

Research article

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Abstract. Angel sharks (*Squatina* spp. Duméril, 1805) are a group of coastal benthic sharks distributed worldwide, currently including threatened and understudied species. Two species are formally described along the East Pacific coast, the California angel shark *S. californica* Ayres, 1859 and the Chilean angel shark *S. armata* (Philippi, 1887). The latter species occurs in the southeastern Pacific and has historically been understudied. Additionally, the original description of *S. armata* lacks sufficient data to confidently identify individuals of this species compared to modern descriptions, and no type specimen is currently available to ensure specimen identification. Detailed morphological descriptions for identifying species are an essential resource for solving taxonomic issues in groups of morphologically similar species and to promote the conservation of critically endangered species. Therefore, a neotype from the type locality is here designated for *S. armata*, and a detailed and standardized morphological characterization based on modern taxonomic works is provided. This work contributes in improving the knowledge on the

Chilean angel shark taxonomy and provides an improved frame of reference for identifying angel sharks in the East Pacific, especially in areas where species may occur in sympatry.

Keywords. Morphology, neotype, southeastern Pacific, species identification, taxonomy.

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Introduction

Angel sharks (Order Squatiniformes) are a group of 24 species that inhabit temperate to tropical waters of continental shelves in all major oceans (Stelbrink *et al.* 2010; Vaz & de Carvalho 2013, 2018; Weigmann 2016; Weigmann *et al.* 2023). They are ambush predators that prefer soft seafloors to bury and feed on unsuspecting prey (Fouts & Nelson 1999; Meyers *et al.* 2017). They have k-selected life histories characterized by slow growth, late maturity, and low fecundity (Colonello *et al.* 2007; Baremore *et al.* 2010), which, in conjunction with their susceptibility to fisheries (Quero 1998; Alvarez Perez & Wahrlich 2005), have rendered them as one of the most threatened coastal chondrichthyan orders worldwide (Dulvy *et al.* 2014, 2021). Consequently, sightings of angel sharks have become increasingly rare and some species have been virtually extirpated from their original distribution areas (Quero 1998; Dulvy *et al.* 2003; Hiddink *et al.* 2019).

Taxonomy is an often overlooked yet fundamental instrument for conservation and management strategies (McNeely 2002; Dubois 2003; Mace 2004; Conix 2019; Ottoni *et al.* 2023). Indeed, successful taxonomic resolution and accurate species identification have preceded changes in the conservation status of elasmobranchs (see Richards *et al.* 2009; White *et al.* 2010, 2013; Gabbanelli *et al.* 2018; Concha *et al.* 2019; Carugati *et al.* 2021). This is especially relevant in groups of limited morphological diversity like angel sharks, for which correct species identification is a recurrent concern (Vaz & de Carvalho 2013; Raoult *et al.* 2017). For example, the lack of clear morphological data resulted in the misidentification of the Sawback angel shark *Squatina aculeata* Cuvier, 1829 and Smoothback angel shark *Squatina oculata* Bonaparte, 1840, which has historically hindered the correct determination of their distribution ranges along the coast of West Africa and affected conservation efforts (Lawson *et al.* 2019). This way, morphology and meristics are paramount instruments in correctly identifying angel sharks (Castro-Aguirre *et al.* 2006; Vaz & de Carvalho 2013; Raoult *et al.* 2017).

Nearly one-third of the known species of angel sharks ($n = 9$) have been described over the last thirteen years (Last & White 2008; Walsh *et al.* 2011; Acero *et al.* 2016; Vaz & de Carvalho 2018; Long *et al.* 2021; Weigmann *et al.* 2023) and during this time, taxonomic uncertainties have also been reported from the Central and Northwestern Atlantic (Vaz & de Carvalho 2018), the Mediterranean Sea (Lawson *et al.* 2019), and the southeastern Pacific (Cañedo-Apolaya *et al.* 2021). Recent efforts in identifying and describing angel sharks have adopted a more integrative approach by combining morphology with other disciplines, such as genetics (Padial *et al.* 2010; Long *et al.* 2021). For example, the identification of the African angel shark *Squatina africana* Regan, 1908 was improved by combining morphology and DNA-barcoding, enabling a better delimitation of its distribution range which was expanded into the southwestern Indian Ocean (Ambily *et al.* 2018). In addition, genetic data have been successfully used in identifying angel sharks and in constructing phylogenies (e.g., Stelbrink *et al.* 2010; Vélez-Zuazo & Agnarsson 2011; Naylor *et al.* 2012; López-Romero *et al.* 2020), which has been particularly useful when studying co-occurring species.

Along the Pacific coast of America, two valid species of angel sharks have been described: the Pacific angel shark *Squatina californica* Ayres, 1859, found along the northeastern Pacific coast and reportedly occurring as far south as northern South America, and the Chilean angel shark *S. armata* (Philippi, 1887), reported from the Pacific coast of South America, from Ecuador to Chile (Puentes *et al.* 2007; Cañedo-Apolaya *et al.* 2021; Fricke *et al.* 2023). Contrary to the Atlantic Coast of South America, where the taxonomy and morphology of endemic angel shark species was revised (Vaz & de Carvalho 2013, 2018), a taxonomic revision of angel sharks from the eastern Pacific coast is still lacking. The distribution limits of *S. armata* and *S. californica* are unclear, and misidentifications are especially common in northern South America, where both species may occur in sympatry (Cañedo-Apolaya *et al.* 2021). This need is further stressed by the recent classification of the Chilean angel shark as Critically Endangered at the IUCN Red List of Threatened Species (Dulvy *et al.* 2020).

Several aspects about *Squatina armata* have been revised, such as its presence as bycatch in different fisheries (Elliott-Rodríguez & Paredes-Bulnes 1997; Hernández *et al.* 2010), its parasitological fauna (Carvajal 1974; Castro Romero & Baeza Kuroki 1987), its feeding habits (Velázquez-Chiquito *et al.* 2021), its phylogenetic position (Stelbrink *et al.* 2010; Cañedo-Apolaya *et al.* 2021), and its neurocranium morphology (López-Romero *et al.* 2020), yet its identification and differentiation from *S. californica* remain problematic. In fact, revisions of morphological traits of *S. armata* are restricted to the short reports by Norman (1937) and Yáñez (1951).

Although Philippi (1887) provided a relatively detailed description of *Squatina armata*, an improved characterization is needed for more accurate identification in the field and in collections. In his description of *S. armata*, Philippi (1887) provided 14 body measurements, including information on the position and size of thorns, and comments on coloration as well as body and fin shape. Nevertheless, Philippi (1887) did not compare the holotype of *S. armata* with the previously described *S. californica*. Clarification based on morphological and meristic differences between these two species is needed given their possible distribution overlap and the existence of potentially undescribed species (Cañedo-Apolaya *et al.* 2021). Moreover, the description and illustration by Philippi (1887) have also been considered insufficient (Norman 1937; Yáñez 1951). Unfortunately, the holotypes of both *S. armata* and *S. californica* are lost (Supp. file 1.1; Fricke *et al.* 2023), and there are no additional types for these species (Fricke *et al.* 2023). Therefore, the need for designating neotypes is urgent to develop better identification tools and avoid misidentifications.

In this study, the Chilean angel shark *Squatina armata* is redescribed based on two specimens collected in 2019 from its type locality (Iquique, Chile) and on the jaw of an additional specimen from Caleta Higuierillas, Chile. Based on these specimens, an expanded and updated morphological description of the species is provided, including molecular data and images. Additionally, based on the literature, morphological comparisons with *S. californica* and other angel shark species from off South America are presented.

Material and methods

Two mature males of the Chilean angel shark *Squatina armata* (1004 mm TL and 10.01 kg; 1040 mm TL and 11.63 kg) were captured by artisanal fishers targeting bony fishes in Iquique, Chile (20°29'1.39" S, 70°9'44.89" W), the type locality of the species, using gillnets. The specimens were collected, immediately frozen, and transported to the National Museum of Natural History (Museo Nacional de Historia Natural de Chile, MNHNCL) of Santiago, Chile. The specimens were thawed, measured and photographed fresh, after which they were preserved in 4% formalin. External hard structures, such as dermal denticles and thorns, were studied using the fresh and preserved condition. The specimens were deposited in the marine vertebrate collection of the MNHNCL (neotype – designated here: MNHNCL ICT 7625; and voucher: MNHNCL ICT 7626). Additionally, the mandible of another mature male was

included, caught as bycatch in the gillnet fishery targeting bony fishes at Caleta Higuierillas, central Chile (32°55'47.51" S, 71°32'19.95" W). However, upon collection this specimen had already been processed by fishers, so it was not possible to obtain full-body measurements. The jaw was cleaned and stored at the facilities of Chondrolab, Universidad de Valparaíso, Chile, as part of the Montemar Chondrichthyan collection (Colección Condrictios Montemar, CCM-1228).

Morphology and meristics

Measurements were taken manually to the nearest millimeter and standardized as a percentage of total length (% TL, Table 1). Morphometric measurements of the entire body were based on the works of Walsh & Ebert (2007) and Last & White (2008), whereas meristic measurements of the skeletal structures were based on Compagno (1984) and Vaz & de Carvalho (2018). Digital radiographs of the neotype were taken at the radiology center at the veterinary clinic of the Chilean National Zoo, using a diagnostic X-ray unit (model PX-30N) and an iCRco[®] scan (30/50 mA/kV 0.40 s) to count the vertebrae and fin rays of the left pectoral fin. Dermal denticles and thorns were observed under a microscope. The left clasper of specimen MNHNCL ICT 7626 was dissected manually, soft tissues were removed using a scalpel, and subsequently submerged in sodium hypochlorite (5%). Morphometric measurements of the examined specimens were compared to those of *Squatina californica* and other congeners from the Atlantic coast of South America (Table 1).

For the comparisons with other specimens and species, we retrieved data from the following publications: holotype of *S. armata* (Phillipi, 1887), *S. californica* Ayres, 1859, *S. argentina* (Marini, 1930), *S. dumeril* Lesueur, 1818, *S. guggenheim* Marini, 1936, *S. occulta* Vooren & da Silva, 1991 (Vaz & De Carvalho 2013), *S. david* Acero, Tavera, Anguila & Hernández, 2016 (Acero *et al.* 2016), and *S. varii* Vaz & Carvalho, 2018 (Vaz & De Carvalho 2018). Some measurements were presented as fractions in their original work (e.g., *S. californica*) and were transformed to percentages for consistency.

