

Least concern or critically endangered? Integrative taxonomy provides insights into the reticulated swellshark *Cephaloscyllium fasciatum* and the formosa swellshark *C. formosanum* (Chondrichthyes: Carcharhiniformes: Scyliorhinidae)

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Abstract. The formosa swellshark (*Cephaloscyllium formosanum*) was historically known only from the reportedly lost holotype collected from southwestern Taiwan. After a decade, the rediscovery of the holotype and the identification of additional specimens from museum collections, suggest high morphological similarity with the sympatric *C. fasciatum*, particularly the colour pattern. In the present study, we reassess the taxonomic status of both species using an integrative approach combining morphological and molecular data. Molecular analyses reveal subtle differences between the two nominal species: Maximum likelihood trees based on COI and NADH2 mitochondrial genes reflect that both species cluster within one clade; two species delimitation analyses support a single molecular operational taxonomic unit; and K2P genetic distances are nearly identical. Morphologically, the open-centred dorsal saddles, previously considered diagnostic for *C. fasciatum*, were reinterpreted as an intraspecific variation within *C. formosanum*, which shows black dorsal saddles with white spots. We therefore propose *C. fasciatum* as a junior synonym of *C. formosanum*. Our revisionary work reflects the importance of a robust taxonomic framework before any further conservation status assessments.

Key words. IUCN red list, Chondrichthyes, West Pacific, systematics, species delimitation

INTRODUCTION

The swellshark genus *Cephaloscyllium* Gill, 1862, containing 18 valid species hitherto, is the most speciose genus within the catshark family Scyliorhinidae (Pollerspöck & Straube, 2025). These sharks are relatively small, ranging from 42 to 150 cm in total length (TL), and are all oviparous, exhibiting two distinct reproductive modes (Nakaya et al., 2020). Their distribution is restricted to the Indian and Pacific Oceans, with the highest diversity in the central Indo-West Pacific (Pollerspöck & Straube, 2025). Swellsharks inhabit warm temperate to tropical waters, typically on continental shelves and upper slopes at depths of 100–700 m, though some species occur nearshore (Ebert et al., 2021).

Although rarely targeted, swellsharks are frequently taken as bycatch in fisheries and are usually discarded (Horn,

2016). Most species are considered stable in population and are categorised as “Least Concern” (LC) by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, given their putatively high abundance and post-release survival rate [e.g., *C. isabellum* (Bonnaterre, 1788); Horn, 2016; Finucci & Kyne, 2018], or their potentially remote habitats forming refuges from fishing pressure (e.g., *C. formosanum* Teng, 1962; Rigby et al., 2021). In contrast, several species reportedly face heavy fishing pressure resulting in significant population decline; for instance, *C. fasciatum* Chan, 1966 is classified as “Critically Endangered” (CR) due to its relatively restricted distribution and high overlap of their habitat with intensive fisheries (Dulvy et al., 2020).

Taiwan hosts one of the richest chondrichthyan fauna in the world, with 187 recorded species (Ng et al., 2025). Four swellshark species are known from Taiwanese waters, *C. fasciatum*, *C. formosanum*, *C. sarawakensis* Yano, Ahmad & Gambang, 2005, and *C. umbratile* Jordan & Fowler, 1903. All except *C. formosanum* are common in fishery bycatch (Nakaya, 2019; Ng et al., 2025). In a recent taxonomic revision of the genus in Taiwan, Nakaya et al. (2013) distinguished *C. fasciatum* from its sympatric congeners by its distinctive patterns of dark lines forming open-centred saddles, contrasting with the dark blotches or spots of other species. Nakaya et al. (2013) also resurrected *C. formosanum* from the synonymy of *C. umbratile*, a species described based on the holotype collected from southwestern Taiwan,

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which was reportedly lost in 2012 (Nakaya et al., 2013). More recently, Nakaya (2019) reported *C. formosanum* from southwestern Taiwan. However, the specimens reported by Nakaya (2019) possess similar colour pattern to those of *C. fasciatum* in Nakaya et al. (2013), therefore raising doubts on the taxonomic status of the two species. Given that colour pattern is the most important character for identifying *Cephaloscyllium* (Nakaya et al., 2013), whether the variation between *C. formosanum* and *C. fasciatum* is interspecific or intraspecific has yet to be tested.

The purpose of this study is to re-evaluate the taxonomic status of *C. fasciatum* and *C. formosanum* by analysing specimens from their known distribution in the South China Sea. We test whether the varying colour pattern between *C. formosanum* and *C. fasciatum* represents a diagnostic character as hypothesised by Nakaya et al. (2013) or an intraspecific variation, using an integrative approach that combines morphological and genetic data. Given the contrasting conservation status of *C. fasciatum* (CR) and *C. formosanum* (LC), a stable taxonomic framework and an accurate distribution range is fundamental for effective management and conservation.

MATERIAL AND METHODS

Specimens examined in the present study were housed in the following institutions: Academia Sinica (ASIZP), Natural History Museum, London (BMNH), National Museum of Marine Biology and Aquarium, Taiwan (NMMB-P), and National Taiwan University Museum (NTUM). During recent searches in other Taiwanese collections, the holotype of *C. formosanum* was recovered by the senior author in 2022. After a decade, the specimen remains in good condition and is now deposited in the Taiwanese Fisheries Research Institute (TFRI). Identification of the two studied species *C. fasciatum* and *C. formosanum* followed Nakaya et al. (2013): specimens exhibiting patterns of dark lines or reticulations forming open-centred saddles were identified as *C. fasciatum*, while those with four close-centred saddles anterior to the first dorsal fin were identified as *C. formosanum*. Sex was determined by the presence (male) or absence (female) of claspers. Maturity in males was assessed based on the calcification stage of the claspers, or wherever necessary, by examining the gonad development through a horizontal incision on the right lateral abdomen in females (Chen & Mizue, 1973). Terminology, measurements, and meristic followed Nakaya et al. (2013), while terminology for egg-case descriptions followed Ebert et al. (2006). Direct measurements were taken using a digital calliper (precision=0.1 mm) or a tape ruler (precision=1 mm). Proportional measurements are presented as a percentage of TL, unless otherwise indicated. A Mann-Whitney U Test was employed to investigate the relationship between total length and body patterns (open-centred saddles or close-centred saddles).

DNA barcoding was conducted using the mitochondrial cytochrome c oxidase I (COI) and NADH dehydrogenase subunit 2 (NADH2) markers for phylogenetic reconstruction

and species delimitation: COI is a widely used barcoding tool for delimitation of fish species, which extensive application and deposition in public repositories [e.g., Barcode of Life Data Systems (BOLD), <https://bench.boldsystems.org/index.php>]; NADH2 typically provides better resolution for delimiting chondrichthyan species (Naylor et al., 2012). Genomic DNA was extracted using Dneasy Blood and Tissue Kit on a QIAcube Connect automatic extractor (Qiagen, Düsseldorf, Germany). The target gene regions were amplified via Polymerase Chain Reaction (PCR) using the following primer pairs: FishF1 (5'-TCAACCAACCACAAAGACATTGGCAC-3') and FishR1 (5'-TAGACTTCTGGGTGGCCAAAGAATCA-3') for COI (Ward et al., 2005), and ILEM-Mustelus (5'-AAG-GAC-CAC-TTT-GAT-AGAGT-3') and ASN-Mustelus (5'-AAC-GCT-TAG-CTGTTA-ATT-AA-3') for NADH2 (Naylor et al., 2005). Each 15 µl PCR mixture contained 7.5 µl of EmeraldAmp MAX HS PCR Master Mix (Takara Bio., USA), 0.3 µl of each primer, 1.5 µl of template DNA, and 5.4 µl of sterile distilled water. The thermal cycling profile consisted of an initial denaturation at 94°C for three minutes, then subjected to 35 cycles of denaturation at 94°C for 30 seconds, annealing at 50°C for 30 s, and finally extension at 72°C for 90 seconds, and finally an extension at 72°C for 10 minutes. The successfully amplified PCR products were purified using AMPure XP (Beckman Coulter Life Sciences, USA) following the manufacturer's protocol. Sanger sequencing was conducted by Genomics BioSci and Tech Co Ltd (Taipei, Taiwan) using the forward strand (COI) or both strands of the same primers (NADH2) used for PCR.

