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## Erratum for:

Long, D.J., Ebert, D.A., Tavera, J., Acero P., A. & Robertson, D.R. (2021) *Squatina mapama* n. sp., a new cryptic species of angel shark (Elasmobranchii: Squatinidae) from the southwestern Caribbean Sea. *Journal of the Ocean Science Foundation*, 38, 113–130.

Due to a transcription error in the collection data for the specimens, it is necessary to make the following several corrections:

**p. 116 & p.127, collection data:**

**Holotype.** USNM 400784, immature male, 400 mm TL, Panama, Caribbean coast, Comarca de Guna Yala, north-northeast of Puerto Escocés, 8.96˚, -77.45˚, 1190–1259 m, trawl, station MOC11-1, D.R. Robertson & C. Castillo, 6 January 2011.
**Paratype.** USNM 400796, immature male, 325 mm TL, collected with holotype.
**Comparative material.** *Squatina david*: USNM 400759, immature female, 503 mm TL, Panama, Caribbean coast, Comarca de Ngobe-Bugle, off Bocas del Toro, 9.27˚, -81.69˚, 252–289 m, trawl, station MOC11-31, D.R. Robertson & C. Castillo, 12 January 2011.

is corrected to

**Holotype.** USNM 400784, immature male, 400 mm TL, Panama, Caribbean coast, Comarca de Ngobe-Bugle, off Bocas del Toro, 9.27˚, -81.69˚, 260–272 m, trawl, station MOC11-31, D.R. Robertson & C. Castillo, 12 January 2011.
**Paratype.** USNM 400796, immature male, 325 mm TL, collected with holotype.
**Comparative material.** *Squatina david*: USNM 400759, immature female, 503 mm TL, Panama, Caribbean coast, Comarca de Guna Yala, north-northeast of Puerto Escocés, 8.96 ˚, -77.45 ˚, 252–289 m, trawl, station MOC11-1, D.R. Robertson & C. Castillo, 6 January 2011.

**p. 123, Figure 8 caption:** Map of Panama and the southwestern Caribbean with the capture location by the R/V *Miguel Oliver* of the type specimens of *Squatina mapama* (MOC 11-1) and a specimen of *S. david* (MOC 11-31) off the western Caribbean coast of Panama.

is corrected to

Map of Panama and the southwestern Caribbean with the capture location by the R/V *Miguel Oliver* of the type specimens of *Squatina mapama* off the western coast of Panama (MOC 11-31) and a specimen of *S. david* (MOC 11-1) off the eastern Caribbean coast of Panama.

**p. 126, Remarks:** The R/V *Miguel Oliver* expedition did capture a single immature female specimen of *S. david* (Fig. 9: USNM 400759) from a depth of 252–289 m off the western Caribbean coast of Panama (9.27˚, -81.69˚: Fig 8). This represents the westernmost extension of the range of *S. david*, as the previous known western limit of *S. david* was off central Colombia at Bocas de Cenzia (Acero et al. 2016), 750 km east of MOC 11-31. From these limited collections the ranges of *S. mapama* and *S. david* overlap by at least 500 km.

is corrected to

The R/V *Miguel Oliver* expedition did capture a single immature female specimen of *S. david* (Fig. 9: USNM 400759) from a depth of 252–289 m off the eastern Caribbean coast of Panama (Comarca de Guna Yala, 8.96˚, -77.45˚: Fig 8). This represents a modest western extension of the range of *S. david*, as the previous known western limit of *S. david* was off central Colombia at Bocas de Cenzia (Acero et al. 2016). From these limited collections, the ranges of *S. mapama* and *S. david* appear to be allopatric with no apparent overlap of both species.

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# *Squatina mapama* n. sp., a new cryptic species of angel shark (Elasmobranchii: Squatinidae) from the southwestern Caribbean Sea

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## Abstract

Integrating both morphological and genetic data, we describe *Squatina mapama*, a new species of the angel shark genus *Squatina*, found on the upper continental slope off the Caribbean coast of Panama. Distinguishing characters of *S. mapama* include a wider pectoral and pelvic span; a shorter head length; a narrower mouth; short fringed nasal flaps and barbels; a few large denticles on top of the head; a single dorsal midline row of slightly enlarged denticles from the level of the posterior insertion of the pelvic fin to the first dorsal fin and continuing past the first dorsal fin to the second dorsal-fin origin; and the presence of smaller scattered spots in males, which, in combination, allow separation of this new species from the closely related and sympatric species *Squatina david*. The new species can be distinguished from all other currently recognized *Squatina* species by meristic and morphometric measures, as well as by sequence differences in the mtDNA COI marker. Phylogenetic analysis shows *Squatina mapama* n. sp. to be a basal member of a small clade of western Atlantic *Squatina* species that includes *Squatina occulta*, *Squatina guggenheim*, and *S. david*, which likely evolved in the late Oligocene or Miocene period. We also report a western range extension of *S. david* from Colombia to the western Caribbean coast of Panama.

**Key words:** taxonomy, ichthyology, fishes, Atlantic Ocean, Panama, phylogenetics, clades, DNA barcodes

**Citation:** Long, D.J., Ebert, D.A., Tavera, J., Acero P., A. & Robertson, D.R. (2021) *Squatina mapama* n. sp., a new cryptic species of angel shark (Elasmobranchii: Squatinidae) from the southwestern Caribbean Sea. *Journal of the Ocean Science Foundation*, 38, 113–130.

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## Introduction

Traditional methods of taxonomic analysis over the last three centuries have relied on morphological and meristic comparisons to elucidate and describe different species, but methods of genetic analysis can show high diversity and temporal separation of related species that may not differ a great deal in physical traits (Winston 1999, Jörger & Schrödl 2013). DNA sequencing can show that populations in one morphologically defined species, in both allopatric and sympatric species, may actually represent one or more undescribed taxa (Bickford et al. 2006). These "cryptic species" may show much more genetic divergence than phenotypic differentiation, and among fishes, can expose diverse species complexes (Baldwin et al. 2011), raise implications for zoogeography (Delrieu-Trottin et al. 2018), or demonstrate geologically ancient lineages among related taxa (Colborn et al. 2001). In elasmobranchs, genetic analyses have led to the resurrection of synonymized taxa (Ebert et al. 2010, Daly-Engel et al. 2013, Ebert et al. 2013), the identification of new species within the same genus that shows a great degree of morphological similarity (Karl et al. 2011, Quattro et al. 2013, White et al. 2017, White et al. 2021), and the discovery of diverse genetic and biogeographical species complexes (Fahmi et al. 2021). Such information has applications and important ramifications to fisheries management (Harry et al. 2019). Moreover, Naylor et al. (2012) suggest that ongoing documentation of genetic diversity among elasmobranchs indicate the existence of at least 79 undescribed cryptic species of sharks and rays. However, since their publication, at least 125 new species have been described, representing nearly 10% of all known species (D.A. Ebert pers. database, 18 Sept 2021). For the genus *Squatina*, some cryptic species have been found in sympatry with morphologically similar conspecifics; for example, Cañedo-Apolaya et al. (2021) reported on a likely cryptic species of *Squatina* from the Pacific coast of northern Peru that lies within the range of *Squatina armata* (Philippi, 1887) and possibly *Squatina californica* Ayres, 1859.