Molecular methods and analysis

DNA extraction, PCR amplification and sequencing

Genetic material was extracted from muscle tissue preserved in 90% ethanol using a Blood & Tissue DNA extraction kit (Invitrogen) following the manufacturer's instructions. The amplified genes were cytochrome oxidase 1 (CO1), Nicotinamide adenine dinucleotide dehydrogenase 2 (NADH2) and 16S rRNA (16S) using the following respective forward and reverse primers: LCO 5' TCTACMAAYCACAAAGATATCGG 3' and HCO 5' TAAACTTCTGGGTGRCCRAAGAATCA 3' (Stelbrink *et al.* 2010); ILEM 5' AAGGAGCAG TTTGATAGAGT 3' and ASNM 5' AACGCTTAGCTGTAAATTA 3' (Naylor *et al.* 2005); and L2510 5' CGCCTGTTTATCAAAAACAT 3' and H3080 5' CCGGTCTGAACTCAGATCACGT 3' (Palumbi *et al.* 1991). Each reaction had a total volume of 25 uL, with 13.5 uL water, 2.5 uL 1× Buffer, 1 uL MgCl₂ (50 mM), 2 uL dNTPs 10 pM, 0.5 uL BSA, 1 uL of each primer at 10 pM and 3 uL of DNA were added. The amplification protocol for CO1 and 16S followed Stelbrink *et al.* (2010). NADH2 sequences were amplified using the following touchdown cycling protocol: initial denaturation 4 min at 96°C, 30 s at 96°C, 12 cycles of annealing (-1°C at each cycle) starting at 60°C for 30 s, and extension starting at 72°C for 1 minute and 96°C for 30 seconds; 30 cycles for 30 s starting at 96°C, for 30 s at 48°C, and for 1 min at 72°C; final cycle for 2 min at 72°C and 3 min at 4°C. Amplification success was evaluated in 1% agarose gel and sequencing was done using the Sanger sequencing service of Macrogen Inc. (South Korea). Tissue from the specimens of *Squatina armata* was stored to validate these sequences and be used in future collaborations.

Sequence alignment

DNA sequences obtained from the two collected Chilean angel sharks and additionally downloaded sequences from other angel sharks were manually aligned using ProSeq ver. 3.5 (Filatov 2009). CO1

Table 1. Table of body measurements of *Squatina armata* (Philippi, 1887) and other species of angel sharks. Measurements of the neotype and voucher specimen were done to the nearest millimeter and are also represented as a percentage of the total length (% TL). Measurements with an asterisk indicate cases when a lower sample size was used because of measurements that only apply to males, and the number of individuals used is at the top of each column. All measurements were done on the fresh specimens except for those in grey (total length was measured again, 992 mm TL for MNHNCL ICT 7625 and 1036 mm for MNHNCL ICT 7626). Some measurements of *S. californica* Ayres, 1859 were converted from inches and some of *S. armata* and *S. californica* transformed from fractions to percentages.

	<i>S. armata</i> (neotype, 1004 mm TL)		<i>S. armata</i> (neotype) (%)		<i>S. armata</i> (voucher, 1040 mm TL)		<i>S. armata</i> (voucher) (%)		<i>S. armata</i>	<i>S. californica</i>	<i>S. argentina</i>	<i>S. david</i>	<i>S. dumeril</i>	<i>S. guggenheim</i>	<i>S. occulta</i>	<i>S. varii</i>
Name or n° of specimens	MNHNCL ICT 7625	MNHNCL ICT 7626	MNHNCL ICT 7625	MNHNCL ICT 7626	Holotype (lost)	Holotype (lost)	6	3	2*	141	47	11				
Source	This study	This study	Phillipi (1887)	Ayres (1859)	Vaz & De Carvalho (2013)	Acero et al. (2016)	Vaz & De Carvalho (2013)	Vaz & De Carvalho (2013)	Vaz & De Carvalho (2013)	Vaz & De Carvalho (2013)	Vaz & De Carvalho (2013)	Vaz & De Carvalho (2013)				
	mm	% TL	mm	% TL	% TL	% TL	% TL	% TL	% TL	% TL	% TL	% TL				
Fork length	948	94.4	992	95.4												
Pre-1 dorsal length	634	63.1	668	64.2	70.87	66.6	62.1-65.1	60.3-65.3	65.9-68.3	60.1-67.5	59.6-69.4	63.5-65.9				
Pre-2 dorsal length	736	73.3	772	74.2				71.6-74.5				73.6-75.3				
Pre-caudal length	838	83.5	884	85.0			84.3-87.1	83.7-85.7	89.3-91.0	81.9-89.6	83.0-90.9	84.5-85.9				
Head length	158	15.7	185	17.8												
Pre-pelvic length	362	36.1	406	39.0				38.6-43.4	38.0-42.8	41.3-44.7	34.9-42.7	36.7-45.7	38.0-41.0			
Pre-pectoral length	181	18.0	196	18.8				19.2-21.0	16.2-21.6	22.5-22.7	17.1-22.3	18.2-23.4	17.9-20.1			
Pre-branchial length	133	13.2	151	14.5				14.6-16.0		15.1-15.8	10.7-17.4	13.8-18.4	12.9-16.4			
Pre-spiracular length	75	7.5	78	7.5				8.4-9.5		7.6-9.3	7.2-10.7	7.8-10.3	6.8-8.5			
Pre-ocular length	64	6.5	66	6.4				4.4-5.9		5.0-5.7	4.5-6.0	4.6-6.4	4.8-6.1			
Pre-orbital length	36	3.6	38	3.7				2.0-3.7	1.7-3.8	3.5-4.1	2.3-4.8	2.5-5.5	2.8-3.8			
Head width at nape	236	23.5	242	23.3	23.30	25.0	16.5-19.4	16.3-17.4	10.4-21.7	15.1-22.6	16.9-19.2					
Orbital head width	142	14.1	176	16.9				12.7-15.7		11.8-11.9	10.9-18.2	11.3-16.0	12.3-13.6			
Mouth width	152	15.1	14.48	14.0				13.7-15.4	12.7-13.6	10.3-11.9	9.9-15.1	10.8-15.6	11.5-13.0			
Head height	67	6.7	68	6.5				5.2-7.4	4.8-6.2	6.8-8.5	5.4-8.9	5.4-9.8	5.3-7.4			
Interorbital distance	97.45	9.7	102.36	9.8				8.8-10.0	7.6-8.9	7.7-8.3	6.4-9.6	6.5-9.9	7.8-8.8			
Eye length	12.66	1.3	14.21	1.4				2.3-2.9	1.2-3.1	-	1.3-2.7	1.6-3.1	1.5-2.1			
Eye height	10.15	1.0	9.87	0.9				1.3-1.9	-	-	0.8-2.2	0.9-1.9	1.0-1.6			
Eye-spiracle distance	24.81	2.5	26.98	2.6				2.4-3.3	2.3-3.3	3.6-3.7	1.9-3.7	2.5-3.8	2.2-3.0			
Internarial distance	73	7.4	72.6	7.0				6.7-7.1		5.7-6.0	4.6-6.9	5.7-7.3	5.4-10.8			
Interspiracular distance	82.44	8.2	87.13	8.4				7.8-9.0	6.7-8.1	7.3-7.9	6.9-9.4	6.9-9.3	7.0-9.4			
Spiracle width	23.26	2.3	21.92	2.1				2.4-3.1	0.9-1.2	1.9-2.3	1.3-3.0	1.6-2.7	2.0-2.5			
Intergill length	28.96	2.9	29.51	2.8				2.1-3.0		3.9*	1.3-4.0	1.5-3.9	2.0-2.8			
Intergill width	116.7	11.6	120.24	11.6				8.2-9.8			7.5-16.3	7.5-10.2	7.9-10.0			
Interdorsal distance	61	6.1	69	6.6				6.0-6.9	5.5-6.9	7.0-7.4	5.3-8.1	5.2-7.5	5.0-7.8			
Dorsal-caudal distance	58	5.8	67	6.4				7.1-8.5		7.3-8.0	6.0-9.6	6.2-9.0	6.9-7.5			
Pectoral-pelvic distance	72	7.2	108	10.4	9.71			9.9-11.7	6.9-14.0	9.1-11.5	7.1-12.3	7.7-12.3	7.9-11.8			
Pelvic(origin)-caudal distance	45	45.4	46.5	44.9				44.0-60.0		49.7*	40.5-68.6	40.0-51.1	45.2-52.6			
Pelvic-caudal distance	343	34.2	370	35.6				30.9-46.8	31.8-37.5	35.9*	29.8-49.0	27.8-36.9	30.2-36.9			
Width at pectoral origins	177	17.8	183	17.7				13.7-15.7		13.1-14.2	12.2-16.6	12.5-17.9	14.4-15.1			
Trunk width	228	22.7	242	23.3	26.21					15.3-19.4	15.3-16.5	12.1-21.2	13.0-22.9	16.0-18.2		
Pectoral fin length	222	22.1	244	23.5		25.0	32.4-36.7			32.7-35.7	23.9-28.7	27.1-33.6	26.7-36.6	33.5-36.0		
Pectoral fin posterior margin	201	20.0	210	20.2	13.11					12.7-15.9						
Pectoral fin anterior margin	252	25.1	259	24.9	29.13					25.2-27.2	27.3-29.4	22.0-25.3	18.1-30.9	22.0-30.9	28.9-30.9	
Pectoral fin base length	115.19	11.5	132.47	12.7						10.5-13.4	8.7-10.9	9.1-10.6	8.3-12.9	9.3-13.3	10.6-12.3	
Pectoral fin width	197	19.6		0.0	16.02					16.5-18.9		14.2-15.7	14.0-20.3	12.0-19.4	17.1-19.8	
Pectoral fin inner margin	119	11.9	120	11.5	8.74					17.1-19.8		10.2-14.1	12.0-17.5	13.3-18.9	17.5-19.4	
Pelvic fin base length	109	10.9	128	12.3						12.5-16.0						
Pelvic fin width	112	11.2	116	11.2						13.0-14.2	12.9-14.4	13.1-13.3	10.2-17.4	9.8-15.5	13.8-16.2	
Pelvic fin length	226	22.5	230	22.1						22.1-23.6	22.9-26.7	17.9-20.9	20.8-27.7	16.5-26.8	25.9-28.6	
Pelvic fin posterior margin	176	17.5	182	17.5												
Pelvic fin anterior margin	128	12.7	143	13.8						10.3-14.6						
Pelvic fin inner margin	118.8	12.0	115	11.1						8.1-10.4		7.8-10.1	6.7-13.3	6.0-12.6	9.9-14.4	
First dorsal fin posterior margin	77	7.7	83.11	8.0												
First dorsal fin anterior margin	103	10.3	104.26	10.0												
First dorsal fin height	72	7.2	81	7.8	8.25					7.5-8.0	7.1-8.8	6.4-7.9	5.5-9.4	6.7-9.2	8.0-10.0	
First dorsal fin inner margin										4.7-5.6	4.4-7.6	3.3-3.8	2.8-6.4	3.3-6.1	5.4-7.0	
First dorsal fin base length	41.76	4.2	39.9	3.8	2.91					2.3-3.2	2.4-3.3	1.6-1.9	1.5-3.4	1.7-3.1	2.2-3.1	
Second dorsal fin posterior margin	67	6.7	74.27	7.1						3.5-4.3	3.6-4.2		2.9-4.5	2.8-4.5	3.7-4.4	
Second dorsal fin anterior margin	93	9.3	97.34	9.4							3.6-5.2					
Second dorsal fin height	65	6.5	76	7.3	8.25					6.8-7.7	7.1-8.3	6.0-7.6	5.1-9.5	6.8-8.6	7.6-9.1	
Second dorsal fin inner margin	19.7	2.0	19	1.8						4.0-5.1	4.7-4	3.50	3.2-5.9	3.1-6.0	5.3-8.8	
Second dorsal fin base length	38.97	3.9	37.65	3.6	2.91					1.9-3.1	2.6-3.2	1.3-1.9	1.6-7.6	1.7-3.6	2.7-3.2	
Dorsal caudal fin margin	125.14	12.5	136.65	13.1						3.1-3.9	3.2-4.1	3.70	2.4-4.4	3.0-4.0	3.4-3.8	
Preventral caudal fin margin	142.84	14.2	151.08	14.5						10.8-11.8	9.7-12.7	10.1*	9.4-17.5	8.9-13.2	11.6-13.6	
Lower post-ventral caudal margin	71.11	7.1	66.35	6.4						14.0-16.3		-	11.8-17.6	10.8-17.5	14.5-17.2	
Sub-terminal caudal margin	25.97	2.6	35.82	3.4												
Upper post-ventral caudal margin	60.35	6.0	57.77	5.6												
Caudal fin height	149	14.8	132	12.7						10.6-14.9		-	9.4-15.1	8.4-14.7	12.0-16.4	
Clasper inner length	217	21.6	215	20.7						10.7-10.8		-	7.7-22.1*	8.5-13.6*	12.5-21.7*	
Clasper outer length	189	18.8	175	16.8						1.7-2.6		7.3-8.3	0.8-8.5*	0.9-3.7*	2.9-6.7*	
Clasper base width	24.93	2.5	23.40	2.3						0.8-1.0		1.60	0.6-3.5*	0.7-1.4*	1.1-2.4*	
Snout-cloacal length	435	43.3	456	43.8						48.5-51.1	44.0-47.3	-	43.7-51.8	45.3-51.7	43.3-47.0	
Cloacal-caudal length	554	55.2	587	56.4						49.2-51.8		-	50.4-57.2	47.8-53.7	37.7-54.2	
Caudal peduncle width	34.57	3.4	40.27	3.9												
Girth	531	52.9	542	52.1												
Anterior nasal flap length	12.02	1.2	15.65	1.5												
Nostril width	17.88	1.8	19.99	1.9						0.4-0.9						
Upper lip arch length	9.88	1.0	12.72	1.2												
Upper lip arch width	43.05	4.3	44.69	4.3												

