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A new record of *Squalus montalbani* (Chondrichthyes: Squaliformes: Squalidae) from the Nansha (Spratly) Islands, South China Sea

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Abstract

The Indonesian greeneye spurdog (or a dogfish shark), *Squalus montalbani* Whitley, 1931, is widely distributed in the warm temperate to tropical waters of Indonesia, Philippines, the island of Taiwan, and Australia. Previous studies suggested that the distribution of dogfish shark species in the South China Sea is composed of two species, *Squalus mitsukurii* Jordan et Snyder, 1903 and *Squalus brevirostris* Tanaka, 1917. In March 2020 a dogfish shark specimen was collected from the Nansha (Spratly) Islands, South China Sea. We identified it as *S. montalbani* based on morphology and mitochondrial DNA barcoding. Our results confirmed the presence of *S. montalbani* in the South China Sea, leading us to conclude that it represents a new species record of the genus *Squalus* in the region. Furthermore, our findings demonstrate that the combined approach is highly effective in identifying *Squalus* species that share similar morphological characteristics.

Keywords

fish taxonomy, mitochondrial DNA barcoding, new record, South China Sea, *Squalus montalbani*

Introduction

The family Squalidae includes 2 genera, 39 species. Among these species, 36 species represents dogfish sharks (genus *Squalus*) (Ziadi-Künzli et al. 2020; Ariza et al. 2022; WoRMS Editorial Board 2023). Due to difficulties in morphological characteristics between different dogfish sharks, species in *Squalus* have a high taxonomic complexity (Viana et al. 2016). Thus, studies related to the taxonomy, evolution, and new species records are especially meaningful. Species of the genus *Squalus* are mainly distributed in the continental shelf waters, upper slope waters, and underwater cracks of the Atlantic, Pacific, and Indian oceans (Viana et al. 2016).

It has been reported that there were 9 species of *Squalus* genus distributed in China, including *Squalus acanthias* Linnaeus, 1758; *Squalus mitsukurii* Jordan et Snyder, 1903; *Squalus brevirostris* Tanaka, 1917; *Squalus blainville* (Risso, 1827); *Squalus formosus* White et Iglésias, 2011; *Squalus japonicus* Ishikawa, 1908; *Squalus megalops* (MacLeay, 1881); *Squalus montalbani* Whitley, 1931; and *Squalus suckleyi* (Girard, 1855) (see Zhu et al.

1963, 1984; Cheng and Zheng 1987; Shao 2023; Zhang 1960; Zhu 1960; White and Iglesias 2011; Straube et al. 2013). Among these species, *S. montalbani* has been found off the island of Taiwan, Australia, Philippines, Indonesia, in eastern Indian Ocean and Western Central Pacific regions (Graham 2019). Previous reports suggested that the distribution of dogfish shark species in the South China Sea is limited to only two species, namely *S. mitsukurii* and *S. brevirostris* (see Zhu 1962, 1979, 1984; Zhang et al. 2018).

A single dogfish shark specimen, at our disposal, collected in the middle of the South China Sea prompted us to identify it using morphological methods and DNA barcoding technique. The specimen could potentially represent a new record of a dogfish species for the studied area.

Material and methods

A single dogfish shark specimen was collected by Jianwei Zhou, at the Dianjian Fishing Harbour Marina, Beihai (mainland China), on March 2020. The fish originated from in the Nansha Archipelago (known also as the Spratly Islands), South China Sea (09°47′57″N, 114°5′35″E). The specimen was identified based on morphological characteristics used by Last et al. (2007).

A piece of muscle tissue was cut from the specimen, stored in 95% ethanol, and DNA was extracted with a DNA Extraction Kit of Tiangen, then PCR amplification. 5′-TCGACTAATCATAAAGATATCGGCAC-3′ and 5′-ACTTCAGGGTGACCGAAGAATCAGAA-3′ were used as primer sequences for cytochrome oxidase I (COI) amplification (Ivanova et al. 2007). PCR amplifications were performed in 25 μL volume including 1 μL of forward primer (F, 10 uM · L^{-1}), 1 μL of reverse primer (R, 10 uM · L^{-1}), 2 μL of dNTPs (2.5 mM · L^{-1} each), 0.15 μL of EasyTaq DNA Polymerase (5 U · μL^{-1}), 2.5 μL of 10 × PCR buffer (25 uM · L^{-1}), 1 μL of DNA template (50 ng · uL^{-1}). The PCR conditions consisted of use of 95°C for 5 min for initial denaturation, 35 cycles of 94°C for 35 s, annealing at 54°C for 35 s, and extension at 72°C for 35 s, with a final extension at 72°C for 10 min. The above reactions were conducted through Biometra thermal cycler (Gottingen, Germany). Finally, the PCR products were stored in 4°C environment. Agarose gel was used for electrophoresis and was sequenced. Subsequently, the COI gene sequence of this specimen was obtained and revised through DNASTAR software (DNASTAR Inc., Madison, WI, USA).

