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Lost and found: recovery of the holotype of the ocellated angelshark, *Squatina tergocellatoides* Chen, 1963 (Squatinidae), with comments on western Pacific squatinids

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Abstract

The ocellated angelshark, *Squatina tergocellatoides*, Chen, 1963 is redescribed from the holotype, which was thought to be lost. Its recent recovery has allowed for a revised description, including new data, and comparison to other Western Pacific squatinids. *Squatina tergocellatoides* can be distinguished from its congeners by three pairs of prominent large black spots, each with a diameter greater than eye length; two on each pectoral fin at anterior and posterior angles and one on each side near the tail base; another three pairs of lesser defined spots, one large spot on base of each dorsal fin and one located laterally on each side of tail located below first dorsal fin. Ventral surface is uniformly white to cream coloured, and margins of pectoral fins and tail similar in colour to dorsal side. Pectoral fins with angular lateral apices and rounded posterior lobe, pelvic fin tips not reaching origin of first dorsal fin, strongly fringed nasal barbels, small inter-orbital space, head and mouth lengths, broad internarial width and pelvic fin base, a very small pelvic girdle width, and a caudal fin with triangular ventral lobe greater in length than dorsal lobe. Comments on additional specimens are provided, as well as observations on biogeography. A review of western Pacific squatinids is also provided.

Key words: Squatinidae, *Squatina tergocellatoides*, holotype, redescription, Western Pacific, Taiwan

Introduction

The family Squatinidae (Chondrichthyes: Squatiniformes) are a small but highly distinctive group of ‘ray-like’ sharks comprised of a single genus with approximately 20 valid species (Ebert *et al*., 2013). Squatinids are a rather undiverse group with a dorso-ventrally compressed body morphology and appear to have evolved in parallel to the batoids (Compagno, 1973, 1977). These sharks are typically found on continental shelves and upper slopes in temperate waters, although some species occur in tropical waters (Ebert & Winton, 2010; White & Sommerville, 2010). Although squatinids appear to be the sister group to pristiophorids and batoids (de Carvalho, 1996; Shirai, 1996), the interrelationships between these orders and the Echinorhinidae remain unresolved (Naylor *et al*., 2012a, 2012b).

The squatinids as a group are very similar morphologically, lacking well-defined morphological characteristics, and are often misidentified, especially in those regions where multiple members of this genus may occur. A major problem within the group is the poor original descriptions of many species, compounded by subsequent confusion and misidentification in the literature. However, taxonomic research over the past decade has helped clarify the regional status of the group, particularly in the Indo-Western Pacific and southwestern Atlantic (Walsh & Ebert, 2007; Last & White, 2008; Walsh *et al*., 2011; Vaz & de Carvalho, 2013), but much work remains to be done. Given that this group is the subject of target and non-targeted fisheries regionally, and they are known to be a particularly vulnerable group

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to over-exploitation (the IUCN Red List of Threatened Species lists 12 species as being near threatened or higher), improved taxonomic resolution is critical to the conservation and management of this group.

Five valid species are known occur in the western North Pacific (WNP) which include *Squatina caillieti* Walsh *et al*. 2011, *S. formosa* Shen & Ting 1972, *S. japonica* Bleeker 1858, *S. nebulosa* Regan 1906, and *S. tergocellatoides* Chen 1963. Recently, Walsh & Ebert (2007) reviewed the WNP squatinids, excluding *S. caillieti*, in order to provide more detailed species descriptions and to identify and establish key defining characteristics between species. Within this review, limited information was available for *S. tergocellatoides* as the holotype for this species was thought to be lost (Walsh & Ebert, 2007). However, a survey (March 2012) of museum fish collections in Taiwan during a biodiversity study of Taiwanese chondrichthyans, the holotype of *S. tergocellatoides* was found by Hsuan-Ching (Hans) Ho (National Museum of Marine Biology & Aquarium, Taiwan).

Since the original description of *S. tergocellatoides* was limited, recovery of the holotype, combined with more recent biogeographic information, provides an opportunity to redescribe and provide additional morphological characteristics for this species based on new measurements of the holotype. These additional morphological characteristics take into account recent diagnostic features used to describe, identify, and separate other WNP species (Walsh & Ebert, 2007; Walsh *et al*., 2011) and thus fills an informational gap for comparisons between *S. tergocellatoides* and other WNP squatinids. An expanded key to the species of Indo-Western Pacific squatinids is also provided since this region is an area of high biodiversity for squatinids, with the biogeography of several species still remaining undefined.