* 1 specimen *2 specimens *31 specimens *5 specimens

(Cytochrome c oxidase subunit 1 gene) and 16S (16S rRNA) sequences were obtained from Cañedo-Apolaya *et al.* (2021) and Stelbrink *et al.* (2010), and NADH2 (NADH-ubiquinone oxidoreductase chain 2) sequences from Naylor *et al.* (2012), Chai *et al.* (2016), Corrigan *et al.* (2016) and Gao *et al.* (2016). Six NADH2 sequences of *Squatina armata* (GN15495-15497, Coquimbo, Chile) and *S. californica* (GN5245-5246 [Santa Rosalía, Gulf of California, Mexico], GN1800 [California, USA]) were provided directly by Dr Gavin Naylor. Each molecular marker was aligned separately using MUSCLE in MEGA ver. 7.0.26 (Kumar *et al.* 2016). Prior to the phylogeny, alignments were tested separately for their quality for phylogenetic inferences, nucleotide proportions, and proportion of invariant sites in DAMBE ver. 6.4.81 (Xia 2017). The best substitution model for each marker was estimated with jModelTest ver. 2.1.10 (Darriba *et al.* 2012), using the three substitutions scheme to analyze the models included in MrBayes. The selected models for each marker were HKY+I (-lnL = 2859.1778) for CO1, GTR+I+G (-lnL = 1580.0354) for 16S, and HKY+G (-lnL = 3374.5248) for NADH2 after BIC model selection. The three amplified molecular markers were then concatenated using the software Mesquite ver. 3.31 (Maddison & Maddison 2017). The sequences for the three molecular markers obtained from the neotype and voucher specimen were deposited in GenBank under the following respective codes: CO1: OR544405 and OR544406; NADH2: OR567498 and OR567499; 16S: OR557297 and OR557298.

p-distance, Neighbour-Joining and phylogenetic reconstructions

The p-distances between NADH2 sequences were calculated, and Neighbour-Joining (NJ) trees were constructed separately for CO1 and 16S in MEGA to showcase distances among angel shark species found off the American continent. The three genes were then concatenated and used for the Bayesian Inference (BI) phylogenetic analysis in MrBayes on XSEDE ver. 3.2.6 (Ronquist *et al.* 2012). Concatenated genes were used instead of molecular markers in isolation to provide more comparative data for analysis and improve phylogenetic accuracy (Rokas & Carroll 2005). The Japanese sawshark *Pristiophorus japonicus* Günther, 1870 was selected as the outgroup. The BI was set to a temperature of 0.20, four chains, four runs, 10 000 000 generations, a sample frequency of 10 000, and a burn-in fraction of 0.25. Only *Squatina armata* sequences obtained in this study were used, as they corresponded to the same haplotype as the published sequences. Trees were visualized using FigTree ver. 1.4.3 (Rambaut 2016).

Results

Order Squatiniformes de Buen, 1926
Family Squatinidae Bonaparte, 1838
Genus *Squatina* Duméril, 1805

Squatina armata (Philippi, 1887)
Figs 1–7; Table 1

Rhina armata Philippi, 1887: 561. Type Locality: Iquique, Chile.

Common name

“Angelote” (Spanish), “Chilean angel shark” (English).

Material examined

Neotype (designated here)

CHILE • ♂ (1004 mm TL, 10.01 kg); Iquique, near Playa Seremeño; 20.483722° S, 70.162472° W; caught at approximately 20 m depth by artisanal fishers; 3 Jun. 2019; GenBank: OR544405 (CO1), OR567498 (NADH2), OR557297 (16S); MNHNCL ICT 7625.

Other material

CHILE • 1 ♂ (1040 mm TL, 11.63 kg); same collection data as for neotype; GenBank: OR544406 (CO1), OR567499 (NADH2), OR557298 (16S); MNHNCL ICT 7626.

CHILE • 1 ♂ (cleaned jaw, fish TL estimated at 1100 mm); Higuierillas; 32°55'47.51" S, 71°32'19.95" W; caught at approximately 40 m depth by artisanal fishers, only head was possible to recover; 18 Mar. 2020; CCM-1228.

Diagnosis and comparisons

Squatina armata differs from *S. californica* by the following combination of characters: surface of head between orbits flat in *S. armata*, while concave in *S. californica*. Anterior margin of head concave in *S. armata*, while straight in *S. californica*. Anterior nasal flaps of *S. armata* relatively broad with three lobes, outer lobe concave at base with relatively long inner lobe, shorter than outer lobe, central lower margin of nasal flap weakly fringed with narrow and relatively long and straight inner barbel, with spatulated end, while anterior nasal flap simpler in *S. californica*, with relatively long outer margin with spatulated tip, central margin slightly fringed. Anterior margins of pectoral fins of *S. armata* softly sinuate, concave anteriorly to posterior margin of head, slightly convex until pectoral fin apex vs almost straight to softly convex in *S. californica*. Row of medial-dorsal thorns absent in *S. armata*, single small medial-dorsal thorn right anterior to pelvic girdle, with single row of 30 small central-caudal thorns, not reaching origin of first dorsal fin and five interdorsal thorns, while medial-dorsal, caudal, and interdorsal thorns absent in *S. californica*. Pectoral thorns form broad patch near pectoral fin apex in adult males of *S. armata*, while absent in *S. californica*. *Squatina armata* has slightly shorter pre-dorsal length (63.1% vs 66.6%, respectively), shorter head width (23.5% vs 25%, respectively), and shorter pectoral fin length (22.1% vs 33.3% TL, respectively). First dorsal fin insertion at 66.6% of TL in *S. californica*, while at 63.1% TL in *S. armata*. In *S. californica*, pre-orbital length equal to first dorsal fin base length, while in *S. armata* somewhat shorter (3.6% vs 4.2% TL, respectively). First dorsal fin height equal to interorbital distance in *S. californica*, while larger in *S. armata* (7.2% vs 9.7% TL, respectively). Colouration of dorsal surface of body in *S. armata* is brownish, with small white spots and larger darker spots, while is greyish ash dorsally with small whitish spots in *S. californica*. In the original description of *S. californica*, there is no mention of any conspicuous spinulation pattern on pectoral fins or head, but prominent in *S. armata*.

Squatina armata has softly sinuate pectoral fin anterior margins, while in *S. argentina* this margin is convex and in *S. david*, *S. dumeril*, *S. guggenheim*, *S. occulta* and *S. varii* it is straight or slightly convex. *Squatina armata* has enlarged dorsal thorns organized in one discontinuous line: one medial-dorsal thorn anterior to pelvic girdle; 30 caudal thorns and 5 interdorsal thorns, while *S. argentina* has dorsal mid-line denticles that are morphologically similar to other trunk denticles and barely organized in a row; *S. david* lacks enlarged thorns on dorsal mid-line; *S. guggenheim* has a single row (or multiple in juveniles) over dorsal mid-line, from mid-length of pectoral fin base to origin of first dorsal fin or of caudal fin.

Squatina armata has four pairs of enlarged dermal denticle patches on the head: one first dorsal to the internarial space; one on the pre-orbital area; one on the eye-spiracle space; and one on the interspiracle space; *S. argentina* has no enlarged denticles on the interspiracular surface; *S. david* has moderate tubercles above the mouth and eye crests, a smooth oval patch above the mid-point of the mouth in between the eyes; *S. dumeril* has two clusters on the snout, one anterior and another posterior to the eyes, and a pair of clusters of denticles between the spiracles; *S. guggenheim* and *S. occulta* have a pair of enlarged, conical, and morphologically distinct dermal denticles between the spiracles.

Tooth count corresponded to 9–9/10–10 in *Squatina armata*, 12–12/12–12 in *S. argentina*, and 10–10/10–10 in *S. david*. *Squatina armata* has a lower vertebrae count ($n = 129$) than *S. argentina* ($n = 132$ –136), *S. david* (135–142), *S. dumeril* (130–135), and *S. varii* ($n = 138$ –150).

Squatina armata differs from *Squatina argentina*, *S. dumeril*, *S. guggenheim* and *S. varii* by having a wider head (23.3–23.5% vs 16.5–19.4% in *S. argentina*, 16.3–17.4% in *S. dumeril*, 10.4–21.7% in *S. guggenheim*, and 16.9–19.2% in *S. varii*), and by having a greater width at the pectoral fin origins (17.7–17.8% vs 13.7–15.7% in *S. argentina*, 13.1–14.2% in *S. dumeril*, 12.2–16.6% in *S. guggenheim* and 14.4–15.1% in *S. varii*). From *S. argentina*, *S. david*, *S. dumeril* and *S. occulta*, *S. armata* differs by having a longer first dorsal fin anterior margin (10.0–10.3% vs 7.5–8.0% in *S. argentina*, 7.1–8.8% in *S. david*, 6.4–7.9% in *S. dumeril*, and 6.7–9.2% in *S. occulta*), and by having a larger second dorsal fin anterior margin (9.3–9.4% vs 6.8–7.7% in *S. argentina*, 7.1–8.3% in *S. david*, 6.0–7.6% in *S. dumeril*, and 6.8–8.6% in *S. occulta*).

Squatina armata has a shorter pectoral fin length (22.1–23.5%) than *S. argentina* (32.4–36.7%), *S. david* (32.7–35.7%), *S. guggenheim* (27.1–33.6%), *S. occulta* (26.7–36.6%), and *S. varii* (33.5–36.0%). *Squatina armata* has a shorter pelvic fin width (11.2%) than *S. argentina* (13.0–14.2%), *S. david* (12.9–14.4%), *S. dumeril* (13.1–13.3%), and *S. varii* (13.8–16.2%). *Squatina armata* has a greater first dorsal fin height (7.2–7.8%) than *S. argentina* (4.7–5.6%), *S. dumeril* (3.3–3.8%), *S. guggenheim* (2.8–6.4%), and *S. occulta* (3.3–6.1%). *Squatina armata* has a shorter pectoral fin inner margin (11.5–11.9%) than *S. argentina* (17.1–19.8%), *S. occulta* (13.3–18.9%), and *S. varii* (17.5–19.4%), but longer than *S. david* (6.1–8.2%).