The genus *Squatina*, the only extant genus of the family Squatinidae in the order Squatiniformes, are a group of dorsoventrally flattened sharks well adapted to a benthic lifestyle (Compagno 1990). Although the genus has a lineage extending back to the Cretaceous (Cappetta 2012, Klug & Kriwet 2013, Maisey et al. 2020), they are extremely conservative in their anatomy, providing few characters for morphological differentiation between taxa (Mollen et al. 2016, López-Romero et al. 2020). Species within the genus are distributed globally in cool temperate and tropical seas, primarily on the continental shelves (Ebert et al. 2013). Species divergence appears to be strongly linked to biogeographical processes of vicariance and dispersal (Stelbrink et al. 2010, Acero et al. 2016). The number of valid species varies from 22 to 25, depending on whether several synonymies are correct (see Fricke et al. 2019). This uncertainty reveals our lack of knowledge of their true diversity. Research collecting during the last decade has enabled the identification of 4 new species (including the one described here) in the Western Atlantic leading to 8–10 American species, with three species on the Pacific coast, and the remainder inhabiting the Atlantic side of the continent. Within the Greater Caribbean area, several species of angelsharks are known from the Gulf of Mexico: *Squatina dumeril* Lesueur, 1818; *Squatina heteroptera* Castro-Aguirre, Espinosa-Pérez & Campos, 2006; and *Squatina mexicana* Castro-Aguirre, Espinosa-Pérez & Campos, 2006. The latter two are currently considered synonyms of *S. dumeril* (Fricke et al. 2019). A fourth species, *Squatina david* Acero, Tavera, Anguila & Hernández, 2016 occurs off the northern coast of South America. Until recently, no specimens of *Squatina* were recorded from the Caribbean coast of Central America (Ebert et al. 2013, Acero et al. 2016). Here we report on two specimens of a new species of *Squatina* from the Caribbean coast of Panama, that, while morphologically similar to the sympatric *S. david*, is genetically distinct.

## Materials and Methods

Between 2007 and 2011, a series of research cruises were made by the Spanish research vessel R/V *Miguel Oliver* along the continental shelves and slopes of the Pacific and Atlantic coasts of Central and South America (Robertson et al. 2017). The R/V *Miguel Oliver* is operated by the Spanish Ministerio de Agricultura y Pesca, Alimentación y Medio Ambiente (MAPAMA; http://www.mapama.gob.es). The vessel is a 70 m long, 2495 gross tons, stern trawler that began operation in 2007. Sampling was done using a Lofoten bottom trawl equipped with a

pair of 1,300 kg oval steel doors, each attached to the net by a 100 m long warp. The trawl itself was 32 m long with a mouth opening 23 m wide and 3.5 m high when fully deployed on the bottom and had a cod-end mesh of 35 mm. Rubber rollers along the bottom of the mouth of the net reduced its contact with the substratum. The ship's side-scan sonar was used to locate a suitable area of relatively level, unobstructed bottom prior to each trawl. Bottom times for trawls were typically 30 mins, at speeds of ~5.5–6.4 km/hr. Those cruises, aimed at assessing both the biodiversity of benthic organisms and fishery resources by deploying bottom trawls at depths down to ~1600 m, began with expeditions to Peru, Patagonia, and the Pacific coast of Panama. The second-to-last cruise, in 2010, sampled the outer edge of the continental shelf and the continental slope of Pacific Central America, between Panama and Guatemala. A companion cruise with similar objectives was made on the Caribbean shelf of Central America, between Panama and Belize, in early 2011. Samples were collected on board from a total of 99 localities in the Caribbean, sampled between central Panama (8.56º, -77.25º) and Belize (17.50º, -87.39º), between 6 and 31 January 2011, at depths ranging from 125 to 1482 m. One of us (DRR) was invited to participate in both cruises and decided to acquire fish specimens and photographs thereof for scientific study. Specimens collected during both cruises have been deposited in the National Museum of Natural History, with a representative group being DNA-barcoded by their Laboratories of Analytical Biology. Specimens of the new *Squatina* species described here were collected in one of the trawls off the Caribbean coast of Panama.

Morphometric measurements and terminology (Tables 1 & 2) follow Walsh & Ebert (2007), Last & White (2008), Vaz & de Carvalho (2013, 2018), and Acero et al. (2016). Meristic characters, including vertebral counts, were taken from digital radiographs, and tooth and dermal denticle counts were taken directly from specimens. In addition to validating the new species description, it was decided to explore its evolutionary relationships, and a molecular phylogeny was built using newly generated mitochondrial sequence data plus available GenBank sequences of 19 other extant *Squatina* species, the accession numbers of which are listed in Table 3.

DNA extraction was performed using DNeasy Blood and Tissue (QIAGEN) amplification kit following the manufacturer's instructions. Two mitochondrial markers, cytochrome oxidase I (COI) and 16S were amplified. Both have previously been used in studies of angelshark relationships, by Stelbrink et al. (2010) and Acero et al. (2016). Universal primers used were COI_VF2_t1 (Ward et al. 2005), COI_VR1d_t1 (Ivanova et al. 2007), and 16Sar and 16Sbr (Palumbi 1996). Amplifications were performed in 15 µl reactions containing 0.5 µl of DNA, 0.625 µl of each primer (forward-reverse), and 11.25 µl of Thermo Scientific 1.1X PCR Master Mix (2.5 mM $MgCl_2$). The PCR program consisted of an initial denaturation of 1 to 3 minutes, 30–35 cycles at 94º C for 45 seconds, followed by 45 seconds at an annealing temperature of 52–56º C, and 60 seconds at 72º C with a final extension of 3 minutes at 72º C. Sequencing was performed in one direction on an ABI 3100 automated sequencer (Applied Biosystems, Foster City, CA).

Sequences were cleaned and trimmed with Geneious 9.0 (Biomatters, Auckland, New Zealand), and Muscle (Edgar 2004) was used as the alignment algorithm. Analyses were performed on a concatenated but gene-partitioned matrix. Corrected Aikake Information Criteria in jModelTest2 (Posada 2008) was used to select the substitution model that had the best fit for each gene partition. Phylogenetic relationships were assessed using Maximum Likelihood (ML) and Bayesian Inference (BI). RAxML-GUI 0.93 (Silvestro & Michalak 2012, Stamatakis 2014) was used to produce a starting tree that was transformed into a chronogram using nonparametric rate smoothing (Sanderson 1997). This tree was prepared in TreeEdit to satisfy the temporal constraints associated with fossil calibration. The calibration point included the stem lineage of all extant species of *Squatina* which we dated using a hard-minimum age of 97 my and a standard deviation of 0.2. Fossil information came from Guinot et al. (2012), Klug & Kriwet (2013), Siversson et al. (2016), and Maisey et al. (2020). This time-calibrated phylogeny was assessed in BEAST2 (Drummond & Rambaut 2007, Heled & Drummond 2012). After testing and rejecting the null hypothesis that the data evolved under a strict molecular clock, an uncorrelated lognormal (UCLN), relaxed clock prior was selected as the model of the evolutionary rate. The birth-death process was chosen as the tree prior. BEAST analyses were run three independent times, with 500 million generations, sampling all parameters every 10,000 generations. Mixing and convergence statistics were monitored in Tracer v1.6 (Rambaut et al. 2018). Runs were combined in LogCombiner v2, and TreeAnnotator v2 was used to summarize the maximum clade credibility tree from the resulting trees after discarding the first 25% as part of the burn-in phase.