Thirteen COI sequences of the genus *Squalus* were downloaded from NCBI for phylogenetic study, *Somniosus rostratus* (Risso, 1827) (KJ083255) was selected as the outgroup to root the tree (Table 1). The genetic relation between COI sequences was analyzed by the maximum likelihood method (ML, Felsenstein 1981). Phylogenetic tree construction first used JModeltest (Posada 2008) based on AIC (Akaike 1973) to filter the best alternative model as TPM2uf+I+G, then use RAxML-NG (Kozlov et al. 2019) to construct the ML phylogenetic tree based on Bootstrap method (Felsenstein 1985). The number of Bootstraps is set to 1000 times, and finally, the online tool ITOL (Letunic and Bork 2007) was used to view and adjust the phylogenetic tree (https://itol.embl.de/). The genetic distances of species were calculated in pairs using MEGA7 (Kumar et al. 2016), and thermodynamic maps of genetic distances were constructed using the R software (Ihaka and Gentleman 1996) combination package (Wei et al. 2017).

Table 1. Species and the GenBank accession numbers of the COI sequences used in phylogenetic tree construction.

Species	GenBank accession number	Reference
Squalus montalbani	KF590396	Sembiring et al. 2015
Squalus mitsukurii	MT123865	Ziadi-Künzli et al. 2020
Squalus brevirostris	EF539300	Ward et al. 2007
Squalus acanthias	KJ205210	Knebelsberger et al. 2014
Squalus blainville	KU198594	Kousteni et al. 2016
Squalus megalops	GU130698	Straube et al. 2010
Squalus hemipinnis	KF590514	Sembiring et al. 2015
Squalus nasutus	JN313288	Daly-Engel et al. 2018
Squalus chloroculus	EF539301	Ward et al. 2007
Squalus grahami	EU399028	Ward et al. 2008
Squalus crassispinus	DQ108248	Ward et al. 2005
Squalus formosus	MT123847	Ziadi-Künzli et al. 2020
Squalus cubensis	MG792175	Pfleger et al. 2018
Somniosus rostratus	KJ083255	Moura et al. 2015

Results

Morphological characteristics of the studied specimen of *Squalus montalbani* were shown in Fig. 1. The detailed measurements (in absolute values) were included in Table 2. Those absolute values yielded the relative values presented below.

Diagnosis. Body elongate to robust; trunk depth 12.2% TL; pre-first dorsal length 29.0% TL; pre-second dorsal length 61.2% TL; interdorsal space 25.4% TL; low raked dorsal fins; prepectoral length 22.5% TL; pelvic-caudal space 26% TL; dark spots on upper caudal lobe showing saddle-like extension toward upper caudal lobe margin.

The above morphological characteristics basically conform to the description of the Indonesian greeneye spurdog (dogfish shark), *Squalus montalbani*, in the literature (Last et al. 2007). In addition, based on observations of the morphological characteristics of the sample teeth, dermal denticles tricuspidate and rhomboid were found, in agreement with those described by Viana and De-Carvalho (2018).

The COI gene (655 bp) was sequenced from our sample. The accession number for the sequence submitted to GenBank is OQ826088. The phylogenetic tree was constructed through the downloaded sequences, as shown in Fig. 2. Sample_SM belongs to the genus *Squalus*. *Squalus acanthias*, *Squalus cubensis* Howell Rivero, 1936, *S. brevirostris*, and *S. blainville* are clustered in one group. As an outgroup of phylogenetic tree, *Somniosus rostratus* is a branch alone. Sample_SM and the rest of the species clustered in another group.

The genetic distance thermodynamic diagram shows (Fig. 3) that the genetic distance of COI sequence be-