Squatina armata differs from *S. david*, *S. dumeril* and *S. varii* by having a greater interorbital distance (9.7–9.8% vs 7.6–8.9% in *S. david*, 7.7–8.3% in *S. dumeril*, and 7.8–8.8% in *S. varii*), and by having a greater trunk width (22.7–23.3% vs 15.3–19.4% in *S. david*, 15.3–16.5% in *S. dumeril* and 16.0–18.2% in *S. varii*). From *S. argentina*, *S. occulta*, and *S. varii*, *S. armata* differs by having a shorter eye length (1.3–1.4% vs 2.3–2.9% in *S. argentina* and 1.6–3.1% in *S. occulta*, and 1.5–2.1% in *S. varii*) and by having a greater intergill width (11.6% vs 8.2–9.8% in *S. argentina*, 7.5–10.2% in *S. occulta*, and 7.9–10.0% in *S. varii*).

Squatina armata has a wider clasper base (2.3–2.5%) than *S. argentina* (0.8–1.0%), *S. dumeril* (1.6%), and *S. occulta* (0.7–1.4%). *Squatina armata* has a greater second dorsal fin height (6.5–7.3%) than *S. argentina* (4.0–5.1%), *S. dumeril* (3.5%), and *S. guggenheim* (3.2–5.9%). *Squatina armata* has a shorter dorsal-caudal distance (5.8–6.4%) than *S. argentina* (7.1–8.5%), *S. dumeril* (7.3–8.0%), *S. occulta* (6.2–9.0%), and *S. varii* (6.9–7.5%).

Squatina armata differs from *S. dumeril* and *S. varii* by having a wider mouth (14.0–15.1% vs 10.3–11.9% in *S. dumeril* and 11.5–13.0% in *S. varii*), and by having a longer pelvic fin length (22.1–22.5% vs 17.9–20.9% in *S. dumeril* and shorter than *S. varii* (25.9–28.6%). Compared to *S. argentina* and *S. occulta*, *S. armata* differs by having a greater clasper inner length (20.7–21.6% vs 10.7–10.8% in *S. argentina* and 8.5–13.6% in *S. occulta*), and by having a greater cloacal-caudal length (55.2–56.4% vs 49.2–51.8% in *S. argentina* and 47.8–53.7% in *S. occulta*). Compared to *S. david* and *S. varii*, *S. armata* differs by having a shorter pectoral fin anterior margin (24.9–25.1% vs 27.3–29.4% in *S. david* and 28.9–30.9% in *S. varii*), and by having a shorter second dorsal fin inner length (1.8–2.0% vs 2.6–3.2% in *S. david* and 2.7–3.2% in *S. varii*). *Squatina armata* has a greater pre-ocular length (6.4–6.5%) than *S. argentina* (4.4–5.9%) and *S. dumeril* (5.0–5.7%). *Squatina armata* has a greater pectoral fin base length (11.5–12.7%) than *S. david* (8.7–10.9%) and *S. dumeril* (9.1–10.6%).

Squatina armata has a greater snout-cloacal length (43.3–43.9%), shorter eye height (1%) and shorter pre-spiracular length than *S. argentina* (48.5–51.5%, 1.3–1.9%, 8.4–9.5%). *Squatina armata* has a

greater spiracle width than *S. david* (2.1–2.3% vs 0.9–1.2%), a greater pectoral fin posterior margin (20–20.2% vs 12.7–15.9), greater second dorsal fin posterior margin (6.7–7.1% vs 3.3–5.2%) and greater nostril width (1.8–1.9% vs 0.4–0.9%). *Squatina armata* has a greater orbital head width than *S. dumeril* (14.1–16.9% vs 11.8–11.9%), as well as a greater dorsal caudal fin margin (12.5–13.1% vs 10.1%), greater internarinal distance (7.0–7.4% vs 5.7–6.0%) and greater pectoral fin width (19.6% vs 14.2–15.7%), while having shorter pre-caudal length than *S. dumeril* (83.5–85.0% vs 89.3–91.0%), shorter pre-pectoral length (18.0–18.9% vs 22.5–22.7%), shorter pre-pelvic length (36.1–39.0% vs 41.3–44.7%), shorter pelvic (origin)-caudal distance (45.4–44.9% vs 49.7%), shorter interdorsal distance (6.1–6.6% vs 7.0–7.4%), shorter eye-spiracle length (2.5–2.6% vs 3.6–3.7%) and a shorter intergill length (2.8–2.9% vs 3.9%). Morphometric data on *S. armata* and other South American angel sharks are summarized in Table 1.

Redescription

Morphological measurements of the neotype and complete voucher specimen are summarized in Table 1. The following description is based on the neotype.

COLOURATION. Dorsal surface of body of fresh specimen dark greyish brown, with pairs of prominent, relatively large dark ocelli located on trunk near anterior insertion of pelvic fins, posterior apex of pectoral fins, and tail; white spots on dorsal surface of body, small, scattered. Ventral surface whitish; ventral margins of pectoral fins brownish (Fig. 1). After preservation, the dorsal surface was opaque grey, and the ventral surface was the same as in the fresh specimen.

BODY. Dorsoventrally depressed from head to caudal fin origin.

HEAD. Broad and dorsoventrally depressed; head width about 23.5% of TL, 1.49 times head length (HL). Eyes relatively small, elliptical in shape, positioned dorsolaterally; eye length (EL) 1.3% of TL; eye height (EH) 1.0% of TL; distance between orbits 9.7% of TL, 7.69 times EL. Spiracle length 1.95 times EL. Mouth large, broadly arched, 24.5% of TL, 2.52 times interorbital space; upper labial furrows partially covered by dermal folds; anterior nasal flaps forming semi-oval arch. Nasal aperture presents a posterior nasal flap composed of a single elongated lobe and a relatively broad anterior nasal flap, width 3.5 times the upper lip arch width, composed of an elongated barbel and a broad, low, indented median barbel and a posterior barbel (Fig. 2).

PECTORAL FINS. Large; not fused with head; origin behind 5th gill slit, length 22.1% of TL, length 1.13 times pectoral fin width; anterior margin of pectoral fins softly sinuate; posterior margin of pectoral fins slightly concave; free rear tip of pectoral fins rounded; pectoral fin base 1.05 times pelvic fin base.

PELVIC AND CAUDAL FINS. Relatively large, triangular, with straight margins; pelvic fins length 22.5% of TL, 2.0 times pelvic fin height. Dorsal fins small, trapezoidal in shape; dorsal fin apex and free rear tip rounded; anterior margin of dorsal fins slightly convex; posterior margin of dorsal fins straight, vertically oriented; interdorsal space 6.1% of TL, 1.05 times dorsal caudal fin margin; second dorsal fin slightly smaller than first dorsal fin. Caudal fin hypocercal, with slightly convex dorsal and pre-ventral margins; lower postventral margin of caudal fin 1.14 times as long as posterior margin; upper post-ventral caudal margin slightly convex; lower postventral caudal margin straight; posterior and ventral tips rounded.

VERTEBRAE AND FIN RADIALS. Total vertebrae count 129; 98 pre-caudal vertebrae; 31 caudal vertebrae. Left pectoral fin with 37 radials and pelvic fins with 30 radials ([Supp. file 1.2](#)).

DERMAL DENTICLES AND SPINULATION. Dermal denticles densely covering most of the dorsal surface of the body, absent only on anterior tip of pectoral fins, anterior and posterior insertion of pectoral fins, base and insertion of dorsal fins, insertion of pelvic fins, and dorsal surface of claspers. Dermal denticles on

the head (Fig. 3a), medial dorsal, and caudal area small (Figs 3–4), with posteriorly oriented conical crowns and four to five longitudinal ridges not reaching the crown apex (Fig. 4). Enlarged denticles with variable crown shapes forming four oval pairs of patches on head: some crowns in the patches blunt,

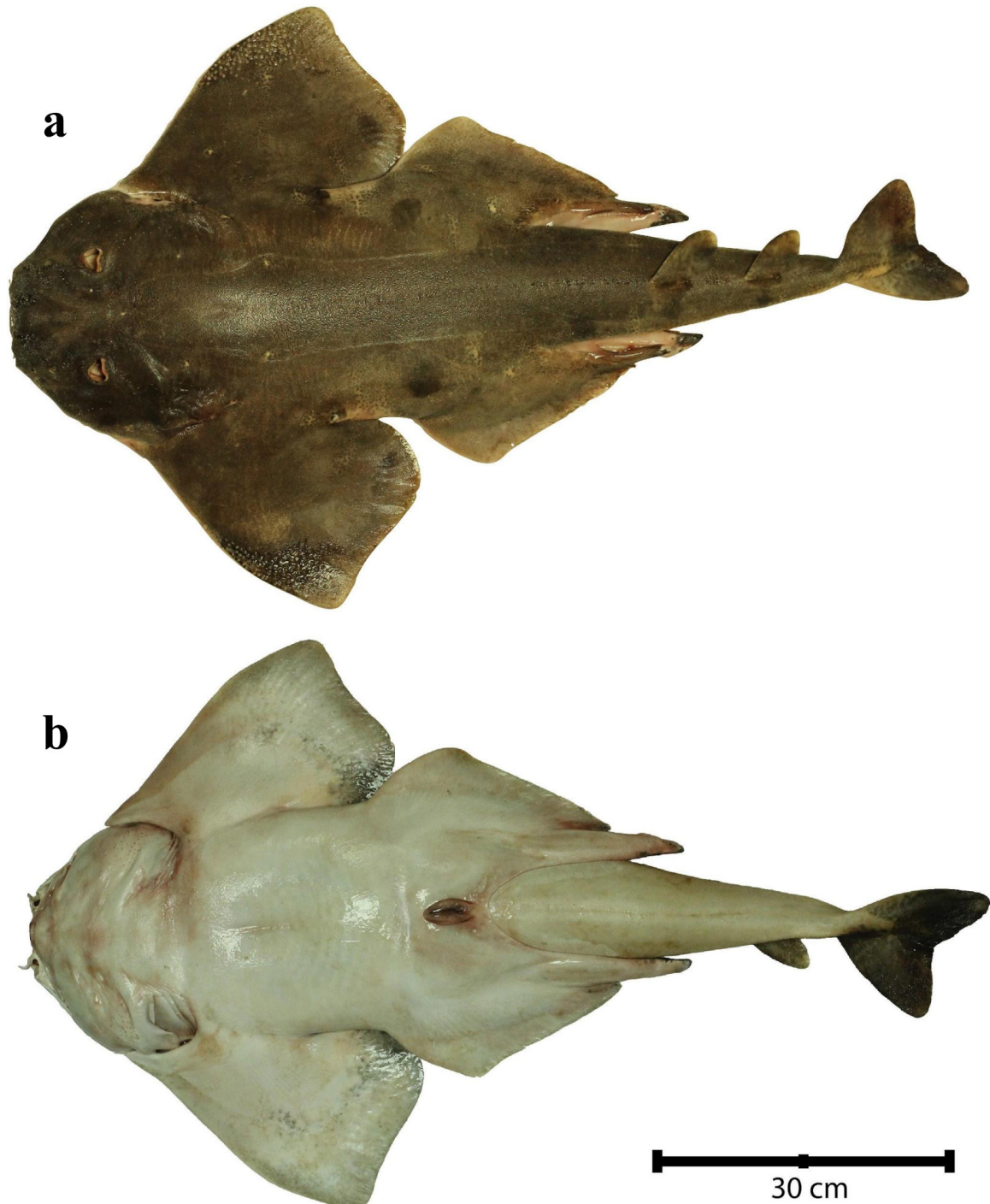


Fig. 1. *Squatina armata* (Philippi, 1887), neotype, ♂ (1004 mm total length; MNHNCL ICT 7625), fresh specimen. **a.** Dorsal view. **b.** Ventral view.