Methods

Morphometric measurements modified after Compagno (2001) and following Walsh & Ebert (2007) and Walsh *et al*. (2011) were taken to the nearest 0.1 mm, and are presented as a percentage of total length (TL) to facilitate direct comparison with other regional squatinid species. It should be noted that the holotype TL measurement presented in the original description by Chen (1963) is slightly larger (625 mm vs. 603 mm TL) to that of the TL from the current measurements due to preservation; the holotype proportional measurements given here are based on our new TL measurement. Vertebral counts were taken directly from digital radiographs, while tooth counts were taken directly from the holotype. Pectoral and pelvic fin radial counts were also taken from the holotype. Additional measurements of a male and female specimen were taken from Yano *et al*. (2005) for comparison to the holotype. Photographs of *S. tergocellatoides* from other geographic regions throughout its range were obtained and used to confirm its occurrence. Abbreviations for institutions and field numbers are as follows: Abbreviations for institutions and field numbers are as follows: Australian National Fish Collection, Hobart, Australia (CSIRO); British Museum of Natural History, London, United Kingdom (NHM); California Academy of Sciences, San Francisco, California, U.S.A. (CAS); Hokkaido University, Laboratory of Marine Zoology, Faculty of Fisheries, Hokkaido, Japan (HUMZ); National Taiwan University, Department of Zoology, Taipei, Taiwan (NTUM); David A. Ebert field numbers (DAE). Tunghai University, Department of Biology, Taichung, Taiwan (THUP). Institutional abbreviations follow Sabaj Pérez (2013).

Family Squatinidae Bonaparte, 1838

Genus *Squatina* Duméril, 1806

Squatina tergocellatoides Chen, 1963

(Figures 1–6, Table 1)

Common name. Ocellated angelshark.

Holotype. THUP 00348, 625 mm TL (original description), 603 mm TL (present study), immature female, Taiwan Strait (Figure 1).

Diagnosis. A squatinid distinct from other WNP squatinids based on a combination of morphological characteristics including dorsal surface with six distinct paired spots with lighter centers, nasal barbels and flaps strongly fringed, and first dorsal fin originating posterior to pelvic fin free rear tips, a condition only found in *S.*

japonicus; predorsal thorns on back absent on *S. tergocellatoides*, present on *S. japonica*; lateral head folds have two rounded lobes on each side; upper lip arch semi-oval, upper lip arch height (1.1), upper lip arch width (4.1); spiracles relatively large, length about 1.2 times eye diameter, 1.1 times eye-spiracle length, with smooth posterior inner margins; pectoral fins acutely rounded at apices, with large prominent dark spots at anterior and posterior angles; pelvic girdle width relatively short (21.5), about equal to head length (20.9); dorsal fins relatively small, angular, prominent spots at base of each fin, interdorsal space (5.9–6.3) smaller than dorsal caudal space (7.5–7.8); caudal fin lobed, ventral lobe triangular with its length greater than dorsal lobe length, upper postventral caudal margin very long (6.1).

FIGURE 1. Dorsal view of *Squatina tergocellatoides* holotype, immature female, 625 mm TL (original description), 603 mm TL (present study). Photograph by D. Ebert.

Description. Proportions as percentages of TL for the holotype and two other specimens from Yano *et al.* (2005) are presented in Table 1.

TABLE 1. *Squatina tergocellatoides* proportional measurements expressed as a percentage of total length (TL%) for the holotype (THUP 00348) and two additional specimens taken from Yano *et al.* (2005) from Malaysia.