Resulting DNA sequences were manually edited and assembled in CodonCode Aligner 12.0.1 (CodonCode Corporation, Dedham, MA, USA). Additional sequences of congeners and selected outgroups were downloaded from Genbank (<https://ncbi.nlm.nih.gov/genbank/>) (COI and NADH2) or BOLD (<https://boldsystems.org/>) (COI). Sequences for each gene were aligned separately using the algorithm 'MUSCLE' (Edgar, 2004) in MEGA12 (Kumar et al., 2024), and the resulting alignments were translated to amino acids to check for stop codons. Maximum likelihood trees employed with the nucleotide substitution model GTR+Γ (Yang, 1994) were reconstructed for each gene using RAXML version 8.2.12 (Stamatakis, 2014) on the CIPRES Science Gateway (<https://www.phylo.org/portal2/home>) (Miller et al., 2010), with 1,000 bootstrap pseudo replicates to determine statistical support for relationships recovered. *Scyliorhinus canicula* (Linnaeus, 1758) and *S. capensis* (Müller & Henle, 1838) were selected as outgroups.

Two molecular species delimitation analyses were employed to test the molecular species hypothesis: the Assemble Species by Automatic Partitioning (ASAP) (Puillandre et al., 2021) and the Bayesian based Poisson Tree Processes (bPTP) (Zhang et al., 2013), which are considered to be effective and robust to test species hypotheses (Magoga et al., 2021). ASAP identifies a significant gap between intra- and interspecific genetic distances based on pairwise genetic distances and further proposes species partitions ranked by a scoring system that does not require biological prior insight

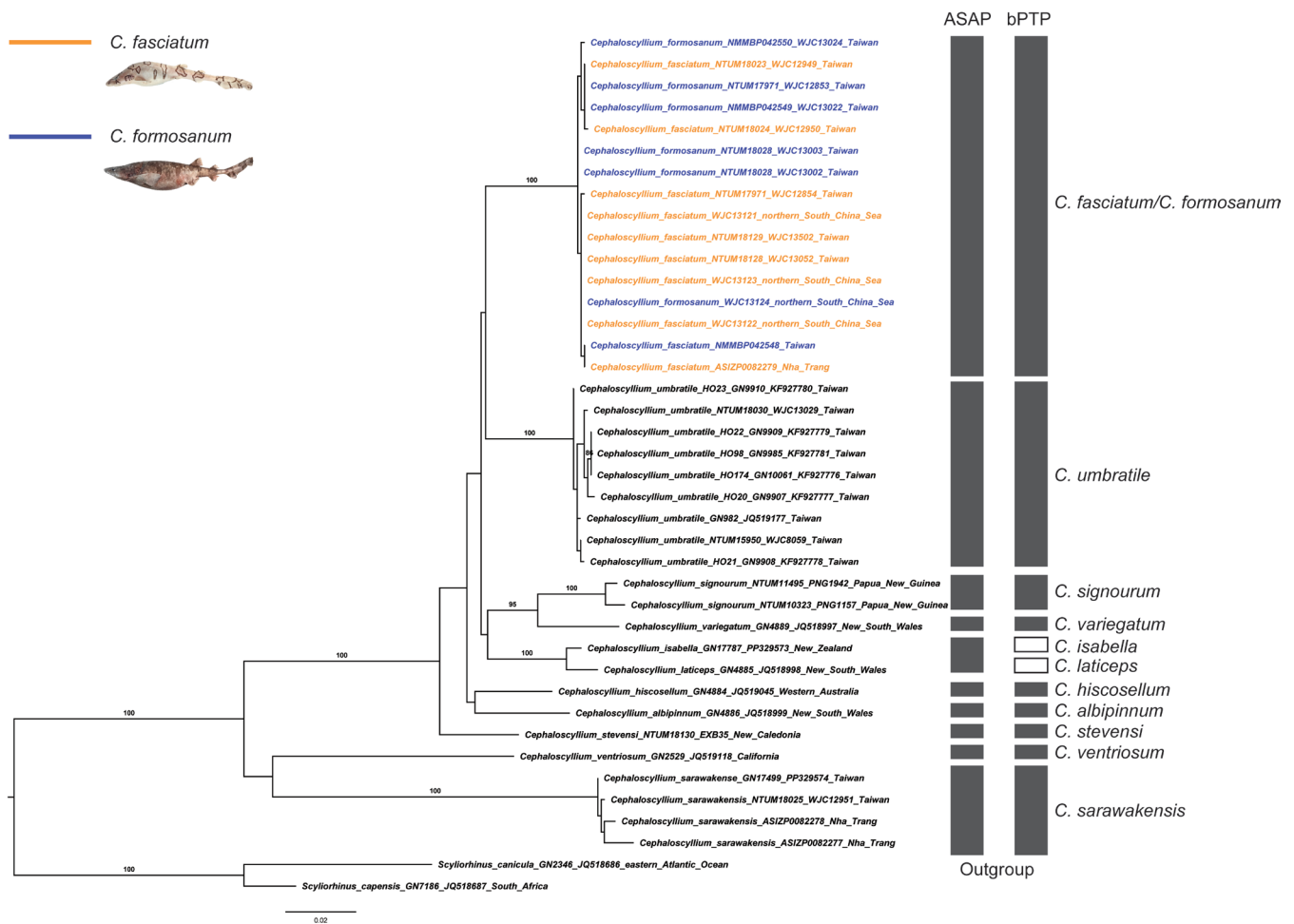


Fig. 1. The maximum likelihood phylogenetic tree reconstructed by the GTR + Γ model with 1000 bootstrap pseudo replicates based on the NADH2 dataset (1,044 bp) and species delimitation analyses of species of *Cephaloscyllium*. Numbers at branches represent bootstrap support values. Bootstrap values below 85% are not shown. Vertical bars on the right side represent the delimited MOTUs. Different colours of bars represent incongruent partitions delimited by species delimitation analyses.

of intraspecific diversity. The analysis was conducted using iTaxoTools (Vences et al., 2021), with default parameters. The bPTP analysis infers Molecular Operational Taxonomic Units (MOTUs) based on the branching events on a rooted tree. Rooted trees with identical sequences removed and the same models and parameters employed as above were inferred as the input tree for bPTP web server (<https://species.h-its.org/>), with the following settings: 100,000 MCMC generations, 100 thinning, burn-in as 0.1, and seed as 123. In addition, the K2P model in MEGA12 was used to quantify the average inter- and intraspecific genetic distances.

RESULTS

The NADH2 dataset comprises 40 sequences (1,044 bp), with 24 generated in the present study (Table 1) and 16 downloaded from Genbank. The maximum likelihood tree suggests that *Cephaloscyllium* forms a monophyletic group with strong support (Bootstrap support, BS=100) (Fig. 1), within which two subclades are resolved: one contains *C. ventriosum* (Garman, 1880) and *C. sarawakensis*; the other one contains all remaining species in the dataset. Within the latter, *C. fasciatum* and *C. formosanum* cluster within

one clade with strong support (BS=100), which forms the sister clade to *C. umbratile*. The ASAP and bPTP analyses delimit 10 and 11 MOTUs, respectively, where both methods delimit *C. fasciatum* and *C. formosanum* as a single MOTU. ASAP also delimits *C. isabella* (Bonnaterre, 1788) and *C. laticeps* (Duméril, 1853) as one MOTU, whereas bPTP separates the two.

The COI dataset consists of 84 sequences (611 bp), with 24 generated in this study (Table 1) and 60 downloaded from online databases. Similar to the NADH2 result, the COI maximum likelihood tree suggests that *Cephaloscyllium* forms a monophyletic group with strong support (BS=100) (Fig. 2), with *C. sarawakensis* representing the sister taxon to the remainder of species. Similarly, *C. fasciatum* and *C. formosanum* cluster within one clade with strong support (BS=98). Notably, a clade containing *C. laticeps*, *C. isabella*, and one sequence downloaded from BOLD (accession number: FNZC311-09), identified as ‘C. sp. B’ also received high support (BS=98). However, the interrelationship between the three species are poorly resolved. The ASAP and bPTP analyses delimit 13 and 18 MOTUs, respectively. As with the NADH2 data, both methods delimit *C. fasciatum* and *C. formosanum* as a single MOTU. Additionally, ASAP

Table 1. Sequences generated from this study. Catalogue number in bold refers to tissue sample number in NTUM (specimen not kept, see Taxonomic account).