## *Squatina mapama,* n. sp.

Small-crested Angelshark; angelote de cresta pequeña

urn:lsid:zoobank.org:act:4F433A27-8764-4FB8-9527-30B339DD3F39

mtDNA COI BIN BOLD:AEC0888 (https://doi.org/10.5883/BOLD:AEC0888)

Figures 1–7; Tables 1 & 2

*Squatina david* (non-Acero, Tavera, Anguila & Hernández) Vaz & Carvalho 2018: 144–159, Fig. 10b, Table 2 (in part) (USNM 400796, Panama).

**Holotype.** USNM 400784, immature male, 400 mm TL, Panama, Caribbean coast, Comarca de Guna Yala, north-northeast of Puerto Escocés, 8.96˚, -77.45˚, 1190–1259 m, trawl, station MOC11-1, D.R. Robertson & C. Castillo, 6 January 2011.

**Paratype.** USNM 400796, immature male, 325 mm TL, collected with holotype.

**Diagnosis.** A *Squatina* species with a combination of: a single row of slightly enlarged dermal denticles along dorsal midline extending between level just anterior of posterior insertion of pelvic fins and anterior base of first dorsal fin and continuing rearwards along dorsal ridge of tail between first and second dorsal fins; a few large denticles on top of head; nasal flap squared with a fine fringe on ventral edge; two short lateral barbels bluntly rounded also with a fine fringed margin; males with a dorsal color pattern of small, scattered, dark spots distributed over a uniform light-brown background; pectoral-fin span 52.0–58.1% TL; pelvic-fin span 30.7–31.0 % TL; pre-pectoral-fin length 19.4–19.8% TL; trunk width 18.1–19.5% TL; head length 16.5–17.5% TL; spiracle length 2.2–2.3% TL; eye-to-spiracle length 2.2–5.0 % TL; mouth width 10.5–12.1% TL; nostril width 1.6–2.3% TL; snout-to-pectoral distance 19.4–19.8%; spiracle width 2.2–2.3% TL; pectoral-fin inner margins 17.5–18.3%.

**Figure 1.** *Squatina mapama*, fresh holotype, USNM 400784, 400 mm TL male, Caribbean Panama (D.R. Robertson).

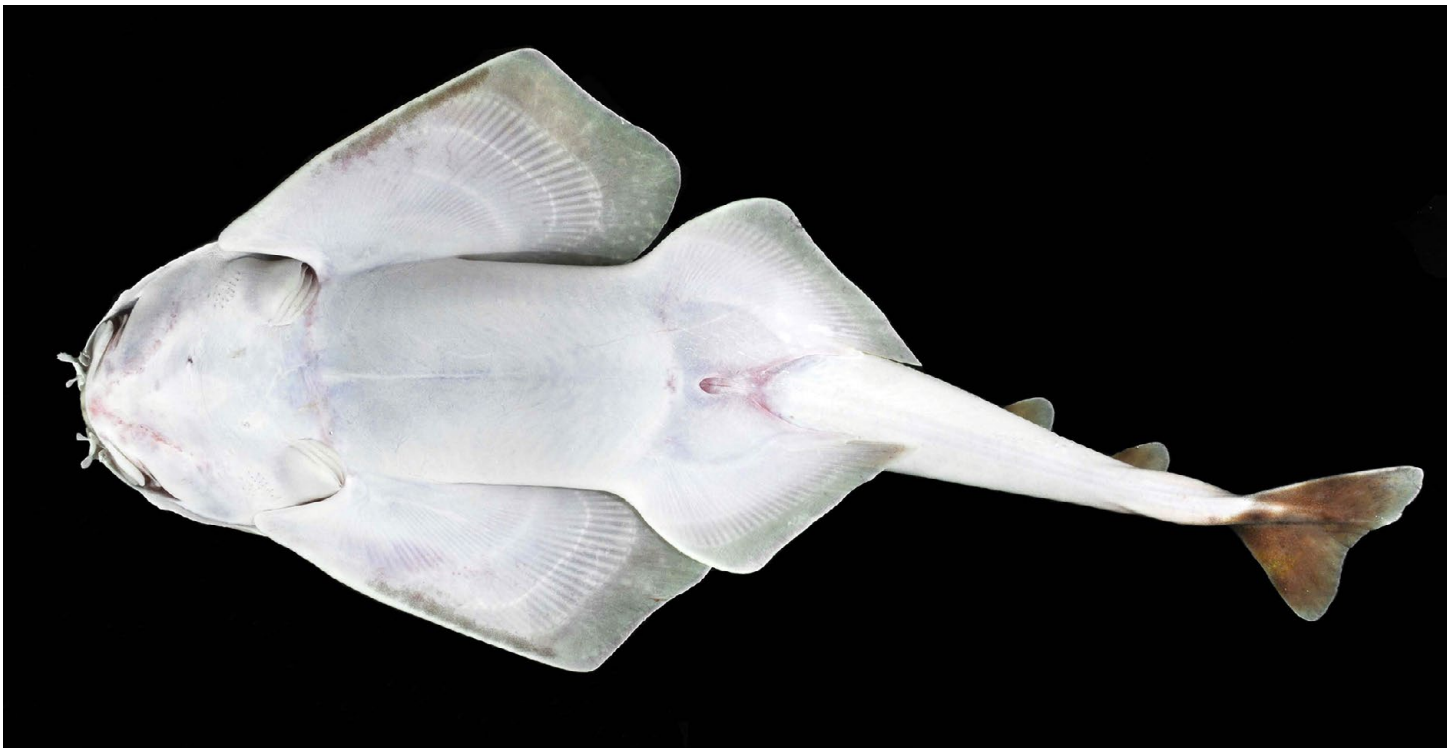

**Figure 2.** *Squatina mapama*, fresh holotype, ventral view, USNM 400784, Caribbean Panama (D.R. Robertson).

**Description.** Body ray-like (head and body dorsoventrally flattened; pectoral fins wide and flattened), with greatest width at tips of fins. Head anteriorly flat at mouth and laterally wide and rounded, head length about 17% (16.5–17.5%) of TL, head width 22.2% TL, with maximum width just anterior to gill opening and over anterior insertion of pectoral fin; interorbital depression shallow, width 8.5–8.9% TL; eyes wide-set, small, and oblong, orbit width 2.3–2.9% TL, slightly raised above lateral edge of upper jaw; spiracle slightly crescentic, width 2.2–2.3% TL, smaller than or equal to orbit width, with tiny papillae along anterior margin; interspiracular space 7.9–8.0% TL, slightly smaller than interorbital space; mouth width 10.5–12.1% TL and 4–5 times mouth height, mouth moderately arched, with double folds in front of each angle of lower jaw; upper-lip arch semi-circular and broader than high; labial furrows extending medially from corners of mouth, upper labial furrow partially