	Holotype	Yano *et al.* (2005)	
	THUP 00348	MSR 130	MSR 359
	Female	Male	Female
Total Length (mm)	603	854	555
Pre-caudal length	85.6	87.2	80.7
Pre-orbital	2.9	2.8	3.2
Pre-spiracle length	7.3	7.4	7.5
Pre-gill length	16.2	12.9	15.9
Head Length	14.6		
Pre-pectoral length	17.8	15.7	22.0
Pre-pelvic length	38.1	39.2	38.7
Snout-vent length	44.4	42.2	44.3
Pre-first dorsal fin length	63.3	66.2	61.8
Pre-second fin dorsal length	73.1	75.5	70.6

...... *continued on the next page*

TABLE 1. (Continued)

	Holotype	Yano *et al*. (2005)	
	THUP 00348	MSR 130	MSR 359
	Female	Male	Female
Inter-dorsal fin length	6.3	6.2	5.9
Dorsal-caudal space	7.8	7.6	7.5
Pectoral-pelvic space	11.2	24.0	17.2
Vent-caudal length	37.8		
Vent length	2.6		
Mouth length	2.7	3.0	2.3
Mouth width	12.0	12.2	12.2
Upper labial furrow length	5.7		
Lower labial furrow length	4.2		
Internarial width	6.4	6.7	7.2
Nostril width	2.0		
Anterior nasal flap length	1.8		
Upper lip arch width	4.1		
Upper lip arch height	1.1		
Eye length	2.0	2.3	2.2
Eye height	1.7	1.5	1.7
Interorbital length	7.8	7.6	8.0
Spiracle length	2.4	2.3	2.5
Eye-spiracle length	2.1		
Head height	5.7		
Head width	20.9		
Trunk height	6.6	6.1	
Trunk width	18.6	15.2	
Caudal peduncle height	2.5		
Caudal peduncle width	4.6		
Pectoral fin length	35.2		
Pectoral fin anterior margin length	28.7	29.3	25.0
Pectoral fin base length	12.3	12.2	11.4
Pectoral fin height	16.9		
Pectoral fin inner margin length	17.6	18.7	19.5
Pectoral fin posterior margin length	12.4	16.4	13.7
Pelvic fin length	24.4	24.0	23.3
Pelvic fin anterior margin	13.5	11.7	12.5
Pelvic fin base length	17.3	12.9	13.9
Pelvic fin height	14.1		
Pelvic fin inner margin length	9.0	3.5	8.9
Pelvic fin posterior margin length	18.2		
Pelvic girdle width	21.5		
First dorsal fin length	6.5	6.3	5.9
First dorsal fin anterior margin length	7.0		
First dorsal fin base length	3.5	3.9	3.4

...... *continued on the next page*

TABLE 1. (Continued)

	Holotype	Yano *et al*. (2005)	
	THUP 00348	MSR 130	MSR 359
	Female	Male	Female
First dorsal fin height	5.6	6.3	4.1
First dorsal fin inner margin length	2.4		
First dorsal fin posterior margin length	4.0	5.7	4.2
Second dorsal fin length	5.9	6.2	7.6
Second dorsal fin anterior margin length	6.7		
Second dorsal fin base length	3.7	4.0	3.4
Second dorsal fin height	5.7	5.6	4.0
Second dorsal fin inner margin length	2.4		
Second dorsal fin posterior margin length	4.0	5.0	4.0
Caudal fin upper lobe length	12.3	13.7	12.9
Caudal fin lower lobe length	14.9		15.3
Caudal lower postventral margin length	4.0		
Caudal upper postventral margin length	6.1		
Caudal subterminal fin margin length	3.4		

Body greatly depressed and ray-like, width at pectoral insertions about 0.8 (0.9) times head length and 4.6 (5.5–5.7) in precaudal length. Head broad, depressed, width about 4.1 in precaudal length; head length to notch about 5.9 times in precaudal length and 1.4 in head width; preorbital space flattened with slight median concave depression, becoming strongly concave between eye orbitals; interorbital length 2.1 in preorbital length; lateral head folds moderately expanded, with two to three rounded lobes on each side (Figures 2a, 2b).

Eyes small, oval, length and height diameters about equal; length about 3.9 (3.3–3.6) in interorbital length; preorbital length greater than eye length. Spiracle inner margin smooth, width subequal to eye length; length slightly greater than eye length; interspiracular length subequal to interorbital length; eye-spiracle length less than eye length (Figure 2a).

FIGURE 2a. Dorsal view of head of *Squatina tergocellatoides* holotype. A small group of electrosensory pores lateral to the spiracles are visible, as are a pair of large auditory pores located central and just posterior to the spiracles. Photograph by D. Ebert.