Original identification	New identification	Locality	Specimen catalogue number	Collection date	Genbank accession (COI)	Genbank accession (NADH2)
<i>C. fasciatum</i>	<i>C. formosanum</i>	Vietnam	ASIZP0082279	29 January 2024	PX869192	PX526999
<i>C. fasciatum</i>	<i>C. formosanum</i>	northern South China Sea	NTUM16808	11 January 2014	–	–
<i>C. fasciatum</i>	<i>C. formosanum</i>	northern South China Sea	NTUM16809	11 January 2014	–	–
<i>C. fasciatum</i>	<i>C. formosanum</i>	Taiwan	NTUM18023	25 March 2022	PX869194	PX526998
<i>C. fasciatum</i>	<i>C. formosanum</i>	Taiwan	NTUM18024	22 July 2022	PX869195	PX526995
<i>C. fasciatum</i>	<i>C. formosanum</i>	Taiwan	NTUM17971-1	25 December 2024	PX869200	PX526990
<i>C. fasciatum</i>	<i>C. formosanum</i>	Taiwan	NTUM18128	25 March 2025	PX869196	PX526994
<i>C. fasciatum</i>	<i>C. formosanum</i>	Taiwan	NTUM18129-1	28 May 2025	PX869197	–
<i>C. fasciatum</i>	<i>C. formosanum</i>	Taiwan	NTUM18129-2	28 May 2025	PX869198	PX526993
<i>C. fasciatum</i>	<i>C. formosanum</i>	northern South China Sea	WJC13121	21 February 2025	PX869204	PX526987
<i>C. fasciatum</i>	<i>C. formosanum</i>	northern South China Sea	WJC13122	21 February 2025	PX869205	PX526986
<i>C. fasciatum</i>	<i>C. formosanum</i>	northern South China Sea	WJC13123	21 February 2025	PX869206	PX526985
<i>C. formosanum</i>	<i>C. formosanum</i>	northern South China Sea	WJC13124	21 February 2025	PX869207	PX526984
<i>C. formosanum</i>	<i>C. formosanum</i>	Taiwan	NMMB-P042549	25 February 2025	PX869199	PX526992
<i>C. formosanum</i>	<i>C. formosanum</i>	Taiwan	NMMB-P042550	14 March 2025	PX869203	PX526991
<i>C. formosanum</i>	<i>C. formosanum</i>	Taiwan	NMMB-P042551	14 March 2025	–	–
<i>C. formosanum</i>	<i>C. formosanum</i>	Taiwan	NMMB-P042548	25 February 2024	–	PX526997
<i>C. formosanum</i>	<i>C. formosanum</i>	Taiwan	NTUM17971-2	25 December 2024	PX869193	PX526996
<i>C. formosanum</i>	<i>C. formosanum</i>	Taiwan	NTUM18028-1	2 March 2025	PX869201	PX526988
<i>C. formosanum</i>	<i>C. formosanum</i>	Taiwan	NTUM18028-2	2 March 2025	PX869202	PX526989
<i>C. sarawakensis</i>	<i>C. sarawakensis</i>	Vietnam	ASIZP0082277	29 January 2024	PX869208	PX526983
<i>C. sarawakensis</i>	<i>C. sarawakensis</i>	Vietnam	ASIZP0082278	29 January 2024	PX869209	PX526982
<i>C. sarawakensis</i>	<i>C. sarawakensis</i>	Taiwan	NTUM18025	11 September 2023	PX869210	PX526981
<i>C. signourum</i>	<i>C. signourum</i>	Papua New Guinea	NTUM11495	26 April 2014	PX869212	PX526979
<i>C. signourum</i>	<i>C. signourum</i>	Papua New Guinea	NTUM10323	17 December 2012	PX869211	PX526980
<i>C. stevensi</i>	<i>C. stevensi</i>	New Caledonia	NTUM18130	13 September 2011	PX869215	PX526978
<i>C. umbratile</i>	<i>C. umbratile</i>	Taiwan	NTUM15950	21 March 2025	PX869213	PX526977
<i>C. umbratile</i>	<i>C. umbratile</i>	Taiwan	NTUM18030	14 April 2018	PX869214	PX526976

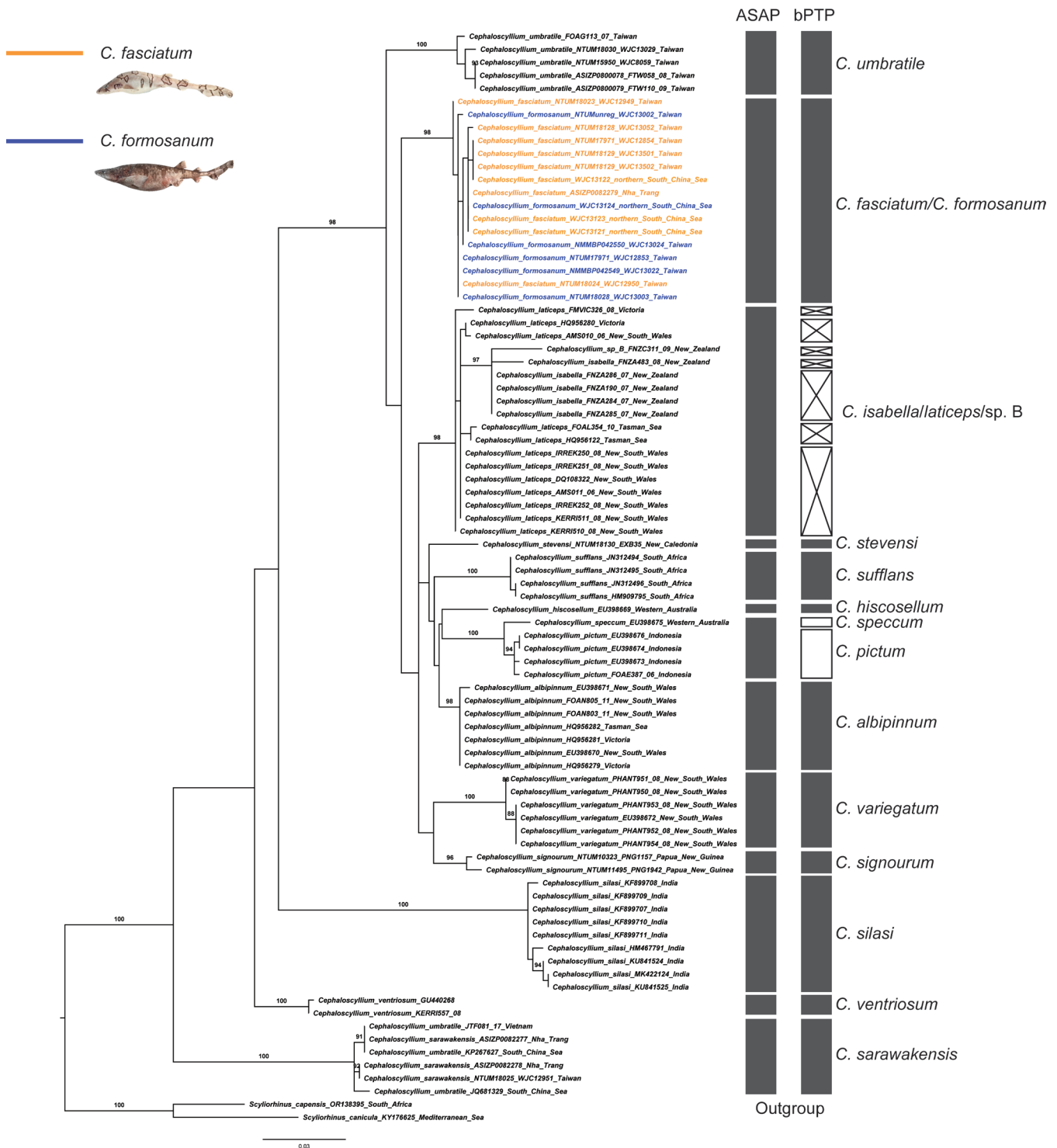


Fig. 2. The maximum likelihood phylogenetic tree reconstructed by the GTR + Γ model with 1000 bootstrap pseudo replicates based on the COI dataset (611 bp) and species delimitation analyses of species of *Cephaloscyllium*. Numbers at branches represent bootstrap support values. Bootstrap values below 85% are not shown. Vertical bars on the right side represent the delimited MOTUs. Different colours of bars represent incongruent partitions delimited by species delimitation analyses. Cross in bars of bPTP represent partitions of the unresolved group associated with polytomies.

groups *C. speccum* Last, Séret & White, 2008 and *C. pictum* Last, Séret & White, 2008 into one MOTU, but bPTP separates them. Moreover, ASAP also groups *C. isabella*, *C. laticeps*, and *C. sp. B* into a single MOTU, whereas bPTP yields extensive splitting within this group, likely reflecting unresolved relationships associated with polytomies in the phylogenetic tree rather than independently evolving lineages.

