											5						5	3	2								
Neomerinthe kaufmani					5				5												1	3	1				5		5								
Neomerinthe procurva					4				4													4					4	2	2								
Parapterois heterura					2	3		2	3												1	3	1			5			1	4							
Parascorpaena aurita					5		1		4											5							5		5								
Parascorpaena maculipinnis					5				5									1	4								5		5								
Parascorpaena mcadamsi					5				5									1	4								5		5								
Parascorpaena mossambica					5				5									1	4								5		5								
Parascorpaena poseidon					5				5										4	1							5		5								
Phenacoscorpius sp.					1				1										1								1			1							
Pontinus tentacularis					5				5										5							1	4		5								
Pteroidichthys acutus					1				1									1									1		1								
Pteroidichthys amboinensis					3				3							1	1	1								3				3							
Pteroidichthys noronhai					1			1									1										1		1								
Pterois lunulata						1					1						1										1			1							
Pterois paucispinula						5				5											4	1					5			5							
Pterois russelii						5				1	4				1	4											5			1	4						
Pterois volitans						5				1	4						5										5			1	4						
Pteropterus antennatus					3	2				1	4								3	1	1						5			5							
Pteropterus radiatus					5					2	3								3	2							5			5							
Rhinopias eschmeyeri					3				3								1		2								3		2	1							
Rhinopias frondosa					3				3								1	2									3		3								
Scorpaena miostoma					5				5										5								5		5								
Scorpaena neglecta					5				5													4	1				5		5								
Scorpaena onaria					2				2											2							2		2								
Scorpaena pepo					5				5										5								5		5								
Scorpaenodes albaiensis						5		1	3	1								1	4								5	1	4								
Scorpaenodes evides						5			5												4		1				5		5								
Scorpaenodes guamensis						5		5													1	4					5		5								
Scorpaenodes kelloggi						5	2	3												2	3						5		5								
Scorpaenodes minor						2		2										2									2		2								
Scorpaenodes parvipinnis						5			5												4	1					5		5								
Scorpaenodes scaber						1		1														1					1		1								
Scorpaenodes varipinnis						5		3	2												4	1					5		5								
Scorpaenopsis cirrosa					5			1	4											2	3						5		5								
Scorpaenopsis cotticeps					2				2											2							2		2								
Scorpaenopsis diabolus					5				5												5						5		5								
Scorpaenopsis macrochir					3			1	2											3							3		3								
Scorpaenopsis neglecta					5				5											3	2						5		5								
Scorpaenopsis orientalis					5				5												5						5		5								
Scorpaenopsis oxycephala					5				5												1	4					5		5								
Scorpaenopsis papuensis					5				5											1		4					5		5								
Scorpaenopsis possi					5				5											5							5		5								
Scorpaenopsis ramaraoi					5				5											1	4						5		5								
Scorpaenopsis sp.					1				1													1					1		1								
Scorpaenopsis venosa					5				4	1										5							5		5								
Scorpaenopsis vittapinna					2				2												2						2		2								
Sebastapistes cyanostigma					5				5									1	4								5		5								
Sebastapistes fowleri					5			1	4									1	4								5		5								
Sebastapistes mauritiana					1				1										1								1		1								
Sebastapistes sp.					1				1									1									1		1								
Sebastapistes strongia					5				5								1	4									5		5								
Sebastapistes tinkhami					3				3										3								3		3								
Sebastes thompsoni						1								1					1								1				1						
Sebastiscus albofasciatus					5							5								4	1						5		5								
Sebastiscus marmoratus					5							5								1	4						5		5								
Sebastiscus tertius					5						1	4									2	3					5		4	1							
Sebastiscus vibrantus					2						1	1										2					2		2								
Setarches guentheri					2				1	1														1	1		2		2								
Taenianotus triacanthus					4	1			1	2	2						4	1									5		1	3	1						
Thysanichthys crossotus						5				1	4								1	4							5		5								

Parascorpaena maculipinnis **Smith, 1957**

Remarks: Five specimens were examined in this study (Tables 3, S1). *Parascorpaena mcadamsi* and *P. maculipinnis* were distinguished from other species of *Parascorpaena* by having 15 to 16 pectoral-fin rays, supraocular tentacle absent or very short, presence of a spine below eye, and presence of a distinct black blotch on spinous dorsal fin in male. *Parascorpaena maculipinnis* can be further distinguished from *P. mcadamsi* by having three suborbital spines (vs. two in *P. mcadamsi*) (Chou and Liao 2022).