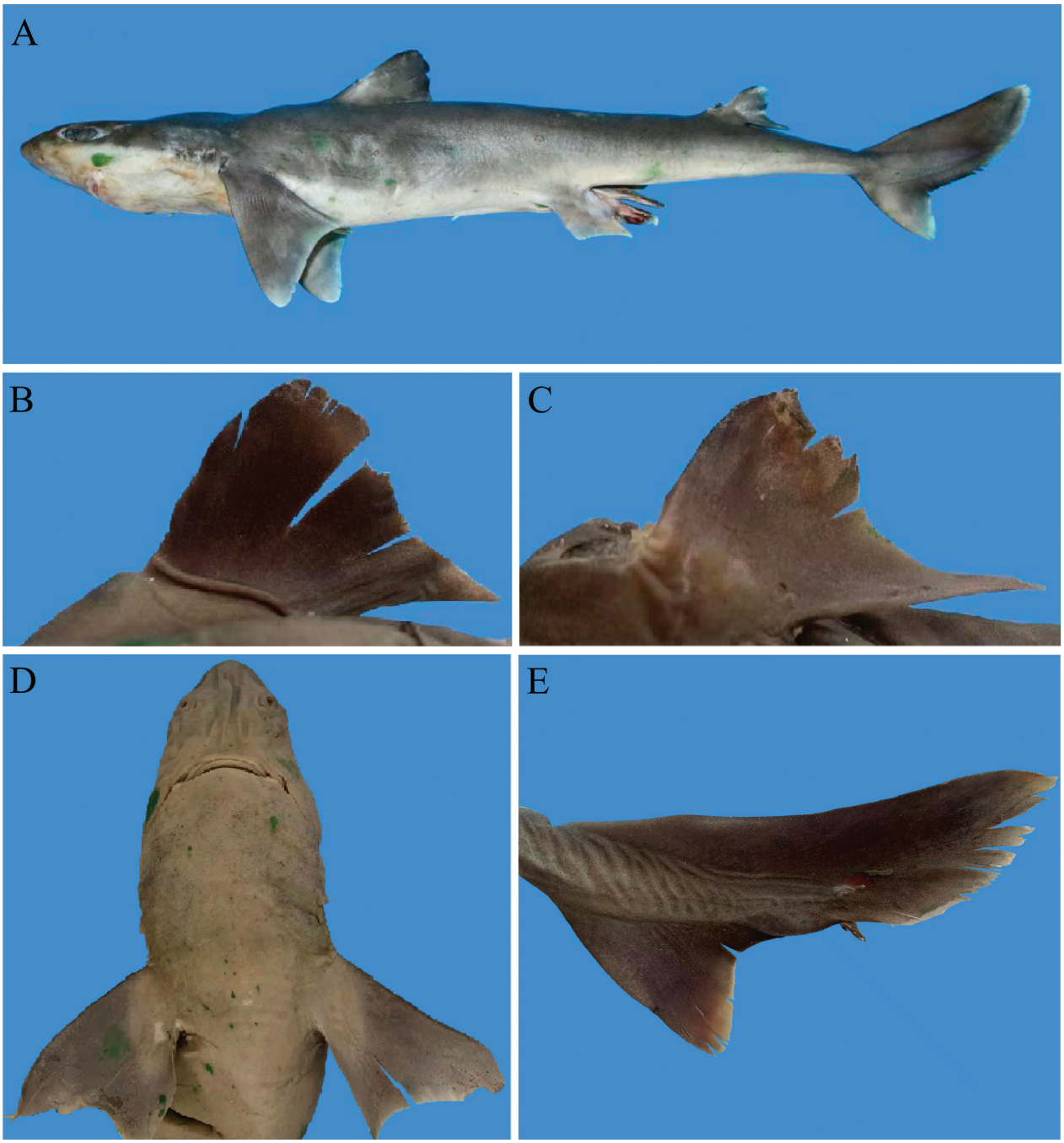

Figure 1. *Squalus montalbani* (sample_SM; length 550 mm TL); (**A**) Left lateral view; (**B**) Lateral view of the first dorsal fin; (**C**) Lateral view of the second dorsal fin; (**D**) Ventral view of the head; (**E**) Coloration of the caudal fin.

tween different species, the intraspecific genetic distance of *Squalus* genus is 0.01–0.09. The genetic distance between sample_SM and *S. montalbani* is 0, and that between sample_SM and *Squalus chloroculus* Last, White et Motomura, 2007 is 0.01, which further proves that sample_SM and *S. montalbani* are the same species having a close relation with *S. chloroculus*. Thus, both the morphological and genetic analysis strongly supports our identification of the newly found dogfish shark specimen as *S. montalbani*. Therefore, the presently studied specimen constitutes a new record of *Squalus montalbani* from the Nansha (Spratly) Archipelago, South China Sea.

Discussion

Due to the unique growth characteristics of the genus *Squalus*, its species have highly similar morphological characters that are difficult to identify, thus hindering taxonomic studies of the genus (Geraci et al. 2017), just as *Squalus montalbani* was once considered by Compagno (1984) to be a junior synonym of *S. mitsukurii*. Over the years, scholars have used ambiguous morphological diagnostic characters to distinguish between different species of the genus *Squalus* and have not achieved uniformity in diagnostic methods for the same species, leading to extensive taxonomic confusion and synonymization in the

Table 2. External measurements of *Squalus montalbani* (based on a single specimen).