Intra- and interspecific genetic distances based on NADH2 and COI genes are shown in Tables 2 and 3. The general mean genetic distance between species of *Cephaloscyllium* is 0.063 for NADH2 and 0.066 for COI. Based on NADH2, the largest interspecific distance is between *C. signourum* Last, Séret & White, 2008 and *C. sarawakensis* (0.152–0.158, $\bar{x}$ = 0.156), and the smallest is between *C. fasciatum* and

Table 2. Intra- and interspecific K2P distance based on NADH2 sequences for selected *Cephaloscyllium* species. Value in bold represents intraspecific distance. Value in parentheses represents the mean.

	<i>C. fasciatum</i>	<i>C. formosanum</i>	<i>C. hiscocellum</i>	<i>C. umbratile</i>	<i>C. albipinnum</i>	<i>C. isabella</i>
<i>C. fasciatum</i>	0.002					
<i>C. formosanum</i>	0–0.005 (0.002)	0.002				
<i>C. hiscocellum</i>	0.049–0.050 (0.049)	0.048–0.050 (0.049)	–			
<i>C. umbratile</i>	0.046–0.052 (0.050)	0.045–0.052 (0.050)	0.050–0.055 (0.052)	0.003		
<i>C. albipinnum</i>	0.054–0.057 (0.055)	0.053–0.055 (0.055)	0.045	0.051–0.056 (0.054)	–	
<i>C. isabella</i>	0.054–0.057 (0.055)	0.053–0.056 (0.055)	0.054	0.046–0.050 (0.048)	0.055	–
<i>C. laticeps</i>	0.056–0.058 (0.055)	0.054–0.057 (0.056)	0.052	0.048–0.052 (0.051)	0.054	0.013
<i>C. variegatum</i>	0.058–0.063 (0.059)	0.058–0.062 (0.060)	0.053	0.061–0.065 (0.063)	0.064	0.056
<i>C. stevensi</i>	0.058–0.061 (0.059)	0.058–0.061 (0.059)	0.048	0.053–0.057 (0.056)	0.058	0.051
<i>C. signourum</i>	0.060–0.065 (0.063)	0.060–0.065 (0.062)	0.065–0.069 (0.067)	0.056–0.063 (0.060)	0.062–0.063 (0.062)	0.057–0.058 (0.058)
<i>C. ventriosum</i>	0.126–0.128 (0.127)	0.126–0.128 (0.127)	0.130	0.123–0.127 (0.125)	0.122	0.122
<i>C. sarawakensis</i>	0.142–0.157 (0.148)	0.142–0.155 (0.148)	0.146–0.153 (0.149)	0.131–0.141 (0.136)	0.127–0.134 (0.130)	0.143–0.150 (0.146)
	<i>C. laticeps</i>	<i>C. variegatum</i>	<i>C. stevensi</i>	<i>C. signourum</i>	<i>C. ventriosum</i>	<i>C. sarawakensis</i>
<i>C. laticeps</i>	–					
<i>C. variegatum</i>	0.059	–				
<i>C. stevensi</i>	0.053	0.063	–			
<i>C. signourum</i>	0.064–0.065 (0.065)	0.041–0.045 (0.043)	0.066–0.066 (0.066)	0.009		
<i>C. ventriosum</i>	0.122	0.138	0.127	0.145–0.147 (0.146)	–	
<i>C. sarawakensis</i>	0.146–0.153 (0.149)	0.152–0.158 (0.155)	0.129–0.136 (0.132)	0.152–0.158 (0.156)	0.126–0.132 (0.130)	0.007

Table 3. Intra- and interspecific K2P distance based on COI sequences for selected *Cephaloscyllium* species. Value in bold represents intraspecific distance. Value in parentheses represents the mean.

	<i>C. fasciatum</i>	<i>C. formosanum</i>	<i>C. hiscocellum</i>	<i>C. umbratile</i>	<i>C. albiginnum</i>	<i>C. isabella</i>
<i>C. fasciatum</i>	0.003					
<i>C. formosanum</i>	0–0.006 (0.003)	0.003				
<i>C. hiscocellum</i>	0.035–0.042 (0.040)	0.036–0.042 (0.039)	–			
<i>C. umbratile</i>	0.044–0.058 (0.052)	0.046–0.058 (0.051)	0.048–0.054 (0.050)	0.005		
<i>C. albiginnum</i>	0.033–0.042 (0.037)	0.033–0.042 (0.036)	0.022–0.025 (0.022)	0.044–0.054 (0.048)	0.001	
<i>C. isabella</i>	0.038–0.049 (0.042)	0.040–0.049 (0.043)	0.040–0.051 (0.042)	0.044–0.055 (0.048)	0.031–0.046 (0.034)	0.004
<i>C. laticeps</i>	0.036–0.044 (0.040)	0.035–0.044 (0.039)	0.033–0.041 (0.037)	0.038–0.055 (0.043)	0.023–0.033 (0.026)	0.010–0.029 (0.014)
<i>C. variegatum</i>	0.046–0.056 (0.053)	0.048–0.056 (0.052)	0.040–0.044 (0.042)	0.053–0.064 (0.058)	0.040–0.048 (0.043)	0.045–0.059 (0.050)
<i>C. stevensi</i>	0.040–0.046 (0.043)	0.040–0.046 (0.043)	0.034	0.044–0.051 (0.047)	0.022–0.025 (0.022)	0.036–0.047 (0.038)
<i>C. signourum</i>	0.033–0.044 (0.039)	0.035–0.046 (0.040)	0.034–0.038 (0.036)	0.044–0.048 (0.045)	0.029–0.033 (0.030)	0.033–0.044 (0.035)
<i>C. pictum</i>	0.048–0.052 (0.050)	0.050–0.052 (0.051)	0.036–0.036 (0.036)	0.064–0.071 (0.069)	0.033–0.037 (0.033)	0.044–0.055 (0.046)
<i>C. speccum</i>	0.048–0.054 (0.052)	0.050–0.054 (0.051)	0.036	0.066–0.070 (0.067)	0.037–0.040 (0.037)	0.048–0.059 (0.050)
<i>C. sulfflans</i>	0.048–0.054 (0.052)	0.050–0.056 (0.052)	0.036–0.038 (0.037)	0.048–0.054 (0.050)	0.033–0.039 (0.035)	0.046–0.055 (0.049)
<i>C. sp. B</i>	0.052–0.056 (0.054)	0.054–0.056 (0.055)	0.051	0.062–0.064 (0.062)	0.044–0.048 (0.044)	0.016–0.026 (0.018)
<i>C. silasi</i>	0.111–0.130 (0.122)	0.114–0.130 (0.120)	0.120–0.132 (0.125)	0.111–0.128 (0.119)	0.129–0.143 (0.134)	0.120–0.146 (0.130)
<i>C. ventriosum</i>	0.068–0.078 (0.075)	0.070–0.078 (0.074)	0.075–0.077 (0.076)	0.078–0.083 (0.080)	0.074–0.080 (0.075)	0.071–0.081 (0.074)
<i>C. sarawakensis</i>	0.114–0.121 (0.118)	0.114–0.121 (0.117)	0.124–0.127 (0.125)	0.110–0.120 (0.114)	0.122–0.135 (0.128)	0.118–0.128 (0.122)
	<i>C. laticeps</i>	<i>C. variegatum</i>	<i>C. stevensi</i>	<i>C. signourum</i>	<i>C. pictum</i>	<i>C. speccum</i>
<i>C. laticeps</i>	0.003					
<i>C. variegatum</i>	0.037–0.050 (0.045)	0.002				
<i>C. stevensi</i>	0.025–0.037 (0.030)	0.045–0.050 (0.048)	–			
<i>C. signourum</i>	0.030–0.041 (0.034)	0.034–0.039 (0.037)	0.036–0.036 (0.036)	0.007		
<i>C. pictum</i>	0.044–0.052 (0.048)	0.061–0.066 (0.064)	0.042–0.042 (0.042)	0.046–0.050 (0.048)	0.003	
<i>C. speccum</i>	0.044–0.052 (0.049)	0.057–0.062 (0.060)	0.046	0.042–0.046 (0.044)	0.013–0.013 (0.013)	–
<i>C. sulfflans</i>	0.042–0.050 (0.045)	0.048–0.054 (0.052)	0.040–0.042 (0.041)	0.036–0.042 (0.039)	0.050–0.052 (0.051)	0.050–0.052 (0.051)