Phenacoscorpius megalops **Fowler, 1938**

Remarks: No specimen was examined in this study. The record was based on Chen (1981). All specimens (CAS47299) were collected from Taiwan, and the figure and description in Chen (1981) corroborate the original description of *P. megalops*.

Phenacoscorpius **sp.**
(Fig. 4a)

Remarks: The counts of dorsal, pectoral, and anal fins are provided in table 3. The number of total vertebrae is 25. The lateral line is incomplete with only two lateral line scales anteriorly, a diagnostic characteristic of *Phenacoscorpius*. The palatine teeth are present. The specimen could not be identified to any valid species of *Phenacoscorpius* according to diagnostic characters (Motomura 2008; Motomura and Last 2009; Motomura et al. 2012a b; Wibowo and Motomura 2017). This species can be clearly distinguished from other congeners by six anal fin rays (except for *P. adenensis* and *P. eschmeyeri*), two lateral line scales (vs. more than three in other congeners), and presence of black spots on upper pectoral fin (Fig. 4a) (vs. absence in other congeners). In addition, this species could be distinguished from *P. megalops* by presence of palatine teeth (vs. absence in *P. megalops*). The taxonomic status of this specimen is unclear and further study using more specimens is needed.

Pontinus macrocephalus **(Sauvage, 1882)**

Remarks: No specimen was examined in this study. *Pontinus macrocephalus* was morphologically similar to *P. tentacularis* but could be distinguished by the counts of dorsal-fin rays (10 in *P. macrocephalus* vs. 9 in *P. tentacularis*) and pectoral-fin rays (17 in *P. macrocephalus* vs. 16 in *P. tentacularis*) (Eschmeyer 1969; Eschmeyer and Randall 1975). We have checked all specimens of *P. macrocephalus* from the collections in Taiwan, but the counts of dorsal-fin rays and pectoral-fin rays are identical to *P. tentacularis*. The occurrence of *P. macrocephalus* in Taiwan needs to be confirmed.

Pterois lunulata **Temminck & Schlegel, 1843**

Remarks: *Pterois lunulata*, *P. russelii* and *P. volitans* differ from other congeners of *Pterois* by having fewer pectoral-fin rays (< 15). Both *P. lunulata* and *P. russelii* lack black spots on dorsal rays, anal rays, and the caudal fin. *Pterois lunulata* can be distinguished from *P. russelii* by more dorsal-fin rays (10–11 vs. 11–12 in *P. russelii*) and pectoral-fin rays (13–14 vs. 12–13). According to the overlapping meristic characters, we agreed with Wilcox et al.'s (2018) opinion that *P. lunulata* might be a junior synonym of *P. russelii*.

Rhinopias frondosa **(Günther, 1892)**

Remarks: Chen (2003) first recorded *R. aphanes* from Penghu, but we re-identified it from the photo as *R. frondosa* based on the shape of the caudal fin (margin of fin membrane between soft rays strongly notched in *R. aphanes* vs. weakly notched to non-notched in *R. frondosa*) (Motomura and Johnson 2006).

Scorpaena pepo **Motomura, Poss & Shao, 2007**

Remarks: Five specimens were examined in this study (Tables 3, S1). *Scorpaena pepo* is closely related to *S. onaria* occurring in Taiwan, but it can be distinguished from *S. onaria* by its 16 pectoral-fin rays (Table 3) (Motomura et al. 2007).

Scorpaenodes hirsutus **(Smith, 1957)**

Remarks: No specimen was examined in this study. The first record was reported by Chen (1981) based on a single specimen collected from Hengchun, Pingtung. Hoshino and Motomura (2021) recently reported another specimen from Hong Chai, Pingtung.

Scorpaenodes minor **(Smith, 1958)**

Remarks: Motomura et al. (2009b) reported the new record of *Scorpaenodes albaiensis* from East Asia and re-identified Taiwanese *S. minor* as *S. albaiensis*. They indicated the two species are closely related and similar in overall body appearance, but *S. minor* can be distinguished from *S. albaiensis* by larger and fewer scales on longitudinal series (27–32 vs. 37–42 in *S. albaiensis*). We have examined two specimens (NMMB-P007032) with 31–32 scales in longitudinal series that conform with *S. minor*.