Abbr.	Character	Absolute value [cm]
TL	Total length	55.0
PCL	Precaudal length	43.0
PD2	Pre-second dorsal length	33.0
PD1	Pre-first dorsal length	16.0
SVL	Pre-vent length	27.5
PP2	Prepelvic length	27.7
PP1	Prepectoral length	12.4
HDL	Head length	10.8
PG1	Prebranchial length	12.6
PSP	Prespiracular length	6.9
POB	Preorbital length	4.1
PRN	Prenarial length	3.2
POR	Preoral length	5.0
INLF	Inner nostril-labial furrow space	2.6
MOW	Mouth width	4.8
ULA	Labial furrow length	1.5
INW	Internarial space	3.2
INO	Interorbital space	4.5
EYL	Eye length	1.8
EYH	Eye height	1.0
SPL	Spiracle length	0.8
GS1	First gill-slit height	0.8
GS5	Fifth gill-slit height	1.1
IDS	Interdorsal space	14
DCS	Dorsal-caudal space	6.5
PPS	Pectoral-pelvic space	13.0
PCA	Pelvic-caudal space	14.3
D1L	First dorsal length	7.1
D1A	First dorsal anterior margin	5.4
D1B	First dorsal base length	3.8
D1H	First dorsal height	3.2
D1I	First dorsal inner margin	3.0
D1P	First dorsal posterior margin	4.3
P1A	Pectoral anterior margin	7.6
P1I	Pectoral inner margin	4.5
P1B	Pectoral base length	2.7
P1P	Pectoral posterior margin	5.9
P2L	Pelvic length	5.5
P2H	Pelvic height	3.8
P2I	Pelvic inner margin	1.8
CDM	Dorsal caudal margin	11.0
CPV	Preventral caudal margin	5.5
CPU	Upper postventral caudal margin	8.5
CPL	Lower postventral caudal margin	2.4
CFW	Caudal fork width	3.9
CFL	Caudal fork length	4.6
HANW	Head width at nostrils	4.0
HAMW	Head width at mouth	6.0
HDW	Head width	7.0
TRW	Trunk width	6.7
ABW	Abdomen width	5.8
TAW	Tail width	3.7
CPW	Caudal peduncle width	1.8
HDH	Head height	4.2
TRH	Trunk height	5.0
ABH	Abdomen height	5.5
TAH	Tail height	2.6
CPH	Caudal peduncle height	2.0
CLO	Clasper outer length	2.7
CLI	Clasper inner length	3.9
CLB	Clasper base width	1.0

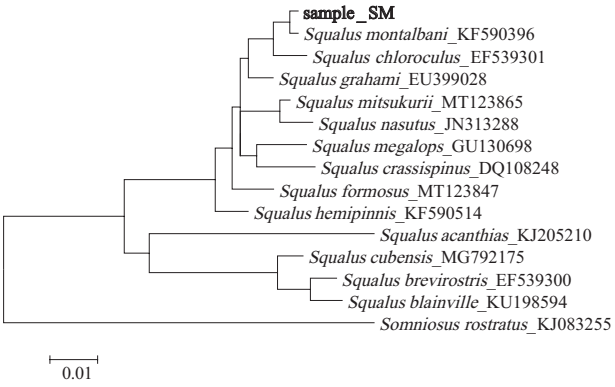

Figure 2. Maximum likelihood phylogenetic tree based on the COI sequence. *Somniosus rostratus* (KJ083255) was chosen as the outgroup to root the tree.

past (Veríssimo et al. 2017). The lack of well-preserved holotypes for many shark species, misidentifications in databases and in the literature, and challenges in retrieving representative series of specimens for comparison are top-down impediments to the proper taxonomic identification and the potential revision of genera (Veríssimo et al. 2014).

On the other hand, the slow growth, low reproductive capacity (Cortés 2000), and ease of capture by trawling and longlining, with a high proportion of bycatch, are the main reasons for the dramatic decline in the population of the genus *Squalus* (see Dulvy et al. 2014). Therefore, the majority of the species of the genus *Squalus* have been included in the IUCN Red List, and they have been classified in five categories according to their threatened level: Data Deficient, Least Concern, Near Threatened, Vulnerable, and Endangered (IUCN 2020). And the majority of the of the species of the genus *Squalus* in the Red List are currently classified as Data Deficient, Least Concern, Near Threatened, while eight species are classified as Vulnerable and Endangered, namely, *S. acanthias*, *S. chloroculus*, *S. brevirostris*, *S. mitsukurii*, *S. japonicus*, *S. montalbani*, *Squalus hemipinnis* White, Last et Yearsley, 2007, *S. formosus* (IUCN 2020). *Squalus montalbani* in Australia most of its range with light or absent fishing pressure, and the deeper parts of its depth range may provide refuge from fishing. Therefore, it is assessed as Vulnerable species (Graham 2019).