FIGURE 2b. Ventral view of head of *Squatina tergocellatoides* holotype. A group of electrosensory pores, located on the lateral side of the head just medial and anterior to the pectoral fins, are visible. Photograph by D. Ebert.

Mouth wide, about 4.4 (4.1–5.3) times mouth length, slightly arched, with double folds in front of each angle of lower jaw. Teeth awl-shaped, slightly curved and directed inwards; three functional series in each jaw; tooth counts by row, upper 10–10, lower 10–10, totals 20 upper and lower, no medial teeth at symphysis. Labial furrows extending medially from corners of mouth; upper labial furrow partially covered by dermal folds, slightly longer than lower labial furrow. Exposed upper lip between bases of anterior nasal flaps forming a narrow high, semi-oval arch; upper lip arch width 4.1, and height 1.1% of TL (Figure 3).

FIGURE 3. Anterior view of head of *Squatina tergocellatoides* holotype, depicting lip arch and fringed nasal barbels and flaps. Photograph by D. Ebert.

Nostrils terminal, separated from mouth by deep furrow, internarial width moderate 6.4 (6.7–7.2)% TL; nostril width 3.2 in internarial width. Nasal flaps large, expanded at tips with moderately strong lobate fringes; flaps extending from dermal folds above mouth; two distinct nasal barbels protruding from nasal flaps; posterior edges of anterior nasal flaps strongly fringed, tips narrowly lobate and not strongly fringed; posterior nasal flaps low, not greatly enlarged (Figure 4).

FIGURE 4. Photograph of nasal flap of *Squatina tergocellatoides* depicting strongly fringed edges. Photograph by W. White.

Dorsal surface covered with rough, tricuspidate denticles; snout, interorbital space, and anterior of spiracles with clusters of small thornlets; mid-dorsal enlarged spines not present, outer margins of all fins smooth; ventral surface smooth with some very fine close-set rough denticles on outer pectoral and pelvic fin anterior margins. Ventral surface of tail covered with close-set imbricate denticles that do not extend to tail base.

Pectoral fins large, originating behind gills, moderately angular in shape, not forming a distinct anterior shoulder; anterior margin mostly straight, extending to acutely rounded lateral apex, length 28.7 (25.0–29.3)% TL and more than three quarters pectoral fin length; angle is more obtuse than right angle; posterior margin slightly concave leading to acutely rounded free rear tip; inner margin convex, approximately half pectoral fin length. Pectoral fin radial count 40.

Pelvic fins broadly triangular, originating anterior to pectoral fin free rear tip; anterior nearly straight, length approximately 2.1 (2.0–2.5) times pectoral fin anterior margin length; base approximately 1.4 (1.1–1.2) times the length of pectoral fin base. Pelvic girdle width between pelvic fin apices moderately broad, 21.5% TL, and about 1.5 times head length. Free rear fin tip tapering posteriorly to acute tip, ending just anterior to first dorsal fin origin; inner margin slightly concave and short, about 2.7 (2.6–2.9) times pectoral fin length. Pelvic fin insertion furrows on ventral surface extends in a narrow ellipse to anterior apogee of vent, vent is within ellipse. Pelvic fin radial count 29.

Dorsal fins small and slightly angular, second dorsal similar in size or slightly smaller than first dorsal; origin of first dorsal fin posterior to pelvic fin tips; interdorsal space is about 0.8 (0.8) of dorsal caudal space; dorsal fin bases about equal in length; dorsal fin margins relatively straight, apices are lobed acutely rounded; posterior margin about 0.6 times length of anterior margin; inner margin approximately 3.5 times the length of anterior margin; first dorsal fin base 1.8 in interdorsal space, and about 2.2 (1.9–2.2) in dorsal caudal space.

Caudal peduncle flattened dorsal-ventrally, with faintly defined longitudinal ridge along each side. Caudal fin triangular in shape, posterior contour concave with lower lobe 1.2 (1.2–1.5) times length of upper lobe; subterminal caudal fin margin slightly more than 0.5 length of upper postventral caudal margin; caudal lower postventral margin slightly convex, approximately 0.7 length of caudal upper postventral margin (Figure 5).

Total vertebrae 137; total precaudal vertebrae 103; monospondylous vertebrae 48; diplospondylous vertebrae to caudal origin 55; diplosondylous precaudal vertebrae to first dorsal fin origin 34.