**Figure 3.** *Squatina mapama*, fresh holotype detail of nasal flaps, USNM 400784, Caribbean Panama (D.R. Robertson).

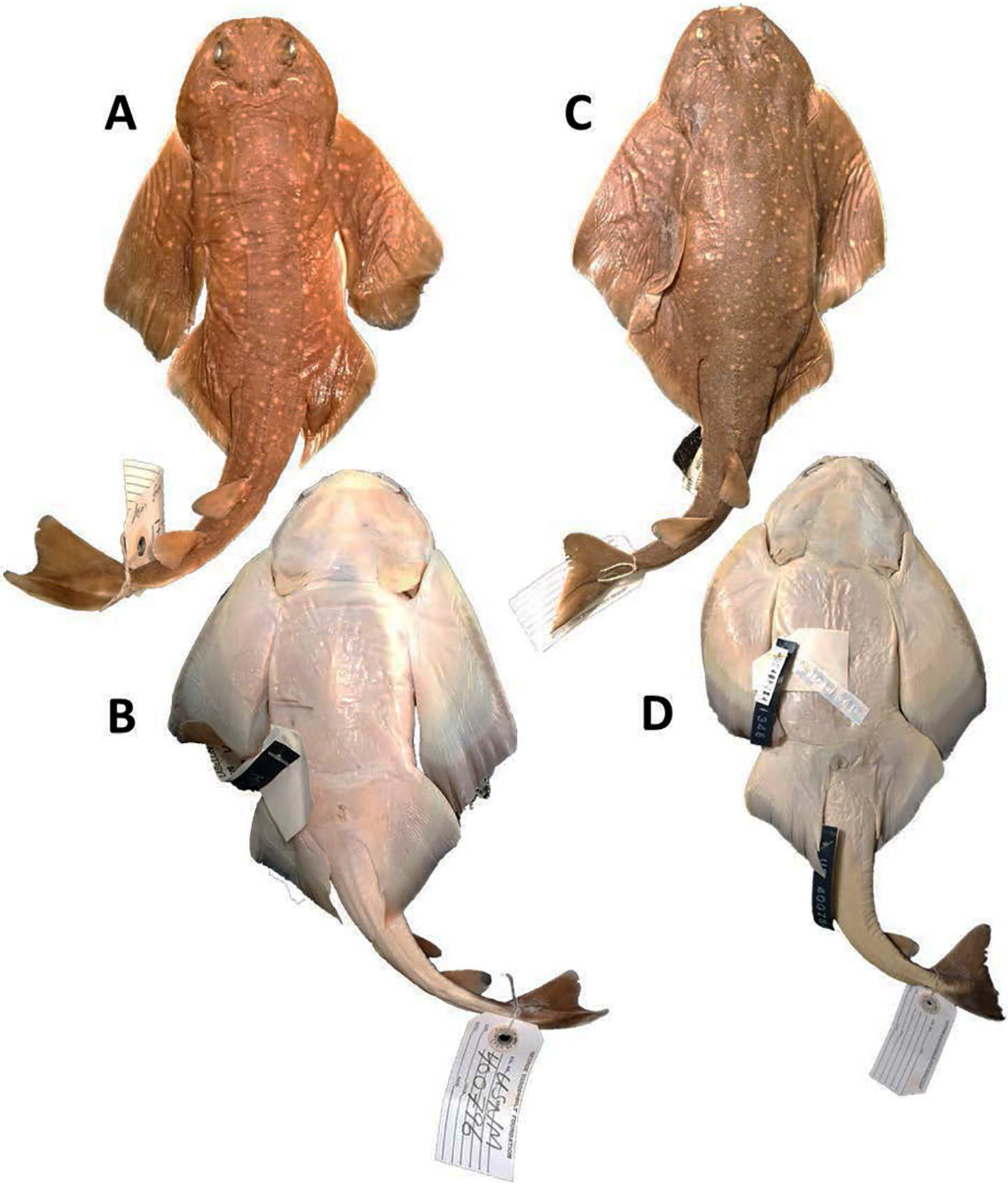


**Figure 4.** *Squatina mapama*, preserved holotype, USNM 400784, 400 mm TL immature male (A & B) and preserved paratype, USNM 400796, 325 mm TL immature male (C & D), Caribbean Panama (D.J. Long).

covered by dermal folds, slightly longer than lower furrow; distinct nasal flaps protruding from dermal folds above mouth, squared with a fine fringe on ventral edge; inner and outer nasal barbels short, flattened, rounded, and bearing a margin of fine short serrations, median barbel largest and widest with a wide, squared-to-slightly rounded terminus, and posterior barbel with a flat wide base with a thin spatulate tip; nostrils large and vertically narrowed, not protruding, with a thin membranous flap externally on lower edge and a second membranous flap interiorly on upper edge; a single shallow dermal fold along exterior of head from corner of mouth to anterior edge of pectoral fin.

Pectoral fins large, length 34.0–34.5% TL, originating behind gills, moderately angular in shape, forming an acute and distinct anterior shoulder that extends under head to behind spiracle, anterior fin margin mostly straight, extending to an acutely rounded lateral apex, posterior margin slightly concave leading to rounded free rear tip; inner margin convex, 17.5–18.3% TL, approximately half (52%) of pectoral-fin length; pectoral-fin radials 37 or 38, divided into 4 propterygial radials, 13 mesopterygial radials, and 20 or 21 metapterygial radials.

Pelvic fins broadly triangular, originating anterior to pectoral-fin free rear tip, anterior border nearly straight to slightly convex, length 1.9 (1.8–2.0) times length of pectoral-fin anterior margin; pelvic-girdle width between pelvic-fin apices moderately broad, free rear tip of pelvic fin tapering posteriorly to acute tip, ending just anterior to first dorsal-fin origin, inner margin slightly concave and short; pelvic-fin-insertion furrows on ventral surface extend in a narrow curve posterior to vent; pelvic-fin radials 26–28.

Dorsal fins small and rounded at the apex; first dorsal fin 6.3–7.2% TL, slightly longer than second dorsal fin 6.0–6.8% TL; base of first dorsal fin 3.8–4.0% TL, slightly longer than second dorsal-fin base 3.2–3.8% TL; origin of first dorsal fin posterior to pelvic-fin tips; interdorsal space 5.7–7.0% TL, shorter than dorsal-fin to caudal-fin space of 8.0–8.3% TL; anterior dorsal-fin margins relatively straight, posterior margins slightly convex; first dorsal-fin base 61% of interdorsal space.

Caudal peduncle flattened dorso-ventrally, with a faintly defined longitudinal ridge along each side; caudal fin triangular, posterior contour concave, with upper lobe 81% length of lower lobe; subterminal caudal-fin margin roughly equal to upper postventral caudal margin; caudal lower postventral margin slightly convex, approximately double length of caudal upper postventral margin.