The genus *Squalus* has a low evolutionary rate (Hara et al. 2018) and its morphology is very similar, so species identification is often carried out by subtle morphological differences. Currently, morphological identification of the genus *Squalus* is based on the color and morphological characteristics of the caudal fin, the morphological characteristics of the head and trunk, and various morphological measurement parameters (Last et al. 2007). Last et al. (2007) have stated that *S. montalbani* and *S. chloroculus* have been confused, and our results show that they are genetically very close to each other; the genetic differentiation between *S. montalbani* and *S. chloroculus* is minimal, so there is a reason for their confusion. Both share the same morphological characteristics: relatively large body size, dark tail, low dorsal fin spines, and small, sloping first dorsal fin. However, there are also

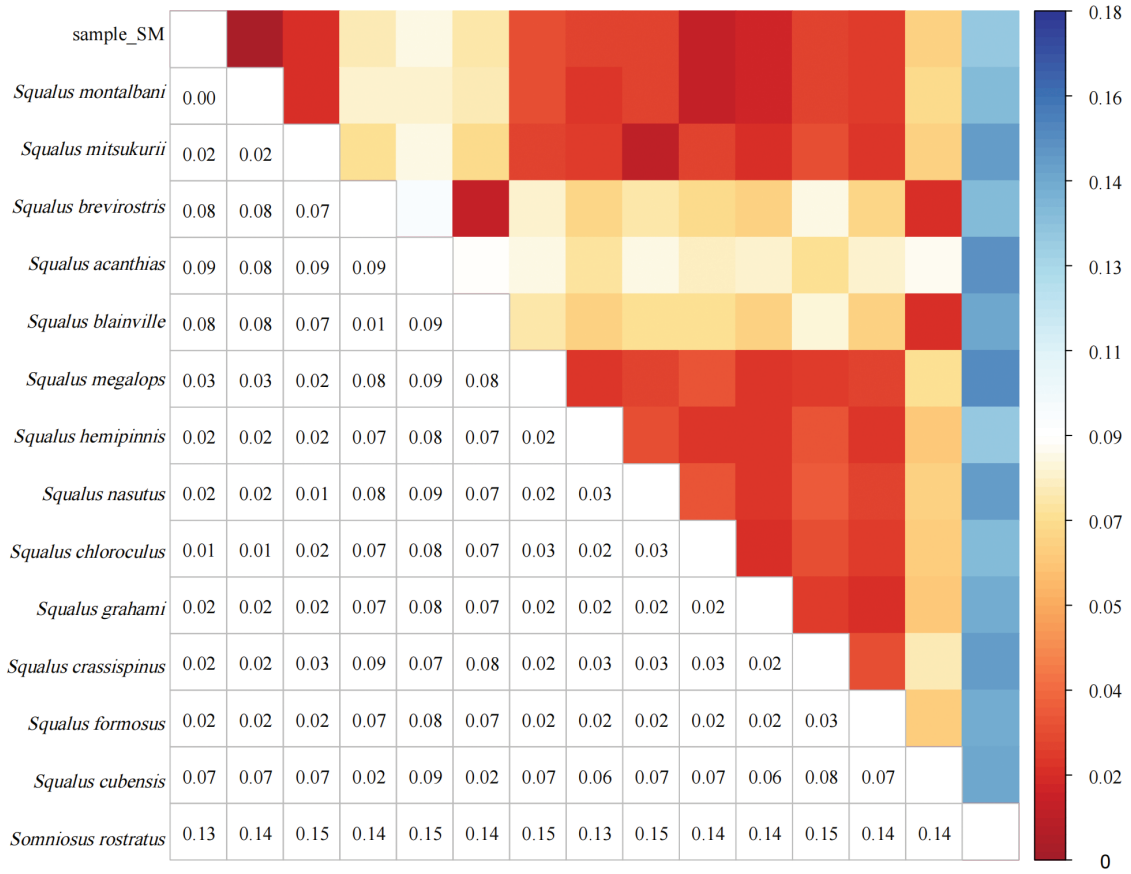

Figure 3. Pairwise comparison of genetic differentiation between the sample in the presently reported study (sample_SM) and other 14 species of the Squaliformes based on COI gene sequence data. The genetic distance relation is expressed according to the color depth of the color block (above diagonal). The genetic distance value (below diagonal).

slight differences between the two, with the dorsal fin of *S. chloroculus* being smaller compared to *S. montalbani*, having a wider base of the fin spines, shorter adult claspers, and the upper postventral caudal margin is short relative to the lower postventral margin, having a marginally higher mean precaudal count (Last et al. 2007).