	<i>C. laticeps</i>	<i>C. variegatum</i>	<i>C. stevensi</i>	<i>C. signourum</i>	<i>C. pictum</i>	<i>C. specum</i>
<i>C. sp. B</i>	0.024–0.032 (0.026)	0.058–0.062 (0.061)	0.051	0.042–0.044 (0.043)	0.056–0.056 (0.056)	0.056
<i>C. silasi</i>	0.120–0.146 (0.130)	0.108–0.122 (0.115)	0.122–0.131 (0.126)	0.115–0.129 (0.122)	0.120–0.130 (0.125)	0.109–0.118 (0.113)
<i>C. ventriosum</i>	0.058–0.084 (0.069)	0.078–0.083 (0.080)	0.083–0.086 (0.084)	0.073–0.084 (0.079)	0.093–0.095 (0.094)	0.093–0.095 (0.094)
<i>C. sarawakensis</i>	0.115–0.130 (0.119)	0.115–0.122 (0.117)	0.117–0.124 (0.121)	0.108–0.115 (0.112)	0.127–0.130 (0.129)	0.120–0.123 (0.122)
	<i>C. sulflans</i>	<i>C. sp. B</i>	<i>C. silasi</i>	<i>C. ventriosum</i>	<i>C. sarawakensis</i>	
<i>C. sulflans</i>	0.001					
<i>C. sp. B</i>	0.062–0.062 (0.062)	–				
<i>C. silasi</i>	0.121–0.131 (0.126)	0.144–0.155 (0.149)	0.005			
<i>C. ventriosum</i>	0.084–0.089 (0.086)	0.090–0.092 (0.091)	0.094–0.105 (0.098)	0.002		
<i>C. sarawakensis</i>	0.122–0.125 (0.124)	0.132–0.140 (0.136)	0.127–0.142 (0.134)	0.094–0.098 (0.096)	0.005	

C. formosanum (0–0.005, $\bar{x}$ =0.002). For COI, the largest interspecific distance is between *C. sp. B* and *C. silasi* (Talwar, 1974) (0.144–0.155, $\bar{x}$ =0.149), and the smallest is again between *C. fasciatum* and *C. formosanum* (0–0.006, $\bar{x}$ =0.003).

Integrating the results from the maximum likelihood trees, the species delimitation analyses and the genetic distances, it is clear that *C. fasciatum* and *C. formosanum* are conspecific. Based on this result, below we provide a redescription for *C. formosanum*.

TAXONOMY

Cephaloscyllium formosanum Teng, 1962

Formosa swellshark

(Figs. 3–7, Supplementary Table 1)

Cephaloscyllium formosanum Teng, 1962: pp. 48–51, fig. 11. Nakaya, 2019: pp. 21, 2 figs.

Cephaloscyllium fasciatum Chan, 1966, pp. 232–236, figs. 6, 7 (a, c), 8, plate (original description); Ebert et al., 2021, pp. 420, pl. 418.

Cephaloscyllium maculatum Schaaf-da Silva & Ebert, 2008, pp. 7, fig. 6.

Cephaloscyllium pardelotum Schaaf-da Silva & Ebert, 2008, pp. 3, fig. 1.

Cephaloscyllium sp. 1 Chiang et al., 2014: pp. 5, fig. 16.

Cephaloscyllium sp. 2 Chiang et al., 2014: pp. 6, fig. 17.

Material examined. 20 specimens. **Holotype:** TFRI 4339, pregnant female 655 mm TL, off Donggang, southwestern Taiwan, 22°25'N, 120°25'E, ca. 366 m, 7 March 1961.

Holotype of *C. fasciatum*: BMNH 1965.8.11.1, immature female 422 mm TL, off east-southeast of Cape Bantangan, Vietnam, 15°55.7'N, 109°28.5'E, 205–315 m, 16 September 1963. **Non-types:** ASIZP0082279, female 482 mm TL, Lương Sơn fishing port, Nha Trang, Khánh Hòa, off southeast coast of Vietnam, depth ca. 120–180 m, 29 January 2024, coll. C.-H. Lin; NMMB-P042548, immature female 267.8 mm TL, off Donggang, southwestern Taiwan, ca. 22°N, 120°E, ca. 300 m, 9 May 2024, coll. Y. Su & Y.-C. Hsu; NMMB-P042549, female 290.7 mm TL, off Donggang, southwestern Taiwan, ca. 22°N, 120°E, ca. 300 m, 25 February 2024, coll. K.-H. Wu; NMMB-P042550, mature male 783 mm TL, NMMB-P042551, mature male 817 mm TL, off Fugang, eastern Taiwan, ca. 22°N, 121°E, ca. 500 m, 14 March 2025, coll. Y.-C. Hsu; NTUM16808, female 193.6 mm+ (caudal fin broken), exp. NanHai 2014, station CP4115, 20°03'N, 120°24'E, 265–300 m, 11 January 2014; NTUM16808, immature female 223.7 mm, exp. NanHai 2014, station CP4116, 20°03'N, 114°11'E, 262–298 m, 11 January 2014; NTUM17971 (2 specimens), immature male 278.9 mm TL, female 325 mm TL, off Donggang, southwestern Taiwan, ca. 22°N, 120°E, ca. 300 m, 25 December 2024; NTUM18023, immature male 301.8 mm TL, off Donggang, southwestern Taiwan, ca. 22°N, 120°E, ca. 300 m, 25 March 2022; NTUM18024, female 198.7 mm TL, off Donggang, southwestern Taiwan, ca. 22°N, 120°E, ca. 300 m, 22 July 2022; NTUM18028 (2 specimens), mature

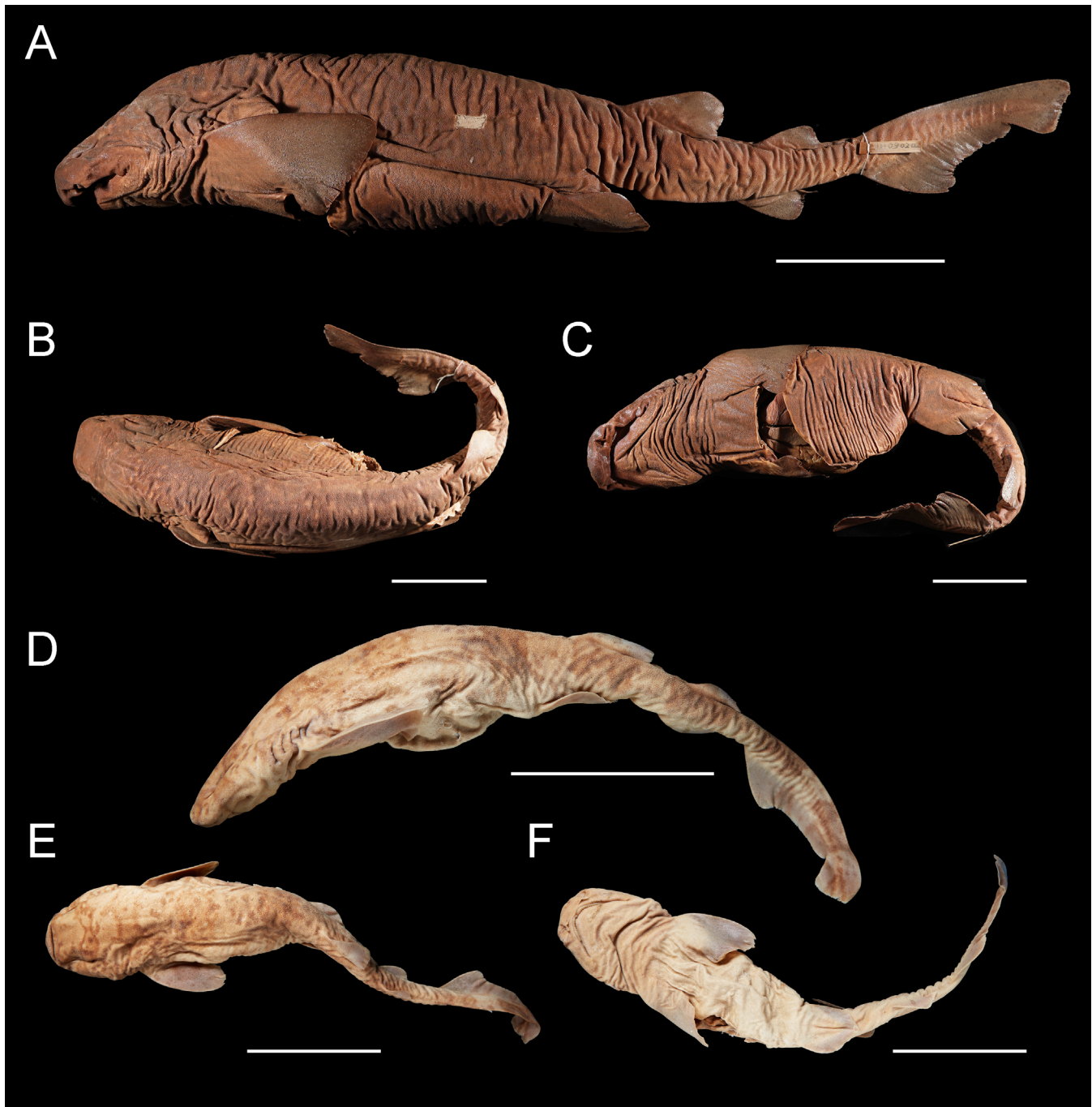


Fig. 3. A–C, holotypes of *C. formosanum* TFRI 4339, pregnant female 655 mm TL and D–F, *C. fasciatum* BMNH 1965.8.11.1, immature female 422 mm TL. A, D: Lateral view. B, E: Dorsal view. C, F: Ventral view. Photos of *C. fasciatum* courtesy of L. Goodayle (BMNH). Scale bars=100 mm.