FIGURE 5. Caudal fin of *Squatina tergocellatoides* holotype, triangular in shape with lower lobe longer than upper lobe. Photograph by D. Ebert.

Colouration. In life, dorsal surface light yellowish brown covered with close-set, small, numerous rounded white spots; fin borders whitish, except at fin bases that are blackish (Figure 6). The most striking feature of this angel shark are the three pairs of prominent large black spots, each with a diameter greater than eye length; two on each pectoral fin at anterior and posterior angle and one on each side near base of tail; another three pairs of lesser defined, spots, one located at based of each dorsal fin and a third spot located laterally on tail about below first dorsal fin. Ventral surface a uniform white to cream colour, margins of pectoral fins and tail similar in colour to dorsal surface. After preservation, colouration fades to a uniform pale yellowish tan, with all major and minor spots becoming indistinguishable. Dorsal and ventral fin borders become greyish after preservation.

Size. Maximum total length to at least 100 cm, with males maturing at about 85 cm TL and females at about 100 cm TL; size at birth is about 30 cm TL.

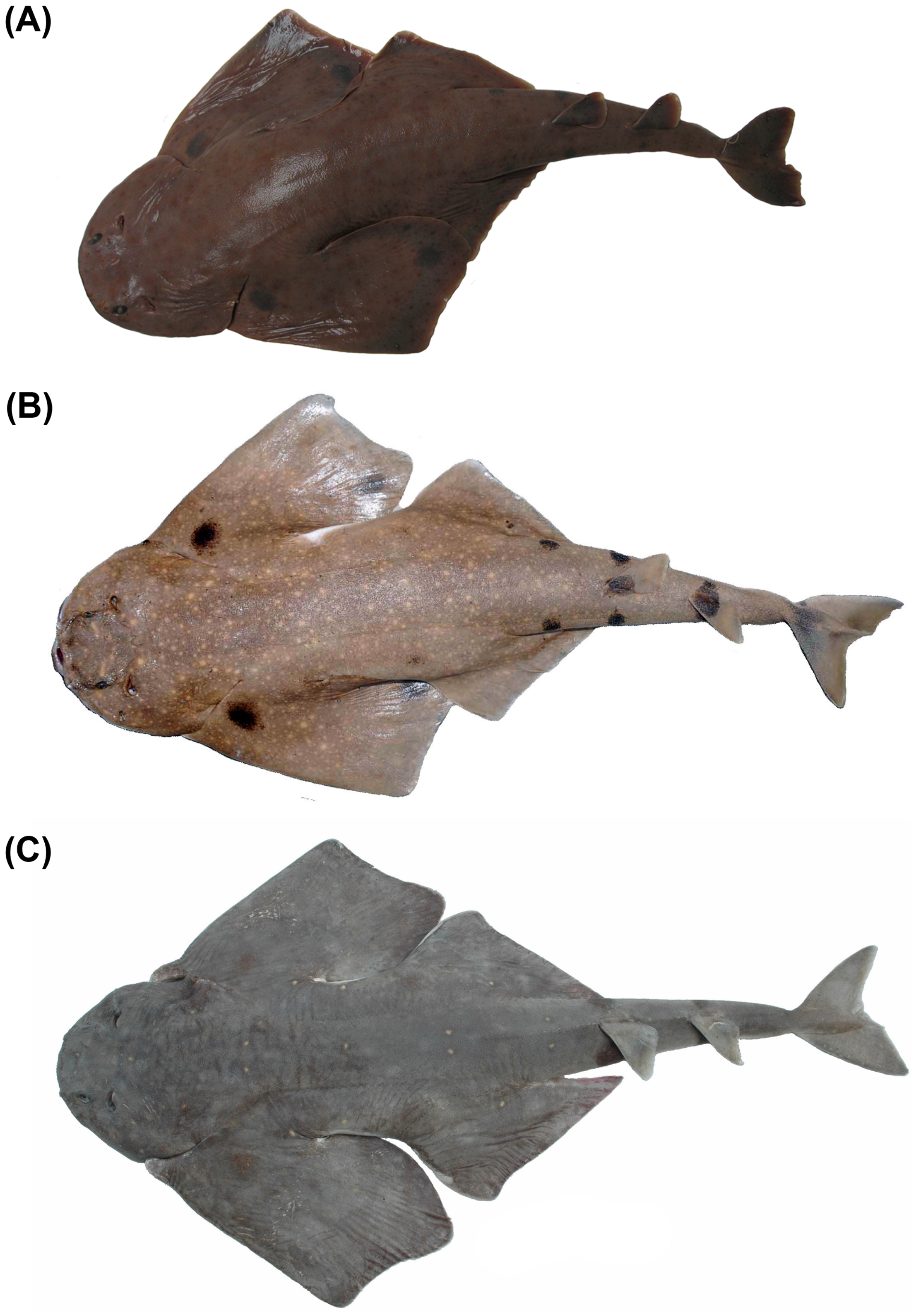

FIGURE 6. Photographs of fresh specimens of *Squatina tergocellatoides* from Hong Kong (A), Vietnam (B) and Taiwan (C) showing variation in colouration and spot patterns between individuals. Photographs by W. White (A) and H.-C. Ho (B & C).

General Biology. Virtually nothing is known about the biology of this rather distinctive angelshark. It is an inhabitant of outer continental shelves and upper slopes in warm temperate to tropical waters found at depths of about 100 to 300 m. Litter size unknown. It may be caught as bycatch by trawlers and other fisheries operating in the western Pacific, especially around Taiwan and possibly Indonesia, but there is no specific catch information on the species. Qualitative observations by one of us (DAE) at fish markets in Taiwan indicate that demersal bony fishes are a primary prey item of this species.

Distribution. Endemic to the western Pacific from the waters surrounding Taiwan in the north, southwards to northwestern Malaysia, including the South China Sea, and the waters off Hong Kong and Vietnam (Compagno *et al*., 2005; Yano *et al*., 2005; Walsh *et al*., 2011).

Discussion