According to the data obtained in this study, the intraspecific genetic distances of the genus *Squalus* mainly ranged from 0.01 to 0.09, which indicates that the differentiation rate of the genus *Squalus* is very low, namely, the genetic expression is relatively conserved, resulting in a very similar morphology of the genus *Squalus*. Therefore, traditional taxonomic methods alone are not sufficient to identify species of the genus *Squalus*, and in recent years, molecular methods have begun to be used to supplement traditional taxonomic methods to make the identification of species of the genus more accurate, but molecular methods cannot completely replace traditional taxonomic methods at present (Schlick-Steiner et al. 2010). It is now customary to use a combination of traditional taxonomic methods and molecular methods of COI or NADH mitochondrial DNA labeling to identify the genus *Squalus*. This combined approach has proven to be very effective in identifying such species (Lim et al. 2022; Cerutti-Pereyra et al. 2012; Gabbanelli et al. 2018).

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References

Akaike H (1973) Maximum likelihood identification of Gaussian autoregressive moving average models. Biometrika 60(2): 255–265. https://doi.org/10.1093/biomet/60.2.255

Ariza AA, Adachi AM, Roque P, Hazin FH, Vianna M, Rotundo MM, Delpiani SM, Díaz de Astarloa JM, Delpiani G, Oliveira G, Foresti F, Cruz VP (2022) DNA barcoding and species delimitation for dogfish sharks belonging to the *Squalus* genus (Squaliformes: Squalidae). Diversity 14(7): e544. https://doi.org/10.3390/d14070544

Cerutti-Pereyra F, Meekan MG, Wei NW, O'Shea O, Bradshaw CJ, Austin CM (2012) Identification of rays through DNA barcoding:

An application for ecologists. PLoS One 7(6): e36479. https://doi.org/10.1371/journal.pone.0036479

Cheng QT, Zheng BS (1987) [A systematic search of Chinese fishes.] Science Press, Beijing, China. [In Chinese]

Compagno LJV (1984) Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1. Hexanchiformes to Lamniformes. FAO, Rome.

Cortés E (2000) Life history patterns and correlations in sharks. Reviews in Fisheries Science 8(4): 299–344. https://doi.org/10.1080/10408340308951115

Daly-Engel TS, Koch A, Anderson JM, Cotton CF, Rubbs RD (2018) Description of a new deep-water dogfish shark from Hawaii, with comments on the *Squalus mitsukurii* species complex in the West Pacific. ZooKeys 798: 135–157. https://doi.org/10.3897/zookeys.798.28375

Dulvy NK, Fowler SL, Musick JA, Cavanagh RD, Kyne PM, Harrison LR, Carlson JK, Davidson LN, Fordham SV, Francis MP, Pollock CM, Simpfendorfer CA, Burgess GH, Carpenter KE, Compagno LJ, Ebert DA, Gibson C, Heupel MR, Livingstone SR, Sanciangco JC, Stevens JD, Valenti S, White WT (2014) Extinction risk and conservation of the world's sharks and rays. eLife 3: e00590. https://doi.org/10.7554/eLife.00590

Felsenstein J (1981) Evolutionary trees from DNA sequences: A maximum likelihood approach. Journal of Molecular Evolution 17(6): 368–376. https://doi.org/10.1007/BF01734359

Felsenstein J (1985) Confidence limits on phylogenies: An approach using the bootstrap. Evolution International Journal of Organic Evolution 39(4): 783–791. https://doi.org/10.2307/2408678

Gabbanelli V, Diaz de Astarloa JM, Gonzalez-Castro M, Vazquez DM, Mabragana E (2018) Almost a century of oblivion: Integrative taxonomy allows the resurrection of the longnose skate *Zearaja brevicaudata* (Marini, 1933) (Rajiformes: Rajidae). Comptes Rendus Biologies 341(9–10): 454–470. https://doi.org/10.1016/j.crvi.2018.10.002

Geraci ML, Ragonese S, Norrito G, Scannella D, Falsone F, Vitale S (2017) [Chapter 2] A tale on the demersal and bottom dwelling Chondrichthyes in the south of Sicily through 20 years of scientific survey. Pp. 13–37. In: da Silva Rodrigues Filho LF, de Luna Sales JB (Eds.) Chondrichthyes—Multidisciplinary approach. IntechOpen, London, UK. https://doi.org/10.5772/intechopen.69333

Graham KJ (2019) *Squalus montalbani*. The IUCN Red List of Threatened Species 2019: e.T161404A68645208. [Accessed on 29 April 2023] https://doi.org/10.2305/IUCN.UK.2019-1.RLTS.T161404A68645208.en

Hara Y, Yamaguchi K, Onimaru K, Kadota M, Koyanagi M, Keeley SD, Tatsumi K, Tanaka K, Motone F, Kageyama Y, Nozu R, Adachi N, Nishimura O, Nakagawa R, Tanegashima C, Kiyatake I, Matsumoto R, Murakumo K, Nishida K, Terakita A, Kuratani S, Sato K, Hyodo S, Kuraku S (2018) Shark genomes provide insights into elasmobranch evolution and the origin of vertebrates. Nature Ecology and Evolution 2(11): 1761–1771. https://doi.org/10.1038/s41559-018-0673-5

Ihaka R, Gentleman R (1996) R: a language for data analysis and graphics. Journal of Computational and Graphical Statistics 5(3): 299–314. https://doi.org/10.1080/10618600.1996.10474713

IUCN (2020) The IUCN Red List of Threatened Species. Version 2020-1. IUCN, Gland, Switzerland.