Scorpaenodes quadrispinosus Greenfield & Matsuura, 2002

Remarks: No specimen was examined in this study. The Taiwanese record was reported by Motomura et al. (2010a) based on two specimens collected from southern Taiwan.

Scorpaenopsis obtusa Randall & Eschmeyer, 2002

Remarks: No specimen was examined in this study. Motomura et al. (2011) reported a single specimen (NMMB-P0007637) of *S. obtusa* from Dongsha in the South China Sea, but no specimen was

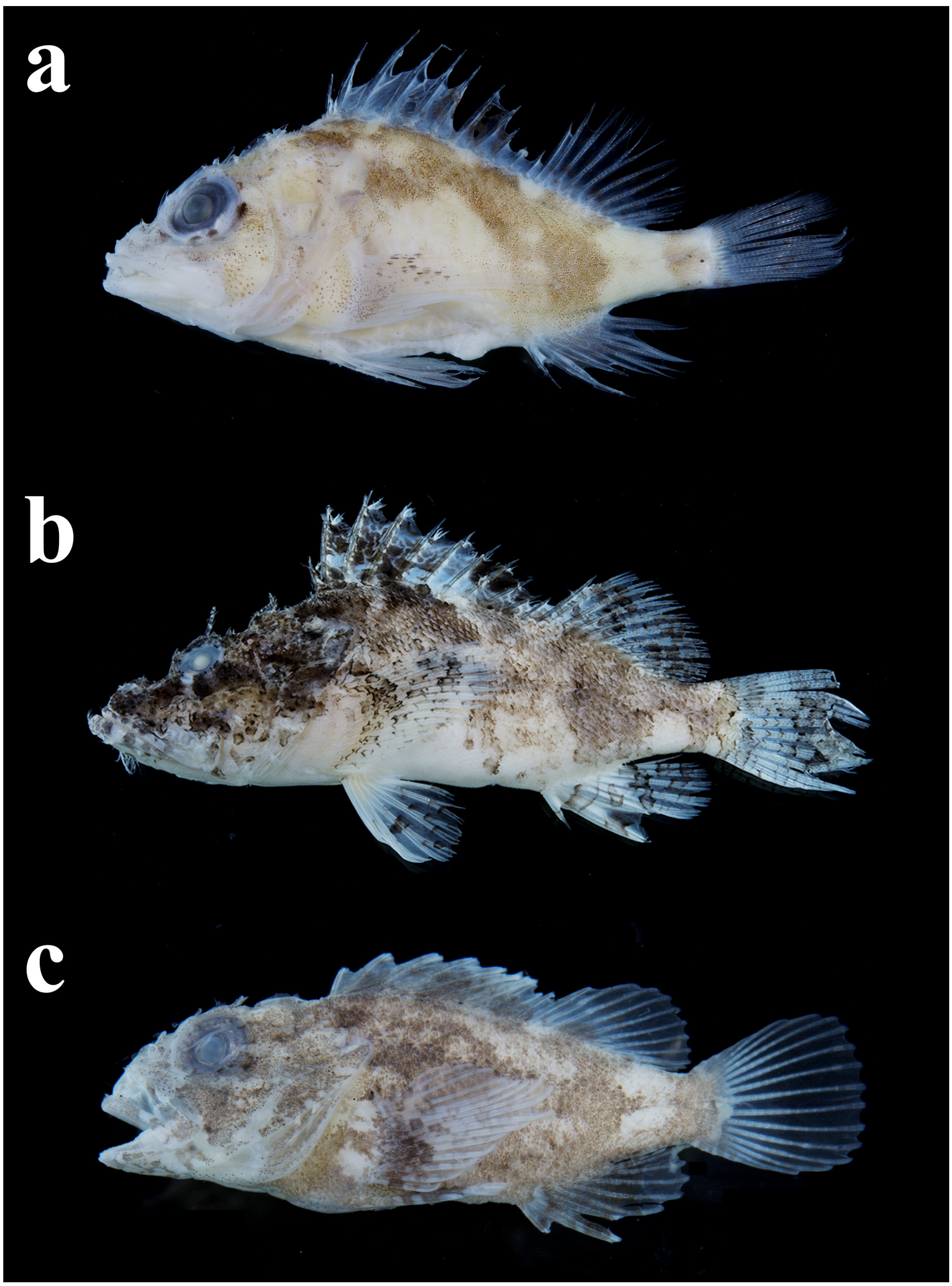

Fig. 4. Preserved specimens of the three taxonomically uncertain species. (a) *Phenacoscorpius* sp., NMMB-P036068, 46 mm SL. (b) *Scorpaenopsis* sp., DOS08531, 137 mm SL. (c) *Sebastapistes* sp., DOS08051, 17 mm SL.

collected from waters around the Taiwan Island. This species can be clearly distinguished from congeners by its distinct short snout. It has been recorded but misidentified as the juvenile of *Synanceia verrucosa* and *Scorpaenopsis diabolus* in the plates of Shao et al. (1993, p. 55) and Chen et al. (2010, p. 99), respectively, both from Kenting, Pingtung.

Scorpaenopsis orientalis Randall & Eschmeyer, 2002

Remarks: This species belongs to the *Scorpaenopsis oxycephala* species group due to its long snout (Randall and Eschmeyer 2002). This species group contains five species, including *S. cacopsis*, *S. cirrosa*, *S. papuensis*, *S. orientalis* and *S. oxycephala*. *Scorpaenopsis orientalis* can be distinguished from others by its 18 pectoral fin rays, and V-shaped and deep interorbital space.

Scorpaenopsis sp.
(Fig. 4b)

Remarks: The counts of dorsal, pectoral, and anal fins are provided in table 3. The specimen has three suborbital spines. This species belongs to the *Scorpaenopsis oxycephala* species group due to its long snout (Randall and Eschmeyer 2002), and it is morphologically most similar to *S. oxycephala* and *S. papuensis*. *Scorpaenopsis* sp. can be distinguished from *S. oxycephala* by having fewer scales in longitudinal series (53 vs. 59–67 in *S. oxycephala*) and differs from *S. papuensis* by absence of an occipital pit (vs. presence of a shallow occipital pit). The taxonomic status of this specimen is unclear, and further studies are needed.