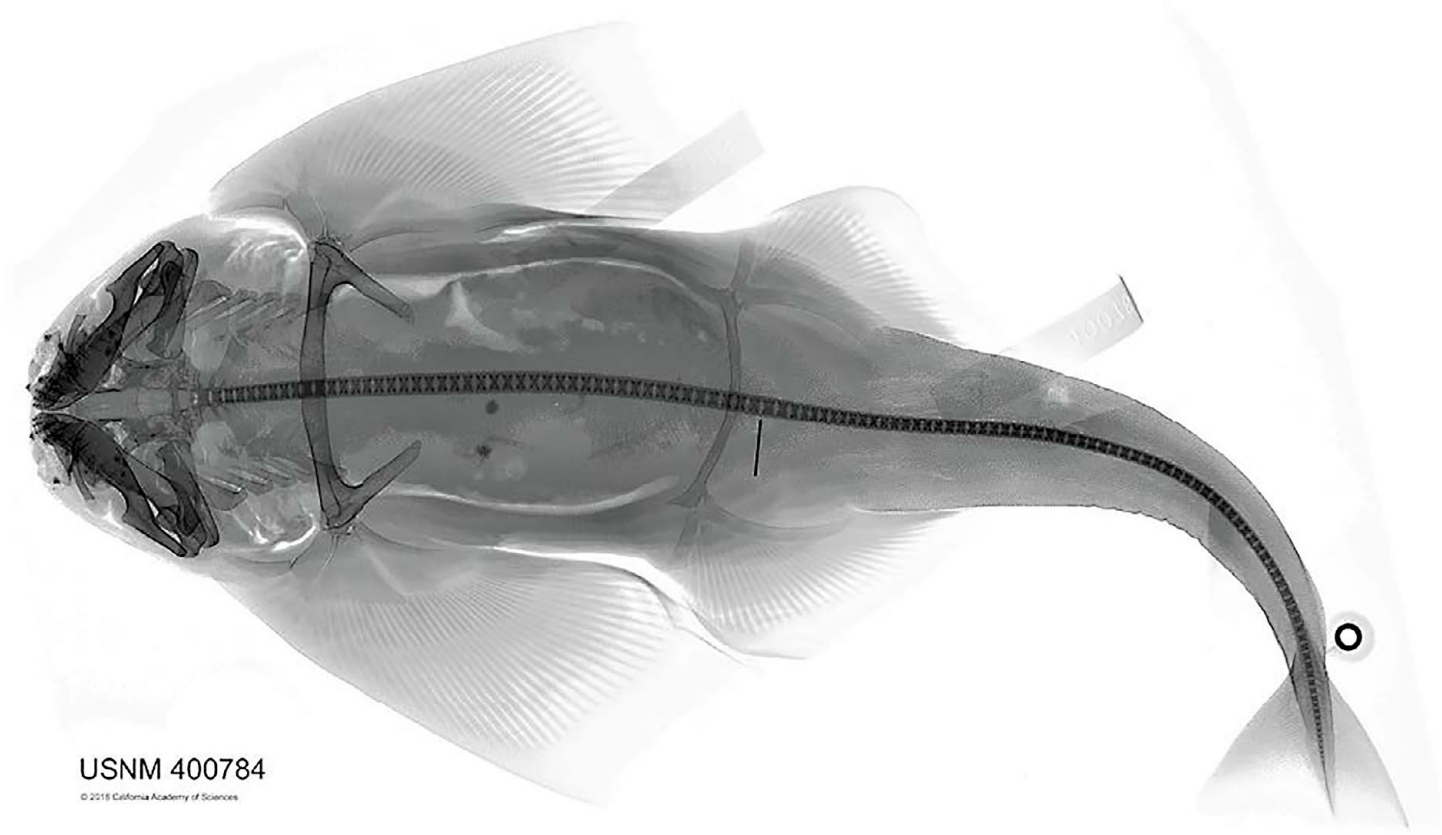


**Figure 5**. *Squatina mapama*, radiograph of holotype, USNM 400784, Caribbean Panama (J.D. Fong).

TABLE 1

Proportional measurements of type specimens of *Squatina mapama,* n. sp. as percentages of total length

| | holotype USNM 400784 | | paratype USNM 400796 | | | holotype USNM 400784 | | paratype USNM 400796 | |
|---|---|---|---|---|---|---|---|---|---|
| Total length (mm) | 400 | % TL | 325 | % TL | Total length (mm) | 400 | % TL | 325 | % TL |
| Precaudal length | 342.0 | 85.5 | 271.0 | 86.0 | Caudal peduncle height | 8.0 | 2.0 | 6.0 | 1.9 |
| Preorbital length | 12.0 | 3.0 | 11.0 | 3.5 | Caudal peduncle width | 14.0 | 3.5 | 11.0 | 3.5 |
| Prespiracle length | 33.0 | 8.3 | 28.0 | 8.9 | Pectoral fin span | 199.0 | 58.1 | 164.0 | 52.0 |
| Prebranchial length | 63.0 | 15.8 | 46.0 | 14.6 | Pectoral fin anterior margin | 118.0 | 29.5 | 88.0 | 27.9 |
| Head length | 66.0 | 16.5 | 55.0 | 17.5 | Pectoral fin length | 138.0 | 34.5 | 107.0 | 34.0 |
| Head width | 89.0 | 22.3 | 69.0 | 21.9 | Pectoral fin base | 43.0 | 10.8 | 33.0 | 10.5 |
| Prepectoral fin length | 79.0 | 19.8 | 61.0 | 19.4 | Pectoral fin height | 68.0 | 17.0 | 52.0 | 16.5 |
| Prepelvic fin length | 156.0 | 39.0 | 156.0 | 39.0 | Pectoral fin inner margin | 73.0 | 18.3 | 55.0 | 17.5 |
| Snout-vent length | 180.0 | 45.0 | 143.0 | 45.4 | Pelvic fin span | 124.0 | 31.0 | 97.0 | 30.7 |
| Pre 1st dorsal fin length | 257.0 | 64.3 | 205.0 | 65.1 | Pelvic fin posterior margin | 55.0 | 13.8 | 40.0 | 12.7 |
| Pre 2nd dorsal fin length | 298.0 | 74.5 | 233.0 | 74.0 | Pelvic fin length | 95.0 | 23.8 | 70.0 | 22.2 |
| Interdorsal space | 28.0 | 7.0 | 18.0 | 5.7 | Pelvic fin anterior margin | 50.0 | 12.5 | 35.0 | 11.1 |
| Dorsal caudal space | 32.0 | 8.0 | 26.0 | 8.3 | Pelvic fin base | 56.0 | 14.0 | 39.0 | 12.4 |
| Pectoral pelvic space | 42.0 | 10.5 | 39.0 | 12.4 | Pelvic fin height | 42.0 | 10.5 | 38.0 | 12.1 |
| Vent caudal length | 150.0 | 37.5 | 112.0 | 35.6 | Pelvic fin inner margin | 37.0 | 9.3 | 37.0 | 11.7 |
| Vent length | 8.0 | 2.0 | 6.0 | 1.9 | Pelvic fin posterior margin | 70.0 | 17.5 | 53.0 | 16.8 |
| Mouth length | 8.0 | 2.0 | 10.0 | 3.2 | First dorsal fin length | 29.0 | 7.2 | 20.0 | 6.3 |
| Mouth width | 42.0 | 10.5 | 38.0 | 12.1 | First dorsal fin anterior margin | 35.0 | 8.8 | 22.0 | 7.0 |
| Upper labial furrow | 18.0 | 4.5 | 14.0 | 4.4 | First dorsal fin base | 16.0 | 4.0 | 12.0 | 3.8 |
| Lower labial furrow | 15.0 | 3.8 | 10.0 | 3.2 | First dorsal fin height | 25.0 | 6.3 | 16.0 | 5.1 |
| Internarial width | 24.0 | 6.0 | 21.0 | 6.7 | First dorsal fin inner margin | 12.0 | 3.0 | 9.0 | 2.9 |
| Nostril width | 9.0 | 2.3 | 5.0 | 1.6 | First dorsal fin posterior margin | 19.0 | 4.8 | 15.0 | 4.8 |
| Anterior nasal flap | 9.0 | 2.3 | 9.0 | 2.9 | Second dorsal fin length | 27.0 | 6.8 | 19.0 | 6.0 |
| Upper lip arch width | 14.0 | 3.5 | 13.0 | 4.1 | Second dorsal fin anterior margin | 33.0 | 8.3 | 21.0 | 6.7 |
| Upper lip arch height | 6.0 | 1.5 | 4.0 | 1.3 | Second dorsal fin base | 15.0 | 3.8 | 10.0 | 3.2 |
| Eye horizontal diameter | 9.0 | 2.3 | 9.0 | 2.9 | Second dorsal fin height | 22.0 | 5.5 | 13.0 | 4.1 |
| Eye vertical diameter | 7.0 | 1.8 | 6.0 | 1.9 | Second dorsal fin inner margin | 11.0 | 2.8 | 8.0 | 2.5 |
| Interorbital width | 32.0 | 8.0 | 27.0 | 8.6 | Second dorsal fin posterior margin | 17.0 | 4.3 | 13.0 | 4.1 |
| Spiracle length | 9.0 | 2.3 | 7.0 | 2.2 | Caudal fin upper lobe length | 49.0 | 12.3 | 35.0 | 11.1 |
| Interspiracle width | 32.0 | 8.0 | 25.0 | 7.9 | Caudal fin ventral lobe length | 57.0 | 14.2 | 46.0 | 14.6 |
| Eye-spiracle length | 9.0 | 2.2 | 5.0 | 1.6 | Lower postventral caudal margin | 31.0 | 7.8 | 17.0 | 5.4 |
| Head height | 24.0 | 6.0 | 18.0 | 5.7 | Upper postventral caudal margin | 16.0 | 4.0 | 9.0 | 2.9 |
| Head width | 89.0 | 22.3 | 69.0 | 21.9 | Subterminal caudal fin margin | 15.0 | 3.8 | 10.0 | 3.2 |
| Trunk height | 31.0 | 7.8 | 23.0 | 7.3 | Pelvic girdle width | 80.0 | 20.0 | 63.0 | 20.0 |
| Trunk width | 78.0 | 19.5 | 57.0 | 18.1 | | | | | |