Ivanova NV, Zemlak TS, Hanner RH, Hebert PD (2007) Universal primer cocktails for fish DNA barcoding. Molecular Ecology Notes 7(4): 544–548. https://doi.org/10.1111/j.1471-8286.2007.01748.x

Knebelsberger T, Landi M, Neumann H, Kloppmann M, Sell AF, Campbell PD, Laakmann S, Raupach MJ, Carvalho GR, Costa FO (2014) A reliable DNA barcode reference library for the identification of the north European shelf fish fauna. Molecular Ecology Resources 14(5): 1060–1071. https://doi.org/10.1111/1755-0998.12238

Kousteni V, Kasapidis P, Kotoulas G, Megalofonou P (2016) Evidence of high genetic connectivity for the longnose spurdog *Squalus blainville* in the Mediterranean Sea. Mediterranean Marine Science 17(2): 371–383. https://doi.org/10.12681/mms.1222

Kozlov AM, Darriba D, Flouri T, Morel B, Stamatakis A (2019) RAxML-NG: A fast, scalable and user-friendly tool for maximum likelihood phylogenetic inference. Bioinformatics 35(21): 4453–4455. https://doi.org/10.1093/bioinformatics/btz305

Kumar S, Stecher G, Tamura K (2016) MEGA7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. Molecular Biology and Evolution 33(7): 1870–1874. https://doi.org/10.1093/molbev/msw054

Last PR, White WT, Pogonoski JJ (2007) Descriptions of new dogfishes of the genus *Squalus* (Squaloidea: Squalidae). Hobart Tas. CSIRO Marine and Atmospheric Research c: 55–69.

Letunic I, Bork P (2007) Interactive Tree of Life (iTOL): An online tool for phylogenetic tree display and annotation. Bioinformatics 23(1): 127–128. https://doi.org/10.1093/bioinformatics/btl529

Lim KC, White WT, Then AY, Naylor GJ, Arunrugstichai S, Loh KH (2022) Integrated taxonomy revealed genetic differences in morphologically similar and non-sympatric *Scoliodon macrorhynchos* and *S. laticaudus*. Animals 12(6): 681. https://doi.org/10.3390/ani12060681

Moura T, Silva MC, Figueiredo I (2015) Barcoding deep-water chondrichthyans from mainland Portugal. Marine and Freshwater Research 66(6): 508–517. https://doi.org/10.1071/MF14095

Pfleger MO, Grubbs RD, Cotton CF, Daly-Engel TS (2018) *Squalus clarkae* sp. nov., a new dogfish shark from the Northwest Atlantic and Gulf of Mexico, with comments on the *Squalus mitsukurii* species complex. Zootaxa 4444(2): 101–119. https://doi.org/10.11646/zootaxa.4444.2.1

Posada D (2008) jModelTest: Phylogenetic model averaging. Molecular Biology and Evolution 25(7): 1253–1256. https://doi.org/10.1093/molbev/msn083

Schlick-Steiner BC, Steiner FM, Seifert B, Stauffer C, Christian E, Crozier RH (2010) Integrative taxonomy: A multisource approach to exploring biodiversity. Annual Review of Entomology 55(1): 421–438. https://doi.org/10.1146/annurev-ento-112408-085432

Sembiring A, Pertiwi NP, Mahardini A, Wulandari R, Kurniasih EM, Kuncoro AW, Cahyani NK, Anggoro AW, Ulfa M, Madduppa H, Carpenter KE, Barber PH, Mahardika GN (2015) DNA barcoding reveals targeted fisheries for endangered sharks in Indonesia. Fisheries Research 164: 130–134. https://doi.org/10.1016/j.fishres.2014.11.003

Shao KT (2023) Taiwan Fish Database. [Accessed 3 May 2023] http://fishdb.sinica.edu.tw

Straube N, Iglesias SP, Sellos DY, Kriwet J, Schliewen UK (2010) Molecular phylogeny and node time estimation of bioluminescent lantern sharks

(Elasmobranchii: Etmopteridae). Molecular Phylogenetics and Evolution 56(3): 905–917. https://doi.org/10.1016/j.ympev.2010.04.042

Straube N, White WT, Ho HC, Rochel E, Corrigan S, Li C, Naylor GJ (2013) A DNA sequence-based identification checklist for Taiwanese chondrichthyans. Zootaxa 3752(1): 256–278. https://doi.org/10.11646/zootaxa.3752.1.16