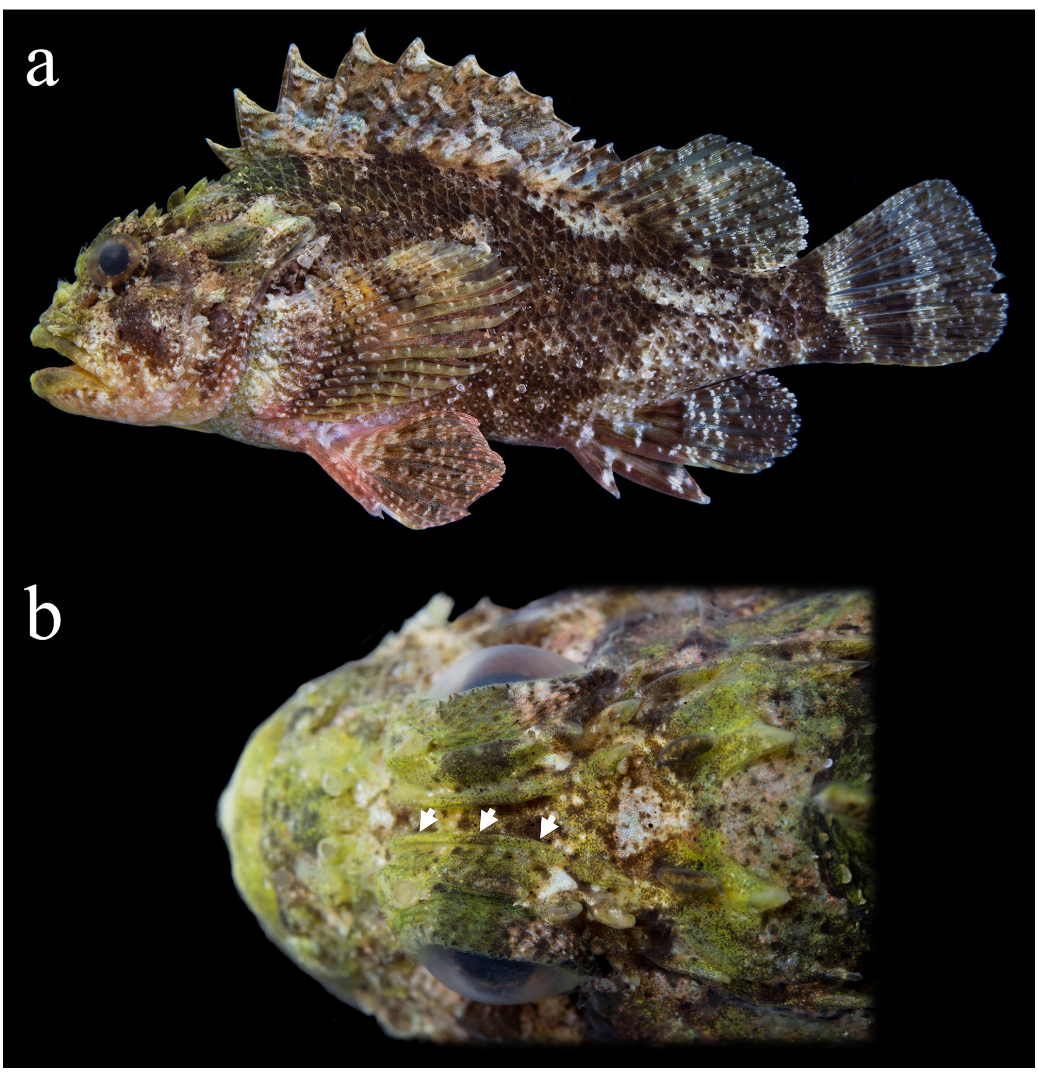

Fig. 5. Fresh specimen of a new record species, *Sebastapistes mauritiana*, from Taiwanese waters. DOS08337, 71 mm SL. (a) Lateral view, (b) dorsal view. White arrows indicate the coronal ridge.

Sebastapistes mauritiana **(Cuvier, 1829)**
(Fig. 5)

Remarks: The species is newly recorded from Taiwanese waters based on a specimen in the current study. The counts of dorsal, pectoral, and anal fins are provided in table 3. This species differs from congeners of *Sebastapistes* by having a strong coronal ridge with a spine (Fig. 4b).

Motomura et al. (2014) have synonymized *Scorpaena hatizyoensis* with *S. mauritiana*. There is one specimen of *S. hatizyoensis* (NTMP0678) collected from Taiwan in 1945 which is supposed to be *S. mauritiana*. However, we re-identified this specimen as a misidentification of *Scorpaena neglecta* according to the image of NTMP0678 in the National Taiwan Museum digital archive information system, with a large body size of 370 mm in total length.

Sebastapistes **sp.**
(Fig. 4c)

Remarks: The counts of dorsal, pectoral, and anal fins are shown in table 3. The specimen was identified as a member of *Sebastapistes* by 12 dorsal-fin spines, presence of teeth on palatines, posterior lacrimal spine directed posteroventrally, complete lateral line, and lack of a deep occipital pit (Motomura et al. 2014). This species and *Sebastapistes strongia* can be distinguished from other congeners based on pectoral-fin rays usually 15 (vs. usually 16 in other congeners), and presence of several white bands on the mandible (vs. absence), but *Sebastapistes* sp. can be further distinguished from *S. strongia* by three suborbital spines (vs. one in *S. strongia*). The taxonomic status of this specimen is unclear, and further studies are needed.

Sebastes joyneri **Günther, 1878**

Remarks: No specimen was examined in this study. The record of the species was reported by Chen (1969), but no specimen is known from collections. The presence of *S. joyneri* in Taiwanese waters is uncertain.