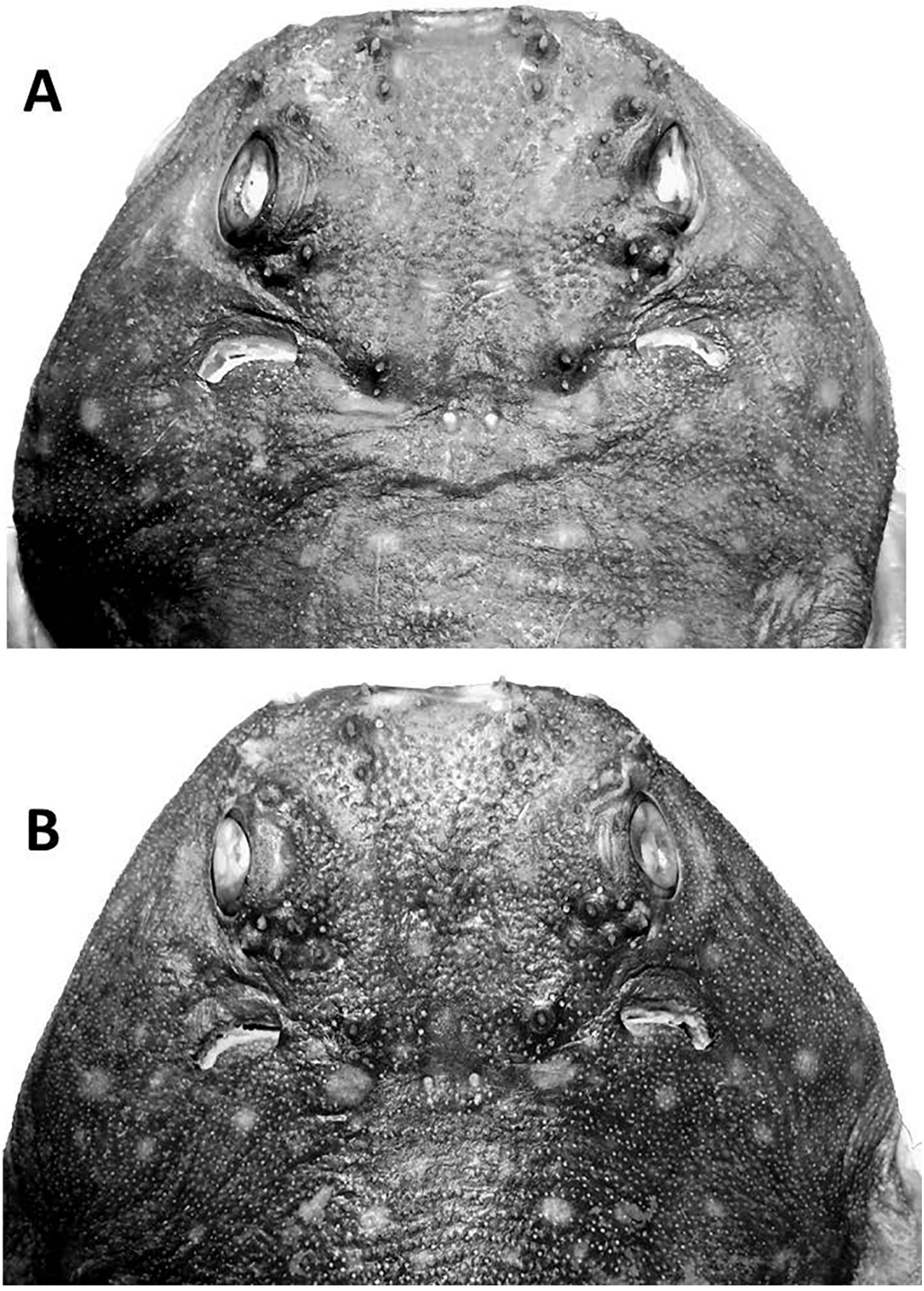


**Figure 6.** *Squatina mapama*, preserved, detail of dorsal head, holotype, USNM 400784, 400 mm TL male (A) and paratype, USNM 400796, 325 mm TL male (B), Caribbean Panama. Images are not to scale relative to each other (D.J. Long).

Total vertebrae 137; total precaudal vertebrae 105; monospondylous vertebrae 47; diplospondylous vertebrae to caudal-fin origin 32 or 33; diplosondylous precaudal vertebrae to first dorsal-fin origin 26 or 27.