some conical, and others thorn-like, being either postero- or latero-dorsally oriented (Fig. 3a); first pair of thorn-like enlarged dermal denticle patches dorsal to internarial space; second patch on pre-orbital area; third patch on eye-spiracle space; and fourth pair on interspiracle space (Fig. 3a). A single patch of thorn-like enlarged dermal denticles on apex of each pectoral fin; pectoral fin thorns hook-shaped, posteromedially oriented (Fig. 3b–c), lacking ridges, similar in size. A total of 36 thorn-like enlarged dermal denticles forming a single longitudinal row on dorsal surface, of similar size (1.5 mm), lacking longitudinal ridges (Figs 3d, 4e): one medial-dorsal thorn, anterior to pelvic girdle; 30 caudal thorns forming a single row; 5 interdorsal thorns forming a single row. Dermal denticles scarce on ventral surface of body. Ventral dermal denticles, small, flattened, with rounded crowns lacking longitudinal ridges, forming patches covering external margins of pectoral and pelvic fins (Fig. 4g), scattered near cloaca, forming a narrow patch on each clasper, covering ventral surface of caudal peduncle except for its anterior portion.

DENTITION (Fig. 5). Tooth count 9–9 in upper jaw, 10–10 in lower jaw; symphyseal teeth absent. Teeth with a single cusp, not serrated; cusps relatively short, lingually bent, drop-shaped; labial face of cusps convex, rounded near base; crown foot broad, projecting laterally on first three series from symphysis on upper teeth, breaking to form a right angle, projecting laterally in the remaining series; roots short, wide, merging from lateral projections of crown feet.

CLASPER EXTERNAL MORPHOLOGY (Fig. 6a). Clasper elongated, flattened ventrally, convex dorsally, broad at base, pointed to tip, extending posteriorly less than one-third of clasper inner length beyond pelvic

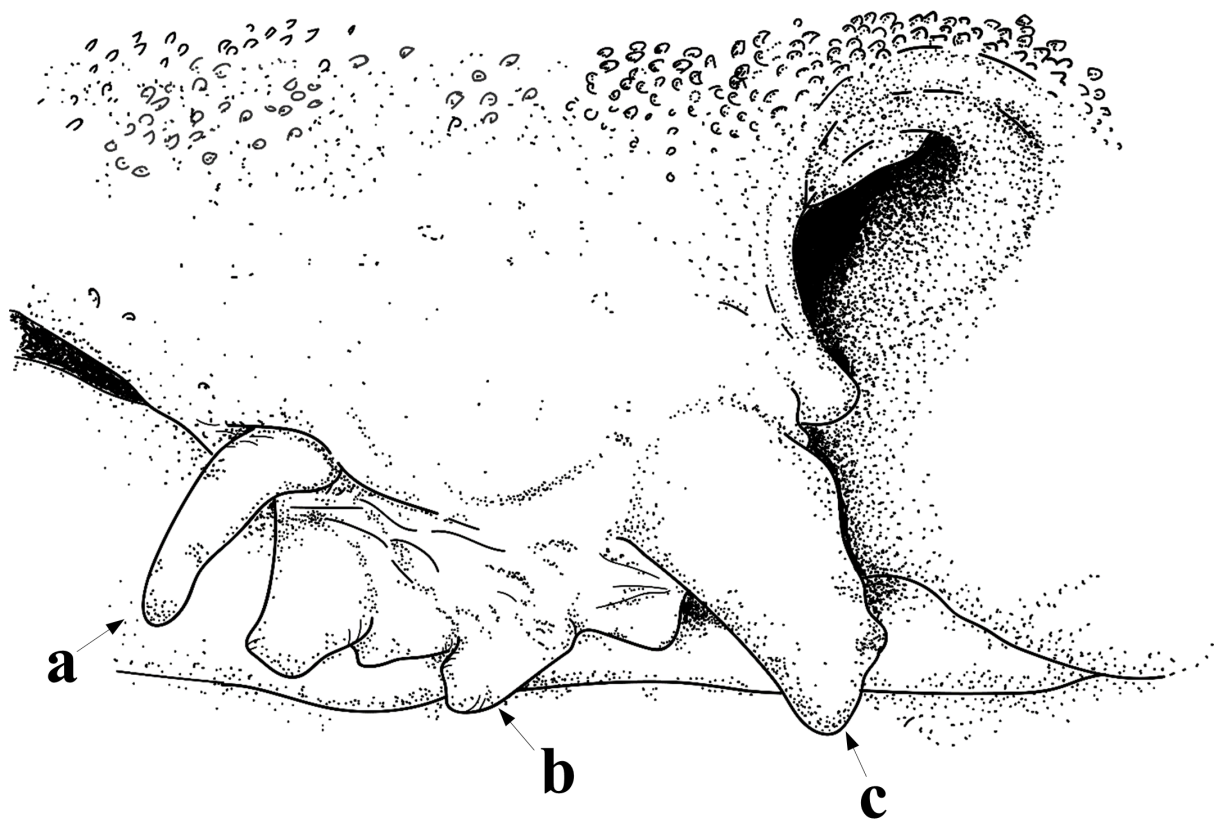


Fig. 2. *Squatina armata* (Philippi, 1887), neotype, ♂ (MNHNCL ICT 7625), illustration of the left anterior nasal flap. **a.** Anterior barbel. **b.** Median barbel. **c.** Posterior barbel. Illustrations by IFC.

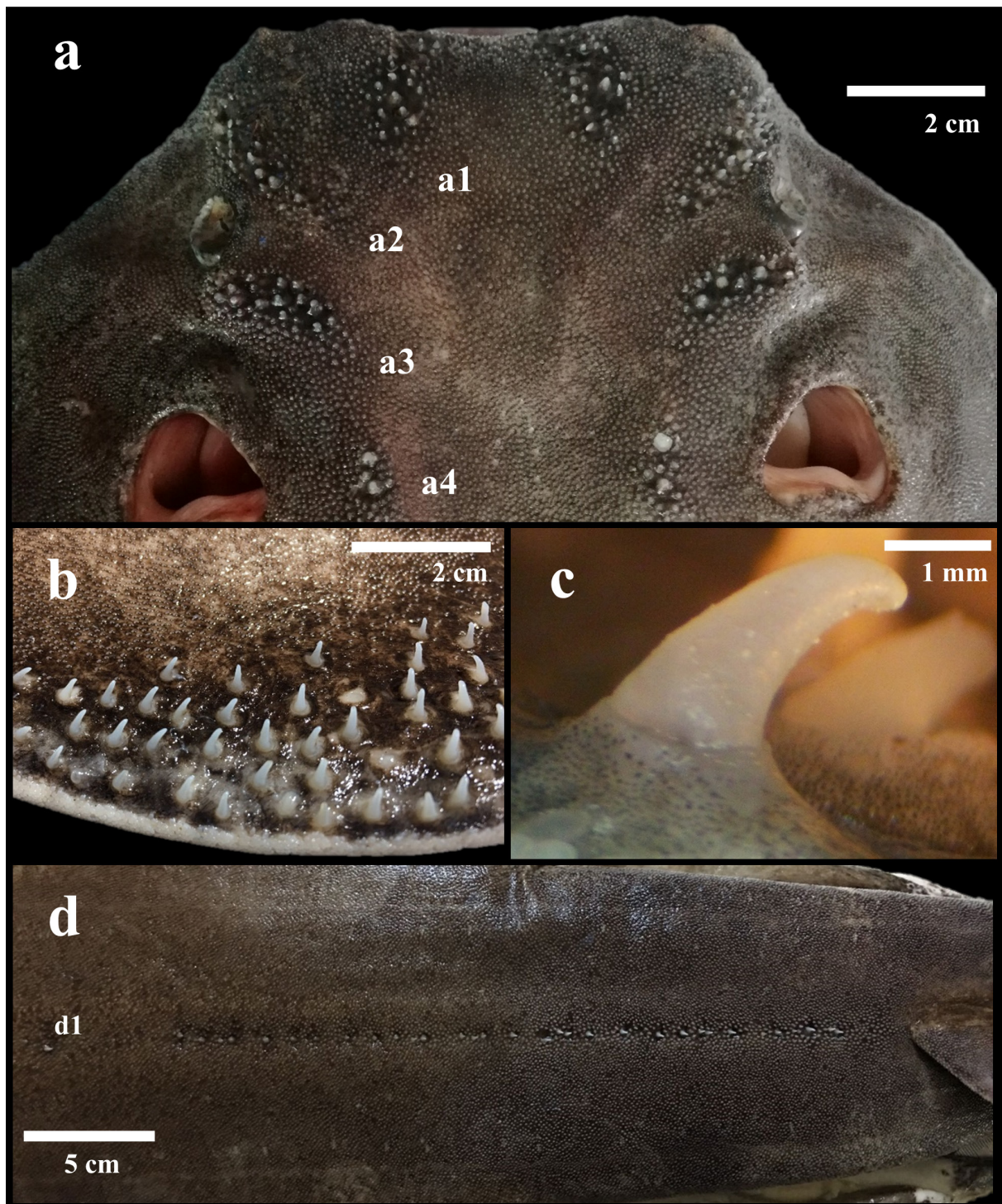


Fig. 3. *Squatina armata* (Philippi, 1887), neotype, ♂ (MNHNCL ICT 7625), dorsal thorns. **a.** Patches of thorns on head forming three pairs; one pair on internarinal space (left one marked a1), second patch on pre-orbital area (a2), third patch on postorbital area (a3), two pairs of interspiracle thorns (a4). **b.** Single patch of 91–93 thorns on apex of each pectoral fin; thorns hooked, inwardly curved. **c.** Close-up of a pectoral fin thorn. **d.** 36 dorsal hooked thorns forming a single row: one medial-dorsal thorn anterior to pelvic girdle followed by 30 caudal thorns and 5 interdorsal thorns (not shown).

free rear tip. Clasper groove elongated, oblique anteriorly to reach dorsal mid-line of clasper, straight on middle, oblique distally; apopyle visible dorsally; globular cartilaginous rod conspicuous along clasper groove, reaching anterior margin of clasper glans; hypopyle anterior on clasper glans, anterior to rhipidion; rhipidion terminal, elongated, flap-like, projecting laterally from hypopyle to base of cover