The recovery of the holotype of *S. tergocellatoides*, previously thought to be lost, combined with additional measurements and photographs of additional specimens, has enabled a more accurate comparison to other regional squatinids based on current morphological measurements for this group of sharks (Walsh & Ebert, 2007). *Squatina tergocellatoides* is similar to other regional squatinids but can be easily identified from other species by several characters. For fresh specimens, colouration involving the three large spot pairs is unique to *S. tergocellatoides* and is lacking for other known western North Pacific species; however, these prominent spot pairs fade after preservation making these sharks indistinguishable from other regional squatinds based solely on colour. Colouration in life varies slightly, and the condition and preservation of specimens appears to affect the visibility of the spots. Specimens from Hong Kong (Figure 6a) and Vietnam (Figure 6b) were a darker and lighter brown, respectively, and covered with small, round light brown spots, while a specimen from Taiwan was dark grey with faded black spots and several small, distinct white spots (Figure 6c). The three major distinct pairs of black spots remain constant although the less prominent pairs of spots, like those described from the holotype and in Yano *et al*. (2005), are not always present. The Hong Kong and Vietnam specimens, both of which lack these aforementioned spots, possess instead a pair of spots on each side of the tail, posterior to the larger spots at the base of the tail.

A recent taxonomic review of WNP squatinids showed that the location of the pelvic fin tips in relation to the first dorsal fin is a distinctive diagnostic feature (Walsh & Ebert, 2007). In *S. tergocellatoides*, the pelvic fin tips do not reach the origin of the first dorsal fin, which is also the case for *S. japonica*. However, *S. tergocellatoides* can be readily distinguished from *S. japonica* by colouration and the lack of mid-back thorns, the latter of which are also missing from *S. caillieti*, *S. formosa* and *S. nebulosa*. The possession of fringed nasal barbels is another defining characteristic of *S. tergocellatoides* and is not found in other WNP squatinids. Potential confusion exists where Yano *et al*. (2005) comments that the barbels of this species are "weakly fringed" but then later states that the "anterior nasal barbels [are] strongly fringed". Photographs from Yano *et al*. (2005) and of recently obtained specimens from Hong Kong and Taiwan, however, confirm that the nasal barbels are indeed strongly fringed as per the original description of the holotype. *Squatina tergocellatoides* also differs from other WNP squatinids by possessing the smallest interorbital length (7.8) and smallest mouth length (2.7). Although a lobed a caudal fin is also present in *S. caillieti*, *S. formosa* and *S. japonica*, the caudal fin of *S. tergocellatoides* has a ventral lobe that is triangular in shape and greater in length than the dorsal lobe.