male 776 mm TL, mature female 738 mm TL, off Fugang, eastern Taiwan, ca. 22°N, 121°E, ca. 500 m, 2 March 2025; NTUM18128, female 167.0 mm TL, off Donggang, southwestern Taiwan, ca. 22°N, 120°E, ca. 300 m, 25 March 2025; NTUM18129 (2 specimens), female 229.2 mm TL, immature male 218.7 mm TL, off Donggang, southwestern Taiwan, ca. 22°N, 120°E, ca. 300 m, 28 May 2025, coll. Y.-Y. Hsu. **Additional material (not retained):** WJC13121, mature male 534 mm TL, WJC13122, mature female 637 mm TL, WJC13123, pregnant female 642 mm TL, WJC13124, pregnant female 697 mm TL, northern South China Sea, 21 February 2025, coll. K-H. Yu.

Diagnosis. A large swellshark species attaining 817 mm TL, differing from other congeners by having a combination of four open-centred or complete dark saddles on dorsal side of body before the first dorsal fin, one open-centred or complete dark blotch on centre of outer surface of pectoral fin, and the surface of egg case smooth, translucent when fresh.

Description. Morphometric and meristic in Supplementary Table 1. Body stout, tail slender (Fig. 3). Head large, slightly depressed. Caudal peduncle slightly tapering. Snout short, considerably depressed, its tip pointed from lateral view, broadly rounded from dorsal view. Interorbital space flat. Nostrils close to mouth. Anterior nasal flap well-developed,

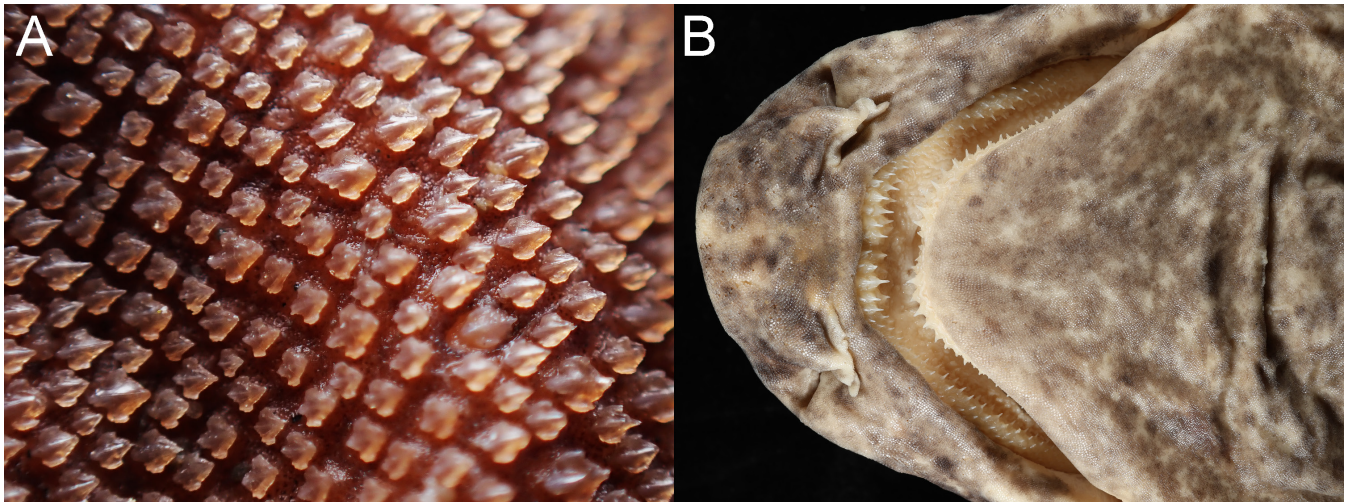


Fig. 4. Placoid scales from below A, first dorsal fin and B, teeth of *C. formosanum*. A: TFR1 4339, pregnant female, 655 mm TL. B: NTUM18028, mature male, 776 mm TL.

broadly triangular, not reaching upper jaw. Posterior nasal flap well developed. Internarial width slightly longer than nostril width. Mouth very broad, almost three times preoral length, strongly arched. Labial furrows poorly defined. Eye small, elliptical. Spiracle small, behind and below eye. Gill openings moderate, the fourth and fifth openings over base of pectoral fin.

Placoid scales robust, tricuspidate, middle cusp longest; medial ridge prominent, several weak ridges present from base to cusp (Fig. 4).

Teeth of holotype missing, description hereafter based on non-types. Tooth-shape similar between upper and lower jaw; main cusp narrowly triangular, usually flanked with 2–4, much smaller cusplets; teeth near symphysis minute (Fig. 4).

Pectoral fin broadly triangular, the apex and free rear tip rounded. First dorsal-fin origin slightly anterior to a vertical through mid pelvic-fin base, apex broadly rounded. Second dorsal fin much smaller than first dorsal fin, origin just posterior to anal-fin origin or over a vertical through mid anal-fin base, base shorter than anal-fin base, apex rounded. Pelvic-fin insertion below a vertical through middle of first dorsal-fin base, apex broadly rounded. Anal fin larger than second dorsal fin, insertion about same level with second dorsal-fin insertion, base length subequal to anal-caudal space, apex rounded, free rear tip pointed, anterior margin convex while posterior margin concave. Caudal fin slender, lower lobe moderately developed, subterminal notch distinct; terminal margin straight in adults, broadly rounded in juveniles. Posterior margin of fins concave in adults, slightly convex in juveniles; free rear tip angular in adults, rounded in juveniles.

Colouration. In fresh specimens (Fig. 5), body background colour pale to dark brown, paler ventrally. Body with prominent and complex patterns and exhibiting remarkable variations: dorsal side of body before first dorsal fin with four saddles extending to mid-lateral body: first connecting upper edges of spiracles, often separated into two horizontally;

second connecting areas above pectoral-fin origins; third connecting areas above pectoral-fin free rear tip; last one positioned approximately one first dorsal-fin base length before first dorsal fin. Saddle formation varying from open-centred dark lines, dark lines encircling blotches, to pure black blotches; saddle shape irregular, from elliptical blotch to narrowly rhombic ‘bars’. Areas below second, third and fourth dorsal saddles sometimes with blotches, sometimes poorly defined or absent. A blotch present below each dorsal fin.

Fins with blotches. Mid-point of outer surface of pectoral fin with a blotch in all specimens examined. Mid-pelvic fin usually with a small blotch. Dorsal-fins lower part with a blotch connecting the blotch under fin bases. A small blotch present at anal-fin origin. Caudal fin with two saddles: first at upper and lower origin extending to about mid-lower lobe, sometimes bifurcated into two separated blotches when viewed laterally; second covering mid-caudal-fin to a vertical through terminal notch, extending to lower lobe. Mid-terminal lobe with a small blotch. Some specimens with a small blotch at mid-upper postventral margin. White and black spots of irregular size usually present except in neonates, scattered across body. White spots usually outnumbered black spots.

Colouration in preservative, similar to that described for fresh specimens. Holotype entirely dark brown, possibly a result of long-term preservation in ethanol solution.

Specimens with close-centred saddles mostly larger (Fig. 6), with a significant relationship between body length and pattern ($U=18$, $p<0.05$). White and black spots on the body usually more prominent in larger individuals.