Sebastiscus tertius **(Barsukov & Chen, 1978)**

Remarks: This species was similar to *Sebastiscus vibrantus*, and both species can be distinguished from the other two congeners by having 19 pectoral-fin rays (vs. 17 in *S. albofasciatus* and 18 in *S. marmoratus*). *Sebastiscus tertius* differs from *S. vibrantus* by having a scaled area on the suborbital bone extending over the anterior margins of the orbit (vs. scaled area does not extend over the anterior margins of the orbit), parietal spine equal to nuchal spine (vs. parietal spine longer than nuchal spine), and a shorter pectoral fin base (9.2–11.7% vs. 11.1–13.2% standard length in *S. vibrantus*) (Morishita et al. 2018). According to our examined materials, the characters matched the description of *S. tertius*, including the state of the scaled area on the suborbital bone, equal lengths of parietal and nuchal spines, and the shorter pectoral fin base of 9.9–10.4% standard length.

Sebastiscus vibrantus **Morishita, Kawai & Motomura, 2018**

Remarks: The comparison between *Sebastiscus tertius* and *S. vibrantus* was provided in the remark of *Sebastiscus tertius*. According to our examined materials, the characters matched the description of *S. vibrantus*, including the state of scaled area on suborbital bone, parietal and nuchal spine, and longer pectoral fin base of 12.4–12.7% SL (Morishita et al. 2018).

DISCUSSION

DNA barcoding of the Scorpaenidae

DNA barcoding has been well known as an effective and rapid tool for identification at the species level and discovery of the biodiversity of marine fishes (*e.g.*, Ward et al. 2005; Steinke et al. 2009; Lakra et al. 2011; Zhang and Hanner 2011 2012; Weigt et al. 2012; Wang et al. 2018; Xing et al. 2018; Thu et al. 2019; Fadli et al. 2020; Huang et al. 2023). However, DNA barcoding for species identification also has its limitations. It works only when *COI* sequences exhibit sufficient interspecific genetic variation. In some cases, the genetic variations of the *COI* gene are unremarkable, such as tunas (*Thunnus* spp.) and most hamlets (*Hypoplectrus* spp.) (García-Machado et al. 2004; Ward et al. 2005; Viñas and Tudela 2009; Victor 2012; Victor and Marks 2018). Additionally, the application of molecular identification can only work when reliable reference sequences with voucher specimens are available (Ruedas et al. 2000; Harris 2003; Savolainen et al. 2005; Ward et al. 2005 2009; Ratnasingham and Hebert 2007; Mitchell 2008; Pleijel et al. 2008; Wang et al. 2012). Moreover, misidentifications of voucher specimens in the Scorpaenidae could also be a serious concern when no taxonomist is involved in the molecular studies (Poss 1999; Randall and Eschmeyer 2002; Randall 2005a b). In the present study, the sequences of 22 species belonging to nine genera were found to have more than one BLAST result with similarities ≥ 98% (Table S2), probably due to misidentifications from online databases. However, voucher specimen photos of some sequences are not available, and this creates a significant drawback to further verification and re-identification. In this study, a reliable DNA barcoding library of the Scorpaenidae from Taiwanese waters has been established based on voucher specimens.

The application of DNA barcoding for demarcating species relies on a gap between minimum interspecific and maximum intraspecific genetic divergences (*i.e.*, barcode gap) (Hebert et al. 2003a 2004; Barrett and Hebert 2005; Wiemers and Fiedler 2007). For fish, the conspecific chance is very high when the genetic divergence of *COI* sequences is less than 2% (Hebert et al. 2003a b; Ward et al. 2009). In the current study, the mean interspecific genetic distance (15.61%) was much higher than the mean intraspecific genetic distance (0.22%) (Fig. 3, Table 2). Although a few species pairs of the Scorpaenidae from Taiwanese waters exhibit low genetic variation in *COI* sequences (less than 2%), reciprocal monophylies were consistently observed in the ML tree (Fig. 2), and these species pairs can be distinguished by their morphological characteristics (Matsunuma et al. 2017; Morishita et al. 2018; Wilcox et al. 2018). The only case of *Pterois lunulata* vs. *P. russelii* may represent an exception, in which the former is potentially a junior synonym of the latter (Wilcox et al. 2018). Some species pairs of the genus *Sebastes* also showed low genetic variation in *COI* gene, but could be clearly distinguished by their morphology, implying recent diversifications or contemporary/historic hybridizations between closely related species (Hyde and Vetter 2007; Steinke et al. 2009; Zhang et al. 2013; Muto and Kai 2023). Most species pairs with low genetic variation observed in this study (except for *P. lunulata* vs. *P. russelii*) are probably a consequence of recent diversifications. Additionally, the majority of high interspecific genetic variations were contributed by species pairs within the genus *Sebastapistes*, such as *S. mauritiana* vs. *S. strongia* (32.3%), *S. mauritiana* vs. *S. fowleri* (30.4%), *S. mauritiana* vs. *Sebastapistes* sp. (30.0%), *S. mauritiana* vs. *S. tinkhami* (27.8%), *S. mauritiana* vs. *S. cyanostigma* (27.0%), and *S. tinkhami* vs. *Sebastapistes* sp. (25.8%). Taxonomic studies of *Sebastapistes* are scarce, and its taxonomic status needs to be re-examined based on comprehensive sampling (Motomura et al. 2014).