The sensory electroreceptor pores on the holotype can be clearly seen on both the dorsal (Figure 2a) and ventral (Figure 2b) sides, as can the pair of relatively large auditory pores located central and just posterior to the spiracles (Figure 2a). The low number of ventral pores is comparable to species from the family Orectolobidae, which share a similar dorso-ventrally compressed body morphology to squatinids, and is likely related to the ambush predatory strategy that members of both families employ (Theiss *et al*., 2011). The concurrent low number of dorsal pores, however, is not typically seen and may suggest that the electrosensory system may not be of relative importance to these species, compared to other sensory systems such as vision (Fouts & Nelson, 1999). The number and distribution of electrosensory pores is consistent among species of the same family, so it is therefore highly likely that other squatinids share a similar electroreceptor pattern to *S. tergocellatoides* (Kempster *et al*., 2012).

Four geographically sympatric species of squatinids are known to occur in Taiwanese waters, making it a hotspot of biodiversity for this genus. The range of two species, *S. japonica* and *S. nebulosa*, appear to occur in more northerly waters extending to Japan and Korea, while the geographic range of *S. formosa* is poorly known and unconfirmed from outside Taiwanese waters at this time. Based on recent records, *S. tergocellatoides* appears to be a more southerly occurring species having been recorded farther south to off Hong Kong, Vietnam, and Malaysia (Yano *et al*., 2005; Walsh *et al*., 2011). The only other known species of WNP squatinid, *S. caillieti*, was caught off Luzon in the Philippine Islands and it is likely that the distribution of this species may overlap the southern distribution of *S. tergocellatoides*, but there are no confirmed records of it from outside the Philippines (Walsh *et al*., 2011). Conversely there are no confirmed records of *S. tergocellatoides* from the Philippines. However, it is likely that *S. tergocellatoides* overlaps in its southern distribution with the tropical *S. legnota*, which has been recorded in Indonesian waters close to Malaysia (Last & White, 2008). This species can be readily distinguished from *S. tergocellatoides* using colouration and position of pelvic fin free rear tips in relation to dorsal fin origin. More specimens of *S. tergocellatoides*, as well as *S. caillieti* and *S. legnota*, are required to confirm suspected distributional localities and ranges.

The IUCN Red List of Threatened Species lists *S. tergocellatoides* as vulnerable mainly due to intense bottom trawl fisheries that occur within its known range (Walsh & Ebert, 2009). This species does not appear to be abundant anywhere, but it is taken in small numbers around Taiwan and elsewhere, including Vietnam, Hong Kong, and Malaysia. Improved species-specific identification of this species and other regional squatinids species will help in the conservation and management of these sharks.

Key to Indo-Western Pacific species of *Squatina*

1a. Nasal barbels strongly fringed and with multiple branches or fine cirri. Posterior edges of anterior nasal flaps between nasal barbels and tips strongly fringed and multi-branched or finely cirrate. . . . . **2**.
1b. Nasal barbels simple or bifurcated. Posterior edges of anterior nasal flaps smooth to moderately fringed . . . ***Squatina legnota***.
2a. Paired ocelli present on back, tail and pectoral fins. . . . . **3**.
2b. No ocelli on dorsal surface. . . . . **4**.
3a. Nasal barbels and anterior nasal flaps greatly expanded and deeply fringed. Lateral head folds low and without rounded lobes. Three pairs of large ocelli with centers resembling mitotic figures on back near bases of pectoral and pelvic fins. . . . . ***Squatina tergocellata***.
3b. Nasal barbels and anterior nasal flaps moderately expanded and finely fringed. Lateral head folds higher and with a pair of low rounded lobes on each side. Six pairs of smaller, light-centered ocelli on back, pectoral and pelvic fins, and tail. . . . . ***Squatina tergocellatoides***.
4a. Interorbital space flat or convex. No orbital thorns. Lower caudal lobe with numerous dark spots. . . . . ***Squatina australis***.
4b. Interorbital space concave. Orbital thorns normally present. Lower caudal lobe with more pale spots than dark spots. . . . . . **5**.
5a. Nasal barbels strongly bifurcate. . . . . **6**.
5b. Nasal barbels weakly or not bifurcate. . . . . **7**.
6a. Upper surface mainly covered with small white, dark-edged spots. Predorsal thorns absent from midline of back. . . . . ***Squatina albipunctata***.
6b. Upper surface mainly covered in bluish spots; a single white spot on nuchal region. A row of small predorsal thorns on back, mostly single . . . . ***Squatina pseudocellata***.
7a. Lateral head folds with two lobes at and in front of mouth corners on each side. . . . . ***Squatina nebulosa***.
7b. Lateral head folds with a single lobe on each side or none. . . . . **8**.
8a. Angle of pectoral apex broadly obtuse, much greater than a right angle. Nasal barbels highly depressed and membranous.. . . . . ***Squatina formosa***.
8b. Angle of pectoral apex narrowly obtuse, usually slightly greater than a right angle. Nasal barbels thickened and subcylindrical.
9a. No enlarged predorsal thorns on back, at most weakly enlarged denticles. . . . . ***Squatina africana***.
9b. A row of enlarged predorsal thorns on back. . . . . ***Squatina japonica***.