Egg case morphology. Egg case translucent, whitish yellow, surface smooth, glossy; no ridges, with numerous thin striations (Fig. 7). Lateral flanges extending entire length of egg case, rounded. Anterior border slightly concave, broad; anterior horns rather long, curved slightly inwards, not touching; tendrils long, tightly coiled. Posterior border much narrower, concave; posterior horns slightly shorter

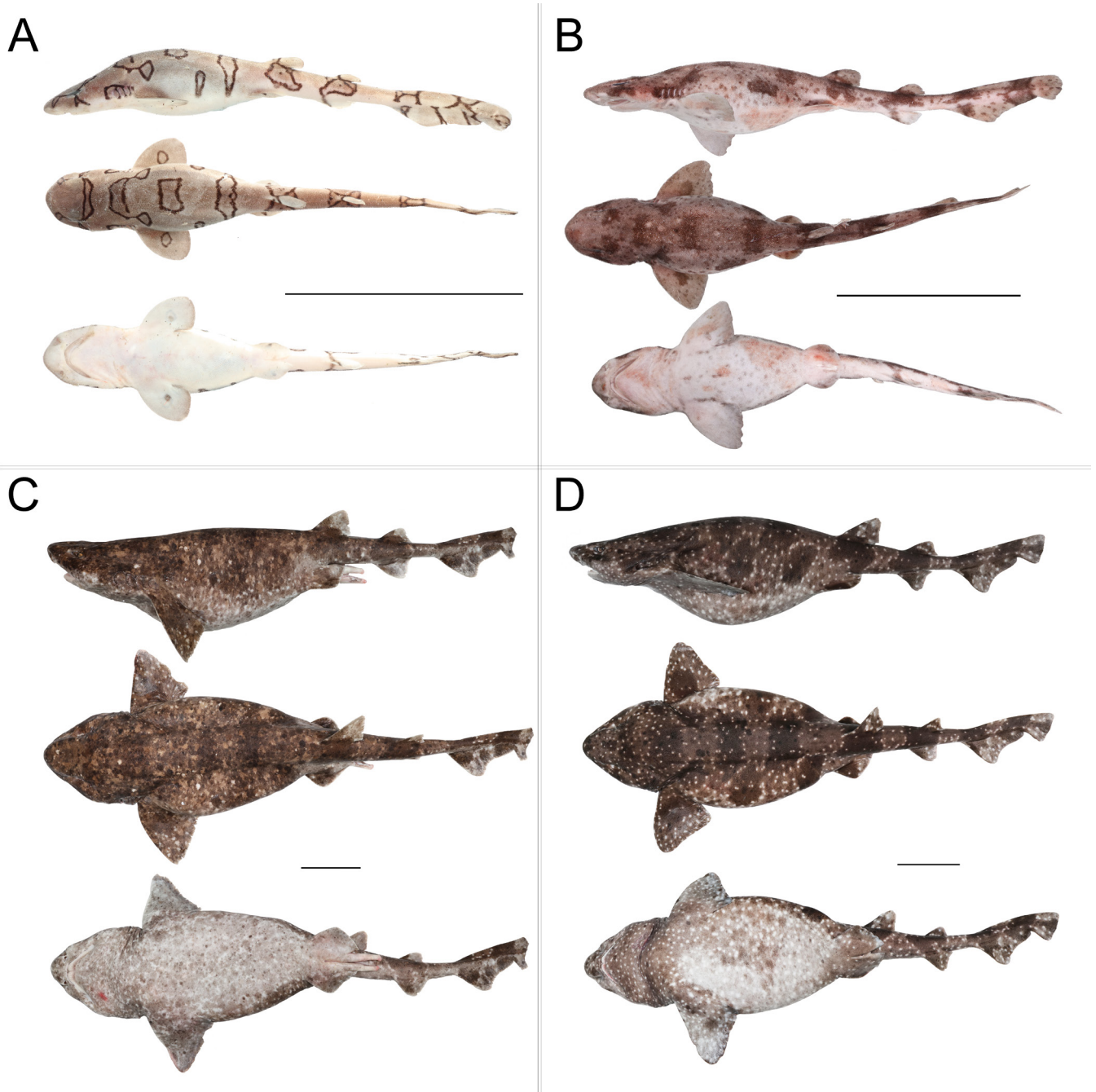


Fig. 5. Fresh specimens of *C. formosanum* showing variation in body patterns. A, NTUM18128, neonate female, 167.0 mm TL. B, NMMB-P042548, immature male, 267.8 mm TL, photo courtesy of Y.-C. Hsu. C, NTUM18028, mature male, 776 mm TL. D, NTUM18028, mature female, 738 mm TL. Scale bars=100 mm.

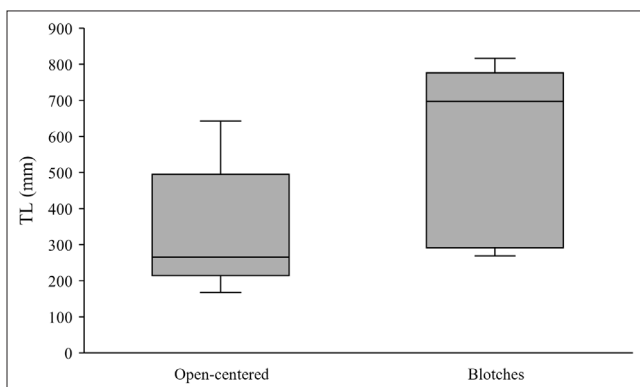


Fig. 6. Relationship between total length and patterns (open-centred saddles and blotches).



Fig. 7. Egg case of *C. formosanum*, 110 mm excluding horns, from WJC13124, pregnant female, 697 mm TL.

than anterior horn, curved inwards, overlapping; tendrils very long, wiry, tightly coiled.

Only one egg case observed in holotype. Two egg cases observed in each of two non-types. No embryos observed inside of egg cases.

Size. Largest specimen recorded 817 mm TL (mature male). Females possibly larger. Size at birth approximately 167 mm TL.

Distribution. Restricted to the tropical northwestern Pacific, from eastern and southwestern Taiwan to the northern South China Sea, and off coasts of Vietnam, at depths of 205–500 m.

Remarks. For a detailed synonym list see Nakaya et al. (2013).

DISCUSSION

Nomenclatural discussion regarding *C. fasciatum*. *Cephaloscyllium fasciatum* was described from specimens collected off the coast of Vietnam. The entire type series possess open-centred saddles, a characteristic that distinguishes it from the sympatric congeners in the northwestern Pacific (Nakaya et al., 2013), including the poorly known *C. formosanum* described from southwestern Taiwan. However, our molecular analyses, including specimens from near the type localities of both *C. fasciatum* and *C. formosanum*, indicate that *C. fasciatum* and *C. formosanum* are conspecific at the molecular level.

From a morphological perspective, several specimens exhibit a colour pattern intermediate between that of the two species, i.e., dark lines encircling black blotches. These intermediates are otherwise indistinguishable from typical *C. fasciatum* (open-centred dark lines) and *C. formosanum* (solid black blotches). Additionally, all specimens share a combination of four dorsal saddles anterior to the first dorsal fin and identical pattern of blotches on the fins. We therefore conclude they represent the same species, so that *C. fasciatum* should be considered a junior synonym of *C. formosanum*. As a result of this taxonomic change, *C. formosanum* should now be recognised as widespread throughout the South China Sea, with its northernmost record off Taitung, eastern Taiwan.

Comparison with North-Pacific congeners. Two species, *C. sarawakensis* and *C. umbratile*, have been reported from Taiwan (Nakaya et al., 2013; Ng et al., 2025). *Cephaloscyllium formosanum* differs from both species by possessing four saddles anterior to the first dorsal fin (vs. two in *C. sarawakensis*; three in *C. umbratile*). Juveniles of *C. sarawakensis* are characterised by having numerous black spots surrounded in white (Nakaya et al., 2013), a feature absent in *C. formosanum*. Large specimens of *C. umbratile* can be easily confused with *C. formosanum* due to the presence of numerous black spots, but *C. umbratile* lacks the white spots commonly found in *C. formosanum*.

Although the three species occur in Taiwanese waters, they do not appear to be sympatric. *Cephaloscyllium umbratile* is commonly found from northern Taiwan to Japan (Nakaya et al., 2013; Ng et al., 2025) but is rarely reported in eastern or southern Taiwan (Ng et al., 2025). While *C. sarawakensis* has a broadly similar geographic distribution in the South China Sea, it is more common in shallow waters around 100 m depth, whereas *C. formosanum* typically occurs in deep waters below 200 m.

Potential size-depth segregation. Size-depth segregation has been reported in deep-water catsharks. Adults of the roughtail catshark *Galeus arae* (Nichols, 1927) from the western-central Atlantic are reported to inhabit deeper waters than juveniles (Király et al., 2003). Here, we propose that a similar situation exists for *C. formosanum*. All mature individuals we examined were captured by deep-sea longliners targeting *Beryx* spp., whereas all immature specimens were collected via bottom trawlers. We hypothesise that juveniles of *C. formosanum* prefer flat, sandy, or muddy seabed, while adults shift to deeper rocky substrates. This is supported by a significant relationship between body pattern and size, with smaller individuals of *C. formosanum* exhibiting a significantly higher proportion of open-centred saddles encircled by dark lines, whereas specimens >600 mm TL almost exclusively possess completely black saddles, typically with complex black and white spots scattered over the body. The complex pattern of adults may provide beneficial camouflage in rocky habitats. This habitat shift also explains the rarity of adult *C. formosanum* in surveys, as their rocky habitats offer refuge from bottom trawling.