The potential records of the Scorpaenidae in Taiwanese waters

To date, 85 species of 29 genera of the Scorpaenidae have been recorded in Taiwanese waters. Several new records originally known from adjacent waters have been reported in recent studies. *Sebastes thompsoni* was previously considered to inhabit cold waters in the northwestern Pacific but has been recently observed in northern Taiwan (Chou and Tang 2021); *Scorpaenopsis orientalis* was considered a Japanese endemic species but has subsequently been discovered in southern Taiwan (Randall and Eschmeyer 2002; Koeda et al. 2019). *Scorpaenopsis cotticeps* was only known from Japan and the Philippines, and had never been reported from Taiwan until Chou (2021). *Lioscorpius longiceps*, *Lythrichthys dentatus*, and *Scorpaenodes corallinus*, which are distributed in the western Pacific, may also occur in Taiwan (Randall and Lim 2000; Nakabo and Kai 2013; Wada et al. 2021; Hoshino et al. 2023). More scorpaenids are waiting to be discovered in Taiwanese waters.

CONCLUSIONS

In this study, we updated the checklist of the Scorpaenidae from Taiwan. In total, 296 specimens of 85 species placed in 29 genera were examined and literature reviewed using morphological and molecular approaches. Among the 85 species, *Sebastapistes mauritiana* (Cuvier, 1829) is a new record, and the taxonomic status of three species in the genera *Phenacoscorpius*, *Scorpaenopsis*, and *Sebastapistes* remain uncertain. A total of 118 *COI* sequences belonging to 66 species of 28 genera are generated based on properly identified voucher specimens in the present study. The *COI* sequences of *Parascorpaena maculipinnis*, *Scorpaena pepo*, and *Scorpaenopsis orientalis* are new to online databases (GenBank and BOLD systems). For K2P distance of the *COI* gene, the mean interspecific genetic distance (15.61%) was higher than the mean intraspecific genetic distance (0.22%), representing a clear barcode gap which makes DNA barcoding feasible within the Scorpaenidae. Identifying Scorpaenidae species through morphology can be challenging for non-specialists, whereas DNA barcoding offers a rapid and powerful tool that does not require taxonomic expertise.

Acknowledgment: We are grateful to two anonymous reviewers for their constructive comments; S.-P. Huang (ASIZP), C.-H. Chan, T.-W. Wu, H.-C. Ho (NMMB-P), for their curatorial assistances; C.-C. Ku, C.-N. Tang, H.-C. Chen, J.-S. Lin, N.-W. Lai, S.-L. Ng, Y.-H. Yu for collecting specimens. This study is partly support by a grant from National Science and Technology Council to TYL (111-2611-M-110-026).

Authors' contributions: TKC and TYL designed the study. TKC, WCH, and WCJ collected, identified, and examined the specimens. TKC, WCH and WCJ prepared the manuscript. All authors revised the manuscript and approved the final version.

Competing interests: The authors declare that they have no competing interests.

Availability of data and materials: All data are available in the paper.

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

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Supplementary materials

Fig. S1. Photographs of some sequenced/examined voucher specimens. Following the scientific name are the catalog number, standard length (SL), and GenBank accession number of the specimen. NA for the accession number indicates that the specimen was used solely for morphological examination and was not sequenced. (download)

Table S1. List of species, body size, catalog number of specimens, and their accession numbers. Species without examined specimen are denoted by a hyphen (-) representing data as "not available" . (download)

Table S2. List of morphological and molecular identifications. The listed sequences included more than one species after BLAST. (download)