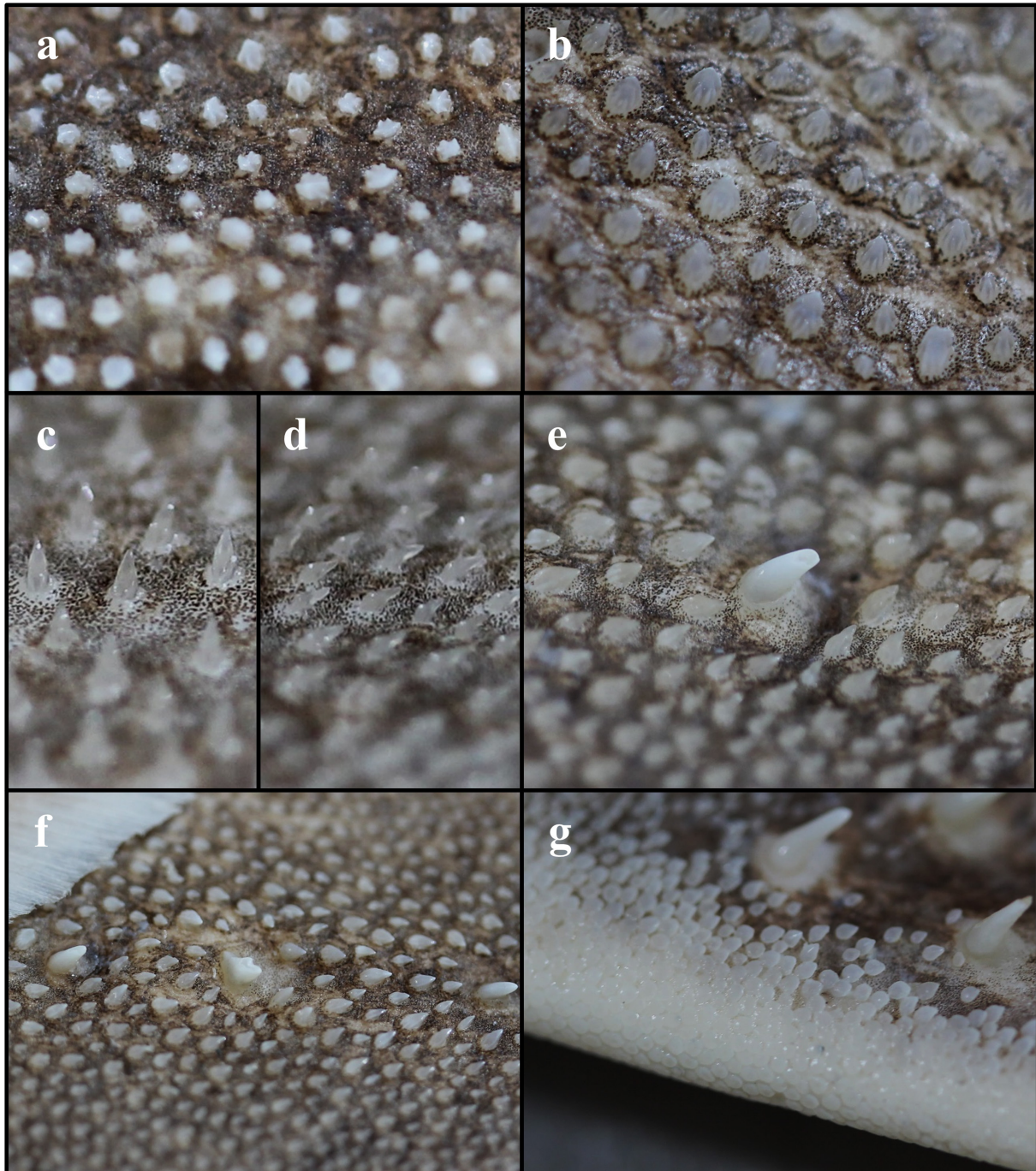


Fig. 4. *Squatina armata* (Philippi, 1887), neotype, ♂ (MNHNCL ICT 7625), dermal denticle shapes and patterns. **a.** Rostral area, frontal view. **b.** Interorbital area. **c–d.** Medial-dorsal denticles in frontal (c) and lateral (d) views. **e.** Caudal area, la

rhipidion, partially covering dorsal surface of glans. Pseudopera not found near hypopyle on clasper glans; cover rhipidion flap-like, relatively thick, well developed, narrow, width about one-fourth of clasper width at pelvic fin free rear tip, positioned terminally on clasper glans. Pseudosiphon absent.

CLASPER SKELETON (Fig. 6b–c). Clasper components surrounding axial cartilage. Axial cartilage elongated, slightly flattened. Dorsal terminal cartilage elongated, narrow, and distally pointed. Dorsal terminal 2 cartilage narrow, flattened, and shorter than dorsal terminal cartilage. Dorsal terminal 3 cartilage small, visible on x-rays but probably lost during preparation. Dorsal marginal cartilage triangular, narrow anteriorly, broadens distally, fused anteriorly with axial cartilage and fused laterally with accessory dorsal marginal cartilage. Accessory dorsal marginal cartilage triangular, longer than dorsal marginal cartilage, posterior apex projected on anterior portion of dorsal terminal 2 cartilage. Ventral terminal cartilage triangular, pointed distally, partially covered by dorsal terminal cartilages in dorsal view. Ventral terminal 2 cartilage broad, outer portion inwardly folded, projected dorsally, partially involving ventral terminal cartilage. Ventral marginal cartilage relatively large, fused proximally with axial cartilage in ventral view, inwardly folded, and projected dorsally.

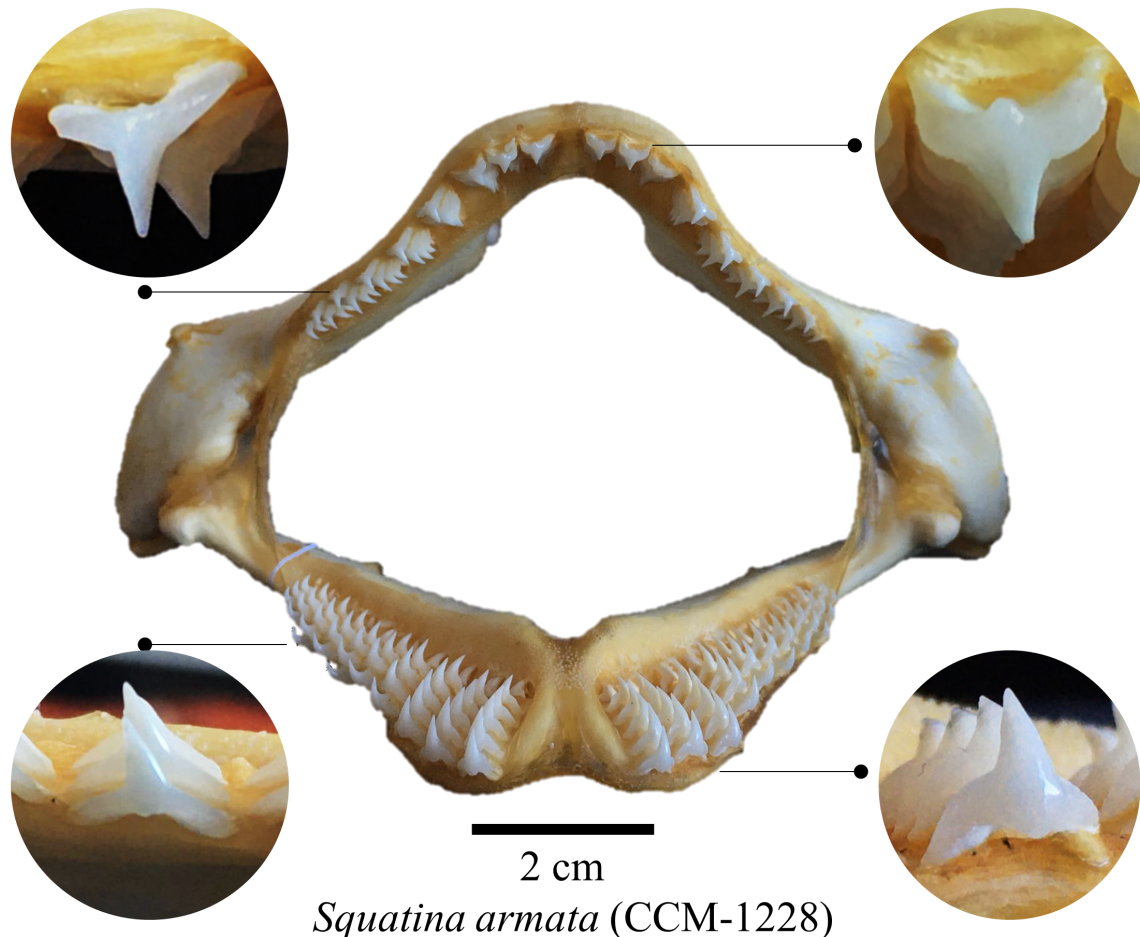


Fig. 5. *Squatina armata* (Philippi, 1887), adult ♂, obtained from the fishmarket of Higerillas, central Chile, date of capture 18 Mar. 2020 (collection code CCM-1228, Chondrolab, Universidad de Valparaíso). Close up of individual teeth not to scale.

Molecular analyses

All markers were successfully amplified in both specimens, which had identical haplotypes for the three markers. A fragment of 675 base pairs (bp) was obtained for CO1, 592 bp for 16S, and 1311 bp for NADH2. The NADH2 sequences were new for *Squatina armata*. Additional n = 18 CO1, n = 18 16S and n = 10 NADH2 GenBank sequences were considered, including CO1 and 16S sequences of other specimens of *S. armata* from a different locality (Supp. file 1.3). Three CO1 sequences of 658 bp and three 16S sequences of 572 bp were obtained from Stelbrink *et al.* (2010), while four CO1 sequences of 610 bp were retrieved from the supplementary material of Cañedo-Apolaya *et al.* (2021). Three unpublished NADH2 sequences of *S. armata* and three of *S. californica* were also included.

The fragment consensus lengths after alignment were 610 bp for CO1, 587 bp for 16S and 1044 bp for NADH2. Each gene showed little saturation according to DAMBE and were concatenated (2289 bp, 11 species).