Fine dermal denticles cover entire dorsum of body, absent on ventral surface except for a small patch on anterolateral edge of pectoral and pelvic fins; a single row of slightly enlarged denticles extends along midline of dorsum from just anterior of the posterior insertion of the pelvic fin to anterior base of first dorsal fin, continuing rearwards along dorsal ridge of tail between first and second dorsal fins, enlarged denticles narrowly triangular or slightly lenticular, with two short lateral ridges on either side of each denticle, terminating in a blunt point that is slightly raised, and base forming a thin, small, rounded shelf embedded in epidermis (Fig. 7); enlarged midline denticles are no more than 50% larger than adjacent denticles; enlarged dermal denticles on head 2 or 3 on upper edge of mouth above barbels, 1 or 2 anterior to orbit, 2–5 posterior to orbit, and one mesial to spiracle (Fig. 6).

Dentition is typical for *Squatina* (teeth show little variation between species): tooth bases are labiolingually narrow and mesodistally wide, teeth have short, narrow, vertical, awl-like cusps with a sharp apex recurved lingually, minor cutting edges lack serrations and have extremely reduced mesial and distal blades; dentition shows monognathic heterodonty with anterior teeth having slightly more erect cusps, with a gradual inclination of cusps in teeth distally; little perceptible dignathic heterodonty between teeth in upper and lower jaws. Both type specimens have 14 teeth in left and right upper and lower jaws with 2 or 3 functional series in each tooth row.

**Color of types.** (Figs. 1–4) Before preservation, body is a uniform pale brown to tan, with scattered, small (<1/3 eye size), round, darker-brown spots, larger along edge of head, on outer half of pectorals and base of pelvic fins; edges of pectoral and pelvic fins fade into a lighter brown with a whitish margin; a few indistinct spots on dorsal fins. After preservation, pale spots are also evident, but much less distinct than dark spots; dorsal surface is overall medium brown with small (<1/3 eye size), round, pale spots of varying sizes scattered evenly over head, body and pectoral and pelvic fins, no spots on dorsal and caudal fins; anterior edges of pectoral and pelvic fins with a whitish margin: ventral surface overall cream; anterior edges of pectoral fins with a grayish-brown mottling, and posterior edges of pectoral and pelvic fins with a light tan margin.

**Size.** Maximum total length is over 40 cm since both type specimens are immature males with undeveloped claspers.

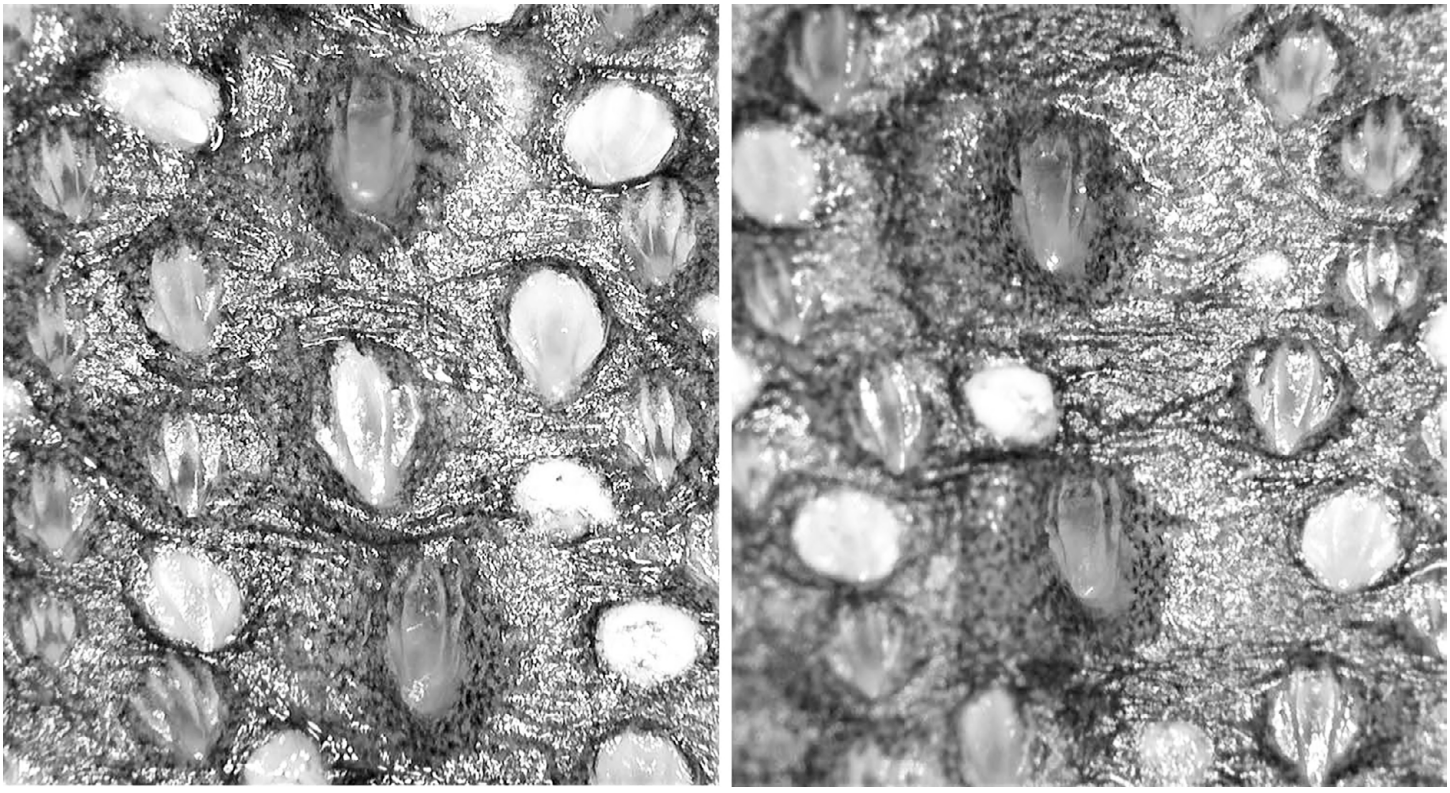

**Figure 7.** *Squatina mapama*, preserved, photomicrograph of dorsal-midline enlarged dermal denticles (central vertical row in each), holotype, USNM 400784, 400 mm TL male (left) and paratype, USNM 400796, 325 mm TL male (right), Caribbean Panama (D.J. Long).

TABLE 2

Meristic values for type specimens of *Squatina mapama,* n. sp.

| | holotype | paratype |
|---|---|---|
| | USNM 400784 | USNM 400796 |
| Total vertebrae | 137 | 137 |
| Monospondylous vertebrae | 47 | 47 |
| Diplospondylous vertebrae to D1 | 26 | 27 |
| Diplospondylous vertebrae to caudal origin | 58 | 57 |
| Caudal diplospondylous vertebrae | 32 | 33 |
| Propterygial radials of pectoral fin | 4 | 4 |
| Mesopterygial radials of pectoral fin | 13 | 13 |
| Metapterygial radials of pectoral fin | 21 | 20 |
| Radials of pelvic fin | 26 | 28 |
| Upper tooth counts | 14+14 | 14+14 |
| Lower tooth counts | 14+14 | 14+14 |

**Etymology.** The specific epithet mapama refers to the acronym MAPAMA, the Ministerio de Agricultura y Pesca, Alimentación y Medio Ambiente, which is the Spanish governmental organization that operates the R/V *Miguel Oliver*. This name recognizes the support of MAPAMA for the research cruises to Central and South America that facilitated the capture of this angelshark, and other new species of deepwater fishes on both sides of the Central American isthmus (Vázquez et al. 2015, Concha et al. 2016, Robertson et al. 2017). Suggested common name of Small-crested Angelshark or angelote de cresta pequeña is in reference to the short and narrow median line of small dermal denticles.