Material examined

Squatina caillieti: *Holotype*: CAS 226473, immature female, 328 mm total length, Taiwan Fisheries Research Institute Fishery Researcher 1 sta. FR1-PHI-02-95, 23 September 1995, 363-385 m, Philippines, Luzon, 13°08.98–09.84'N, 124°04.72–00.01'E, collected by L.J.V. Compagno and P.R. Last.

Squatina formosa: (4 specimens) *Holotype*: NTT7213130 (now labelled as NTUM 01329), immature female, Dong-gang, Pingtung, Taiwan, 31 January 1972; DAE 881805, immature male, Da-xi, Taiwan, May 1988, collected by David A. Ebert; DAE 052105, immature male, Da-xi, Taiwan, May 2005, collected by David A. Ebert; DAE 052305-2, immature female, Da-xi, Taiwan, May 2005, collected by David A. Ebert.

Squatina japonica: (4 specimens) HUMZ 107395, immature female, off Shirahama, Shimoda City, Shizuoka prefecture, Japan, 27 January 1986, caught with a bottom gill net at 30 m; HUMZ 105913 immature male, off Itado, Shimoda, Shizuoka prefecture, Japan, 19 Nov 1985, caught with a bottom gill net at 10m; CAS 20955: immature male, Japan, Tokyo market, collected by R/V Snyder and Sindo as part of the "Albatross 1906 cruise"; CAS 20956, immature male, Japan, Tokyo market, collected by R/V Snyder and Sindo as part of the "Albatross 1906 cruise."

Squatina legnota: (1 specimen) *Paratype*: CSIRO H 6565-01, adult male, 1252 mm TL, Tanjung Luar fish landing site, Lombok, Indonesia, 08º 45'S, 116º 35' E, 9 September 2004.

Squatina nebulosa: (8 specimens) *Holotype*: BMNH 1862.11.1.89, immature female, Japan; *Paratypes* of *S. formosa*, three specimens, were examined and reidentified as *S. nebulosa* by Walsh & Ebert (2007). These specimens are NTU7222433 (now labelled as NTUM 01327), and NTU7041632 (now labelled as NTUM 01328), immature female, Tashi, Taiwan (24º 56.5'N, 121º 53.0'E) in single trawling net at 100-120 fathoms, 16 April 1970, collected by W.H. Ting; NTU7041632 (now labelled as NTUM 01328), immature female, Tashi, Taiwan, 24 February 1972, collected by W.H. Ting; DAE 882105, immature female, Tashi, Taiwan, May 1988, collected by David A. Ebert; DAE 052305-1, immature male, Tashi, Taiwan, May 2005, collected by David A. Ebert; DAE 052505, immature male, May 2005, collected by David A. Ebert; HUMZ 149422, immature female, caught in trawl net in Okinawa Trough, 25° 37.28'N, 126° 05.35'E to 25° 38.12'N, 126° 07.83'E, 2 August 1994; HUMZ 149423, immature male, caught in trawl net in Okinawa Trough, 25° 37.28'N, 126° 05.35'E to 25° 38.12'N, 126° 07.83'E, Japan, 2 August 1994.

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