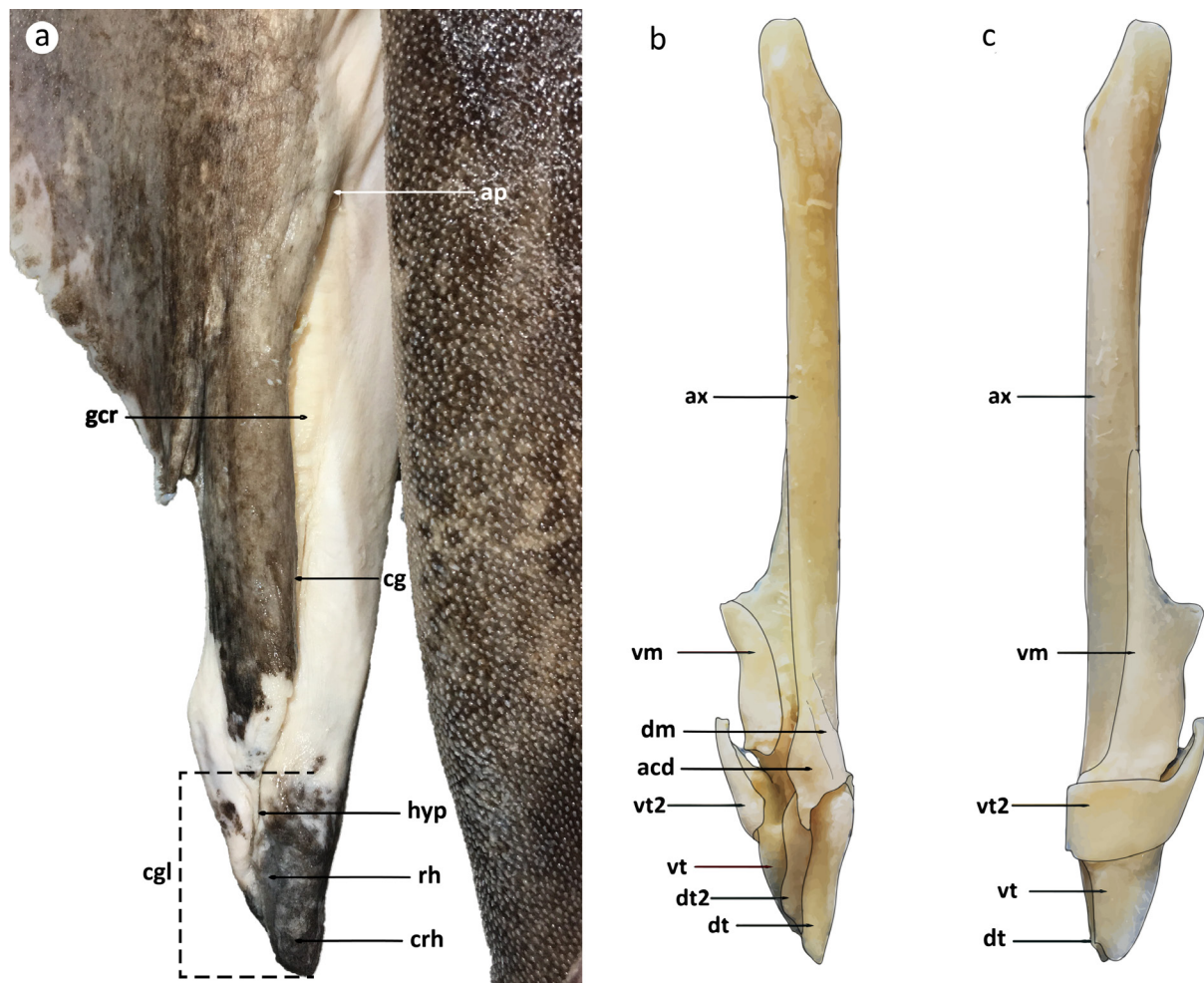


Fig. 6. *Squatina armata* (Philippi, 1887) (voucher MNHNCLICT 7626), clasper morphology. **a.** External. **b–c.** Skeletal dorsal (b) and ventral (c) views. Abbreviations: acd = accessory dorsal marginal cartilage; ap = apophyle; ax = axial cartilage; cg = clasper groove; cgl = clasper glans; crh = cover rhipidion; dm = dorsal marginal; dt = dorsal terminal; dt2 = dorsal terminal 2; gcr = globular cartilaginous rod; hyp = hypopyle; rh = rhipidion; vm = ventral marginal cartilage; vt = ventral terminal; vt2 = ventral terminal 2.

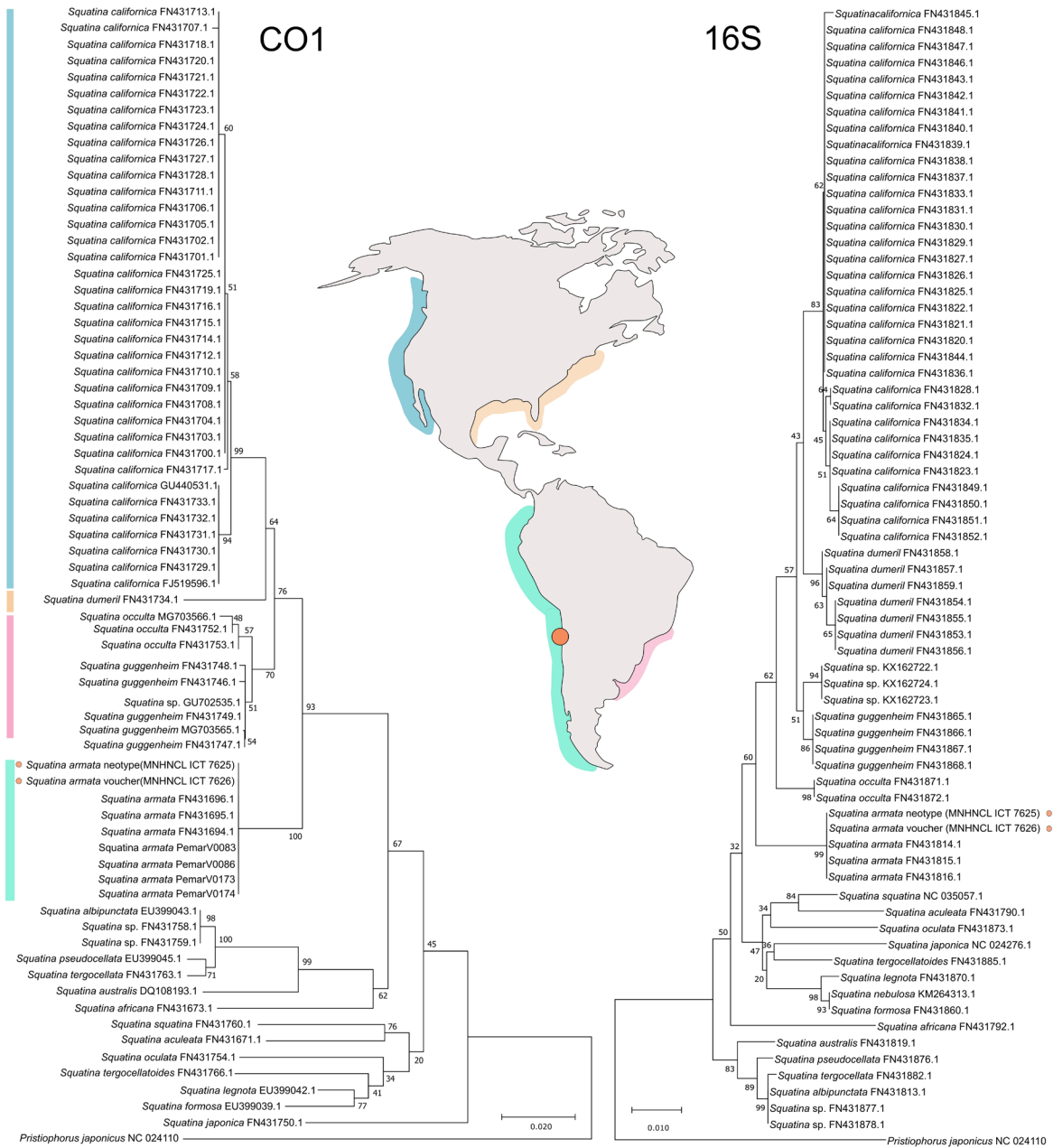


Table 2. The p-distances between angel sharks using the NADH2 sequences. Bold numbers highlight comparisons of the neotype of *Squatina armata* (Philippi, 1887) with other species of *Squatina* Duméril, 1805.

	<i>S. aculeata</i>	<i>S. albipunctata</i>	<i>S. armata</i> (neotype)	<i>S. californica</i>	<i>S. dumeril</i>	<i>S. formosa</i>	<i>S. japonica</i>	<i>S. nebulosa</i>	<i>S. oculata</i>	<i>S. squatina</i>	<i>S. tergocellatoides</i>
<i>S. aculeata</i>	-										
<i>S. albipunctata</i>	0.1178	-									
<i>S. armata</i> (neotype)	0.1092	0.1034	-								
<i>S. californica</i>	0.1111	0.1034	0.0623	-							
<i>S. dumeril</i>	0.1188	0.1082	0.0795	0.0460	-						
<i>S. formosa</i>	0.0891	0.1140	0.0958	0.0939	0.1082	-					
<i>S. japonica</i>	0.0958	0.1188	0.0967	0.1015	0.1188	0.0642	-				
<i>S. nebulosa</i>	0.0891	0.1140	0.0958	0.0939	0.1082	0.0000	0.0642	-			
<i>S. oculata</i>	0.1082	0.1312	0.1063	0.1063	0.1264	0.0833	0.0987	0.0833	-		
<i>S. squatina</i>	0.0862	0.1188	0.0977	0.1063	0.1159	0.0872	0.0967	0.0872	0.0987	-	
<i>S. tergocellatoides</i>	0.1044	0.1303	0.1063	0.1111	0.1216	0.0843	0.0805	0.0843	0.1044	0.1025	-

The p-distances calculated for the NADH2 sequences between the neotype of *S. armata* and other angel sharks ranged between 0.0623 (with *S. californica*) and 0.1092 (with *S. aculeata*) (Table 2). The lowest values were obtained between the species from the American continent (*S. armata*, *S. californica* and *S. dumeril*). The CO1, 16S and NADH2 sequences from the neotype and voucher specimen grouped with the other sequences of *S. armata* in the NJ trees. NJ trees constructed using the CO1, 16S, and NADH2 datasets also showed *S. armata* as sister group to all other American species, *S. californica* and *S. dumeril*, which formed their own clade (Fig. 7).

The Bayesian inference tree had the single Australian species, *S. albipunctata* Last & White, 2008, as a sister group to the remaining ten species, which branched off into two main groups: an American clade (*S. californica* and *S. dumeril*, and *S. armata*), and another group composed of a European-African subgroup (*S. aculeata*, *S. oculata*, and *S. squatina*) and an Asian subgroup (*S. formosa* Shen & Ting, 1972, *S. japonica* Bleeker, 1858, *S. nebulosa* Regan, 1906, and *S. tergocellatoides* Chen, 1963) (Fig. 8).

Discussion

Justification for designation of a neotype and comments on *Squatina armata*

To check the loss of the holotype of *Squatina armata*, we contacted the curator of vertebrate zoology at the National Museum of Natural History of Chile, who certified it was lost. The curator informed that the holotype was lost while it was kept at the Faculty of Sciences of the Universidad Austral de Chile for further taxonomic examination, after a fire broke out in the building (Supp. file 1.1). Therefore, in compliance with Article 75.3 of the International Code of Zoological Nomenclature (ICZN 1999), the specimen MNHNCL ICT 7625 is here designated as neotype, in order to clarify the taxonomic status of the Chilean angel shark *Squatina armata*. The neotype was collected from the type locality of *Squatina armata*, and was deposited at the National Museum of Natural History of Chile.

Regarding previously published work on the morphology of *S. armata*, differences in the number of mid-line thorn rows were noted. Norman (1937) reported a mid-dorsal row of large denticles with one or more rows of smaller enlarged denticles on either side. However, he added that “It is with some hesitation that I have identified these specimens with the Chilean species, known only from Philippi’s

Fig. 7 (see previous page). Neighbour-Joining tree of the angel shark CO1, 16S and NADH2 sequences included in this study. Non-American species reduced to one sequence per species for illustrative purposes. Approximate geographic distributions of the species are colour-coded. Sampling location and position in the NJ tree of the *Squatina armata* (Philippi, 1887) vouchers MNHNCL ICT 7625 (neotype) and MNHNCL ICT 7626 are indicated with orange circles.

rather poor description and figure”. Later, the diagram of *S. armata* in Compagno *et al.* (2005) featured a double row of dorsal thorns that runs from the insertion of pectoral fins to the origin of the caudal fin, including the interdorsal space. Later, the description of *S. armata* by Ebert *et al.* (2021) also mentioned a double row of thorns along the mid-line of its back, yet it was only depicted in the coloured plate of the species and not in the diagram that accompanied the morphological characterization. Instead, Philippi (1887) mentioned a single row of recurved thorns running between the nuchal area and interdorsal space. However, this is inconsistent with the associated plate, where it starts at the center of the medial-dorsal area (see Philippi 1887: fig. 1). Finally, both males examined in this study also presented a single row of hooked thorns, which started at the pelvic girdle and lacked nuchal and medial-dorsal thorns.