Necessity for re-evaluation of the population status. The IUCN population assessments for *C. fasciatum* (CR) and *C. formosanum* (LC) contrast starkly (Dulvy et al., 2020; Rigby et al., 2021). The Least Concern status of *C. formosanum* was assigned because it was thought to inhabit deep waters with limited fisheries interaction, similar to other deep-sea sharks [e.g., the lanternshark genus *Etmopterus* (Rafinesque, 1810)]. However, integrating the new taxonomic treatment with fish-market observations indicates that juveniles of *C. formosanum* occasionally encounter fisheries, while adults have less interaction due to their occupancy of complex rocky substrates that are challenging to sample. Consequently, the population status of *C. formosanum* requires re-evaluation.

Future work on the taxonomy of swellsharks. The taxonomy of swellsharks is well-established (e.g., Last & White, 2008; Last et al., 2008a, b; White & Ebert, 2008; Nakaya et al., 2013). However, species hypotheses have rarely been tested using molecular methodologies. In this study, we propose a new species hypothesis based on COI and NADH2 phylogenetic analyses with comprehensive taxonomic coverage, lacking data only for *C. cooki* Last, Séret & White, 2008 and *C. zebrum* Last & White, 2008. This underscores the importance of integrating molecular analyses with morphological examination, particularly for swellsharks that exhibit high intraspecific variation. In addition, the species delimitation analyses successfully delineated most species, except *C. isabella* and *C. laticeps*,

and between *C. pictum* and *C. speccum*, as these species have rather shallow genetic divergence. The incongruence between the two species delimitation analyses based on the two genes may indicate a complex relationship between these taxa. However, caution should be taken, as the sequence data analysed herein is derived largely from online databases, and specimen identification should be considered tentative.

Swellsharks exhibit prominent intraspecific and ontogenetic variation in body patterning (e.g., *C. formosanum*, this study; *C. sarawakensis*, Nakaya et al., 2013). Nevertheless, such variation remains poorly documented for most congeners, particularly those in Australian waters where available material is limited (e.g., *C. zebrum*). Integrating intra- and interspecific, as well as ontogenetic, morphological variations with molecular species delimitation analyses could provide more support for species hypotheses. This, in turn, would establish a more robust foundation for subsequent population assessments and conservation strategies.

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APPENDIX

Supplementary Table 1. Morphometric and meristic data for the holotype and ranges for the non-types of *C. formosanum*.

Specimens	Holotype	Non-types (n=15)		
		Min.	Max.	S.D.
Total length (mm)	655	167	817	
%TL				
Precaudal length	78.0	71.9	82.0	2.5
Prenarial length	1.5	1.5	3.5	0.5
Preoral length	3.4	3.4	6.1	0.7
Preorbital length	5.3	4.9	10.1	1.3
Prespiracle length	9.5	9.5	11.8	0.7
Prebranchial length	17.7	15.1	17.8	0.8
Head length	21.3	19.8	22.7	0.9
Prepectoral length	20.6	18.8	21.0	0.7
Prepelvic length	49.9	44.1	52.2	2.2
Snout-anterior vent length	52.2	45.6	52.2	2.0
Pre D1 length	57.3	47.7	57.3	2.6
Pre D2 length	67.0	60.4	68.4	2.1
Interdorsal space	7.4	7.4	9.8	0.6
D2–caudal space	7.4	7.0	10.2	1.0
Pectoral–pelvic space	20.8	14.6	21.9	2.0
Pelvic–anal space	9.0	7.4	12.6	1.3
Anal–caudal space	5.7	5.7	8.6	0.9
Orbit length	3.3	2.6	4.3	0.5
Interorbital space	7.1	6.8	8.8	0.5
Nostril width	1.9	1.5	5.2	0.9
Internarial length	3.2	3.1	5.9	0.8
Anterior nasal flap length	0.9	0.9	2.0	0.3
Spiracle length	0.3	0.3	1.0	0.2
Eye–spiracle space	1.3	0.6	1.3	0.2
Mouth length	6.4	5.7	8.2	0.8
Mouth width	9.6	8.5	11.3	0.9
Intergill length	4.9	4.3	6.5	0.6
1st gill slit height	2.5	1.0	3.3	0.6
2nd gill slit height	2.8	1.0	2.8	0.5
3rd gill slit height	2.4	1.0	2.4	0.4
4th gill slit height	2.4	0.9	2.4	0.5
5th gill slit height	1.1	0.7	2.1	0.3
Head height	11.6	6.5	11.6	1.3
Head width	14.0	12.6	16.9	1.3

Specimens	Holotype	Non-types (n=15)		
		Min.	Max.	S.D.
Trunk height		9.9	15.8	1.8
Trunk width		10.9	16.4	1.8
Caudal peduncle height	3.1	2.5	3.8	0.4
Caudal peduncle width	2.6	2.2	3.1	0.2
Pectoral fin length	12.3	12.0	14.3	0.7
Pectoral fin anterior margin length	14.9	11.7	17.1	1.5
Pectoral fin base length	8.1	7.8	9.7	0.5
Pectoral fin height	10.9	8.3	13.3	1.5
Pectoral fin inner margin length	4.2	3.6	5.5	0.5
Pectoral fin posterior margin length	10.9	7.6	13.5	1.7
Pelvic fin length	10.9	9.0	12.4	0.9
Pelvic fin anterior margin length	6.1	5.2	8.3	0.8
Pelvic fin base length	8.8	5.6	8.8	1.0
Pelvic fin height	4.9	3.8	6.9	0.9
Pelvic fin inner margin length	2.5	1.9	4.2	0.6
Pelvic fin posterior margin length	6.9	5.0	7.7	0.8
Clasper length outer	-	1.2	1.7	0.2
Clasper length inner	-	4.1	4.6	0.2
Clasper base width	-	0.7	1.0	0.1
D1 length	9.8	8.7	9.9	0.4
D1 anterior margin length	9.6	8.2	10.5	0.6
D1 base length	6.7	6.2	7.3	0.3
D1 height	4.5	3.1	6.1	0.8
D1 inner margin length	3.2	2.3	3.2	0.3
D1 posterior margin length	4.5	2.8	6.1	0.9
D2 length	7.6	6.9	7.9	0.3
D2 anterior margin length	5.5	2.3	7.0	1.1
D2 base length	4.7	4.5	5.3	0.2
D2 height	2.2	2.0	7.1	1.3
D2 inner margin length	2.9	1.9	3.0	0.3
D2 posterior margin length	3.0	1.6	3.8	0.6
Anal-fin length	8.3	8.3	10.4	0.6
Anal-fin anterior margin	6.8	6.5	8.4	0.6
Anal-fin base length	5.7	5.7	7.5	0.6
Anal-fin height	3.5	2.2	6.5	1.0
Anal-fin inner margin length	2.9	2.1	3.3	0.3
Anal-fin posterior margin length	4.1	2.4	5.2	0.8
Caudal dorsal margin	21.9	19.9	26.9	2.2

Specimens	Holotype	Non-types (n=15)		
		Min.	Max.	S.D.
Caudal fork width	10.7	6.7	14.4	1.8
Caudal fork length	9.8	8.8	13.8	1.4
Caudal preventral margin length	9.6	8.8	11.2	0.6
Caudal lower postventral margin	2.7	2.0	4.8	0.7
Caudal upper postventral margin	6.5	6.1	8.3	0.7
Caudal fin subterminal margin	4.6	3.3	5.0	0.6
Caudal fin terminal margin length	5.2	0.0	7.0	1.6
Caudal fin terminal lobe length	6.5	0.0	7.9	1.8
D1 midpoint–pectoral fin insertion	39.2	22.6	39.2	4.3
D1 midpoint–pelvic-fin origin	13.1	6.8	14.1	1.9
Pelvic-fin midpoint–D1 insertion	8.7	7.1	10.1	0.8
Pelvic-fin midpoint–D2 origin	13.7	13.1	16.5	1.0
Monospondylous vertebrae	44	43	47	1.4
Diplospondylous trunk vertebrae	33	33	35	0.7
Precaudal vertebrae	77	77	81	1.3