Veríssimo A, Cotton CF, Buch RH, Guallart J, Burgess GH (2014) Species diversity of the deep-water gulper sharks (Squaliformes: Centrophoridae: *Centrophorus*) in North Atlantic waters-current status and taxonomic issues. Zoological Journal of the Linnean Society 172(4): 803–830. https://doi.org/10.1111/zoj.12194

Veríssimo A, Zaera-Perez D, Leslie R, Iglésias SP, Séret B, Grigoriou P, Sterioti A, Gubili C, Barría C, Duffy C, Hernández S, Batjakas JE, Griffiths AM (2017) Molecular diversity and distribution of eastern Atlantic and Mediterranean dogfishes *Squalus* highlight taxonomic issues in the genus. Zoologica Scripta 46(4): 414–428. https://doi.org/10.1111/zsc.12224

Viana ST, Carvalho MD, Gomes UL (2016) Taxonomy and morphology of species of the genus *Squalus* Linnaeus, 1758 from the Southwestern Atlantic Ocean (Chondrichthyes: Squaliformes: Squalidae). Zootaxa 4133(1): 1–89. https://doi.org/10.11646/zootaxa.4133.1.1

Viana ST, De-Carvalho MR (2018) *Squalus rancureli* Fourmanoir, 1979, a new junior synonym of the blacktailed spurdog *S. melanurus* Fourmanoir, 1979, and updated diagnosis of *S. bucephalus* Last, Séret & Pogonoski, 2007 from New Caledonia (Squaliformes, Squalidae). Zoosystema 40(9): 159–177. https://doi.org/10.5252/zoosystema2018v40a9

Ward RD, Zemlak TS, Innes BH, Last PR, Hebert PD (2005) DNA barcoding Australia's fish species. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 360(1462): 1847–1857. https://doi.org/10.1098/rstb.2005.1716

Ward RD, Holmes BH, Zemlak TS, Smith PJ (2007) DNA barcoding discriminates spurdogs of the genus *Squalus*. Pp. 117–130. In: Last PR, White WT, Pogonoski JJ (Eds) Descriptions of new dogfishes of the genus *Squalus* (Squaloidea: Squalidae). CSIRO Marine and Atmospheric Research Paper 014, Hobart, Australia.

Ward RD, Holmes BH, White WT, Last PR (2008) DNA barcoding Australasian chondrichthyans: Results and potential uses in conservation. Marine and Freshwater Research 59(1): 57–71. https://doi.org/10.1071/MF07148

Wei T, Simko V, Levy M, Xie Y, Jin Y, Zemla J (2017) Package 'corrplot'. Statistician 56(316): e24.

White WT, Iglesias SP (2011) *Squalus formosus*, a new species of spurdog shark (Squaliformes: Squalidae), from the western North Pacific Ocean. Journal of Fish Biology 79(4): 954–968. https://doi.org/10.1111/j.1095-8649.2011.03068.x

Whitley GP (1931) New names for Australian fishes. Australian Zoologist 6: 311–344.

WoRMS Editorial Board (2023) World Register of Marine Species. [Accessed 1 May 2023] https://www.marinespecies.org [at VLIZ. doi:10.14284/170]

Zhang CL (1960) [The survey report of the fishes of Bohai and Yellow Sea.] Science Press, Beijing, China. [In Chinese]

Zhang R, Lin LS, Li Y, Song PQ, Chen YJ, Zhang J (2018) [Species composition and quantity distribution of sharks in the southwestern sea of the Nansha Islands and mouth of the Beibu Bay.] Marine Fisheries (01): 27–37. [In Chinese]

Zhu YD (1960) [Chondrichthyes of China.] Science Press, Beijing, China, 225 pp. [In Chinese]

Zhu YD (1962) [Ichthyography of the South China Sea.] Science Press, Beijing, China. [In Chinese]

Zhu YD, Zhang CL, Cheng QT (1963) [Ichthyography of the East China Sea.] Science Press, Beijing, China. [In Chinese]

Zhu YD, Cheng QT, Meng QW (1979) [Ichthyography of the South China Sea Islands.] Science Press, Beijing, China. [In Chinese]

Zhu YD, Meng QW, Li S (1984) A new species of dogfish from China. Journal of Oceanology and Limnology 15(4): 283–286. [In Chinese]

Ziadi-Künzli F, Soliman T, Imai H, Sakurai M, Maeda K, Tachihara K (2020) Re-evaluation of deep-sea dogfishes (genus *Squalus*) in Japan using phylogenetic inference. Deep-sea Research. Part I, Oceanographic Research Papers 160: 103261. https://doi.org/10.1016/j.dsr.2020.103261