These differences could be an outcome of phenotypic plasticity, sexual dimorphism, or ontogenetic differences. To determine this, a larger number of specimens including different life stages and both sexes should be examined. Intraspecific variability, such as variations in the number of mid-line rows of thorns, has been reported in *S. guggenheim* (Vaz & de Carvalho 2013) and in other elasmobranchs such as the yellownose skate (*Dipturus chilensis* (Guichenot, 1848)), for which nape thorns, commonly considered a diagnostic character, are often absent (Concha *et al.* 2019).

Norman (1937) observed that the ratio between the interorbital distance was 4.5 times the eye height in immature individuals whereas it was approximately two times that value in adults. Moreover, the interdorsal space in immature specimens is shorter than the dorsal-caudal distance, while the contrary is the case for the adult individuals. Considering size difference among specimens (470 mm vs > 1000 mm TL), these might relate to allometric variation in growth.

The original description of *S. armata* expressed the morphological measurements as simple fractions (e.g., “a third of the length”), which could lead to lower precision and potential differences from the actual values. Despite the similar size and sex of the holotype of *S. armata* and the two specimens

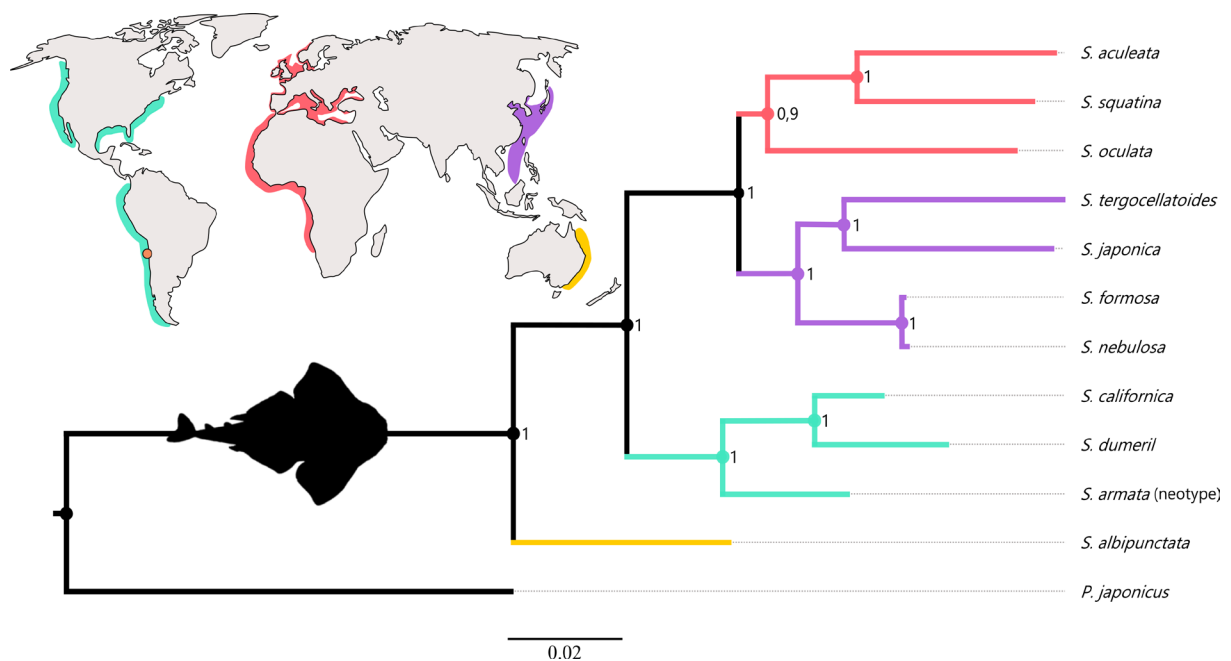


Fig. 8. Bayesian inference phylogenetic reconstruction of 11 species of *Squatina* Duméril, 1805 for which CO1, 16S and NADH2 sequences were available. Species groups are colour-coded in the phylogeny and the geographic distributions on the map. Sampling location of the *S. armata* (Philippi, 1887) vouchers MNHNCL ICT 7625 (neotype) and MNHNCL ICT 7626 is indicated with an orange circle.

reported here, noticeable differences in measurements were obtained. The specimens of *S. armata* reported in this work differ from the holotype in that the former have a larger pectoral fin inner margin (11.5–11.9% vs 8.7%), shorter trunk width (23.3–22.7% vs 26.2%), greater pectoral fin width (19.6% vs 16%), and lower first and second dorsal fin height (7.2–7.8% vs 8.3%; 6.5%–7.3% vs 8.3%), shorter pre-first dorsal fin length (63.2–64.2% vs 70.9%), greater pectoral fin posterior margin (20–20.2% vs 13.1%), shorter pectoral fin anterior margin (24.9–25.1% vs 29.1%), and greater first and second dorsal fin base length (3.8–4.1% vs 2.9%; 3.6–3.9% vs 2.9%). This could be an outcome of differences in how these measurements were taken or of inter-individual variability.

Comments on *Squatina californica*

In the original description of *S. californica*, morphological measurements were also expressed as simple fractions, potentially leading to errors in measurements and limiting comparisons.

The enlarged dermal denticle patches on the apex of each pectoral fin of the male of *S. armata* are a secondary sexual character presented by other mature angel shark males (Bigelow & Schroeder 1948; Colonello *et al.* 2007; Acero *et al.* 2016; Vaz & de Carvalho 2018) and might be a widespread feature (Colonello *et al.* 2007). However, in *S. californica*, this trait appears to be present only in young individuals (Ebert *et al.* 2021), and its effectiveness as a diagnostic marker to differentiate *S. armata* from this species has been described as moderate (Alioto 2012). This feature was not mentioned by Norman (1937) but might be related to the sexual immaturity of the two specimens (male and female of 470 mm and 450 mm TL, respectively). This character needs further revision in *S. armata*, as no females or juveniles were caught for this study. Therefore, further studies are required to validate such characters and evaluate the possibility of ontogenetic differences (Alioto 2012). Consequently, in line with Alioto (2012), the most useful traits observed in this study to distinguish *S. armata* from *S. californica* correspond to the spinulation pattern on the dorsal surface of the head, surrounding the eyes, spiracles, and on the dorsal surface of the pectoral apex, also highlighted by Norman (1937) and Yáñez (1951); the sinuated shape of the anterior margins of the pectoral fins and shape of the head should also be considered.

Notes on comparative material

The range of values of all available life stages and sexes per species were included to account for trait variation in each species and to identify features useful in identifying Chilean angel sharks considering these sources of variability (e.g., ontogeny and sexual dimorphism). Other unnatural sources of variability that might have influenced some comparisons include the condition of some of the specimens and the method by which measurements were done. For example, specimens of *Squatina dumeril* were dry and stuffed, which possibly affected their external morphology and morphometric proportions (Vaz & de Carvalho 2013).

The internal components of the claspers are similar to those of *S. varii* (Vaz & de Carvalho 2018). In dorsal view, the dorsal marginal cartilage of *S. armata* (Fig. 6b) does not show a clear division from the dorsal marginal-accessory dorsal marginal cartilages; yet, there is a soft and barely noticeable groove dividing both structures. Interestingly, the configuration of this side-by-side dorsal marginal-accessory dorsal marginal cartilage group differs from that described for *S. guggenheim* (Vaz & de Carvalho 2013), in which the dorsal marginal-accessory and dorsal marginal cartilage group have a vertical organization, with the dorsal marginal cartilage in the proximal position.

Molecular markers

Sequences of CO1 and 16S of Chilean angel sharks presented the same haplotypes, despite the distance between both localities being approximately 1000 km (Iquique and Coquimbo, Chile). The NADH2 NJ

tree and p-distance results (Fig. 7, Table 2) showed an expected greater similarity between *Squatina armata* and other American angel sharks than between other congeners. The p-distance between *S. californica* and *S. dumeril*, from opposite coasts of the American continent, was lower than their p-distances with *S. armata*, in accordance with their positions in the NJ trees and phylogeny. This comparison expands on previous work that has highlighted how their relationships reflect their geographic distributions (e.g., Stelbrink *et al.* 2010; López-Romero *et al.* 2020) and could be complemented by obtaining NADH2 sequences for more species. The NJ trees (Fig. 7) and the concatenated BI phylogeny (Fig. 8) also show *S. armata* as a sister group to all other American angel sharks, in agreement with previous work (see Stelbrink *et al.* 2010).

Conservation

Because of their coastal and shallow-occurring habits, angel sharks are inherently more exposed to human activities, such as fishing, coastal development, and habitat degradation (Dulvy *et al.* 2021). Their greater vulnerability to these threats compared to other groups highlights the urgent need for effective and efficient conservation policies supported by robust taxonomic and molecular data. To this end, taxonomy is the first and indispensable requisite. However, despite the interdependence of both disciplines, their synergic and harmonic application has not been as frequent as needed. Recent taxonomic studies on angel sharks (Vaz & de Carvalho 2013, 2018) and other successful examples of combining taxonomy and genetics (Ambily *et al.* 2018), with this updated morphological characterization of the Chilean angel shark, questions on geographic range, estimations of abundance, and real incidence in landings can be clarified to ultimately inform better conservation practices of this critically endangered species (Dulvy *et al.* 2020) and other angel sharks on the Pacific coast of America.

Limitations

Ideally, the redescription of a species should include specimens of both sexes and as many ontogenetic stages as possible to assess sexual dimorphism and general morphologic variability among individuals within the species. The redescription in this study was based on two mature males; hence data were limited. Similarly, an updated description of *Squatina californica* would also have been useful in objectively resolving identification issues between these species. However, logistic and funding difficulties restrained including these tasks. Nonetheless, we believe that this study greatly improves the current state of the knowledge of the Chilean angel shark and will prove useful in future taxonomic work and conservation efforts when newly collected material of *S. armata* and *S. californica* may become available.

Lastly, we followed the methodology proposed in recent publications (Vaz & de Carvalho 2013, 2018) to perform standardized and comparable measurements. However, considering that some original descriptions, mostly the oldest ones, do not include a detailed definition of how measurements were taken, some differences among the morphometric data provided in this and previous studies can be due in part to differences in the methods rather than to the morphometry of the examined specimens themselves. However, in this work, other included traits are not necessarily affected by differences in measurement methods, like for instance the shape of the fins or the number and position of thorn patches, among others. Fortunately, consistency among taxonomic methods has been reached thanks to the efforts of different authors acknowledging limitations in doing taxonomic descriptions and lack of standardized methods (see Last *et al.* 2008, 2016; Vaz & de Carvalho 2013, 2018).

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1. Certificate of loss of the *Squatina armata* (Philippi, 1887) holotype issued by the Chilean National Museum of Natural History.

2. Composite dorsal X-ray image of the fresh *Squatina armata* (Philippi, 1887), neotype, ♂ (MNHCL ICT 7625). Image was created based on several close-ups to the body, and because of constraints during radiography the left pectoral fin had to be mirrored.

3. Table detailing the gene markers that were found for each of the species of *Squatina* Duméril, 1805 and outgroup included in the molecular analyses. Respective GenBank accession numbers are provided.