**Distribution.** Presently known only from the type location off Panama (Fig. 8).


**Figure 8**. Map of Panama in the southwestern Caribbean with the capture location by the R/V *Miguel Oliver* of the type specimens of *Squatina mapama* (MOC 11-1) and a specimen of S. david (MOC 11-31) off the western Caribbean coast of Panama.

**Comparisons.** These two new southwestern Caribbean *Squatina* specimens are both immature males, therefore they do not convey the total range of morphological characters within the species (e.g. due to individual variation, ontogenetic development, or sexual dimorphism). However, they still can be unequivocally separated from all previously described northwestern Atlantic angelshark species through a combination of coloration, meristic and morphometric features, as well as by genetic comparisons. Although *Squatina mapama* n. sp., resembles the only other known species of angelshark from the Atlantic waters of Panama, *S. david* (Fig. 9), several morphological and color differences are present that allow their separation.

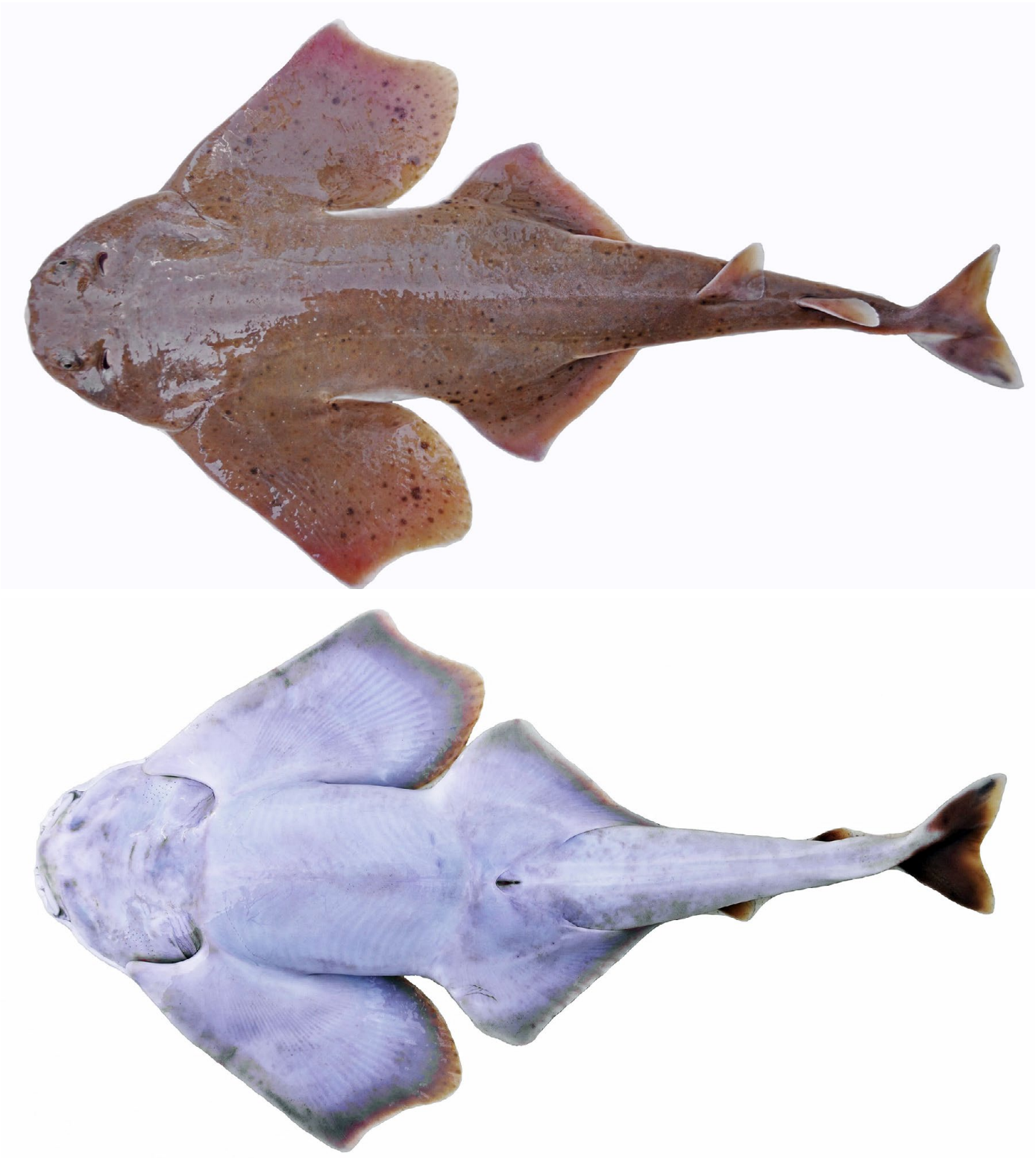

**Figure 9.** *Squatina david*, fresh specimen, immature female 503 mm TL, USNM 400759, Caribbean Panama (D.R. Robertson).

First, *S. david* lacks a line of enlarged denticles along the dorsal midline, whereas a line of slightly enlarged denticles runs along the dorsal midline in *S. mapama* (Fig. 7). In *S. dumeril*, a single row of enlarged dermal denticles extends along the dorsal midline from the nuchal region of the head to the caudal peduncle, while in *S. mapama* the row of denticles begins just anterior of the posterior insertion of the pelvic fin and terminates at the anterior base of the first dorsal fin, then continues on the dorsal midline between the first and second dorsal fins. Although Vaz & de Carvalho (2013) described immature *Squatina occulta* Vooren & da Silva, 1991 as having a similar dorsal midline row of slightly enlarged denticles, Acero et al. (2016) noted no such midline row of denticles in either immature or mature specimens of *S. david*. Since no mature adult specimens of *S. mapama* are available, it is unclear whether this trait may vary ontogenetically in this species. In *S. occulta*, the subdermal base of the dorsal midline dermal denticles are much wider than in *S. mapama* and have a more elongated and acute apex.

In addition, there are several differences in the nasal barbels (Fig. 3). In *S. david*, the nasal flap is a rounded triangle pointing downward, without fringes or serrations, while in *S. mapama* the nasal flap is more squared ventrally and has a short, fine serration or fringe. Furthermore, in *S. david* both the inner and outer nasal barbels are elongated, rod-like, and lack any fringe or cirri, while in *S. mapama* the inner and outer nasal barbels are shorter, flattened with a rounded margin, and bear a margin of fine, short serrations.

*Squatina david* has a smooth oval patch between the eyes above the midpoint of the mouth, where *S. mapama* has a few coarse denticles (Fig. 6). Finally, *S. david* has pronounced papillae along the inner margin of the spiracles, which are very reduced in *S. mapama* (Fig 6).

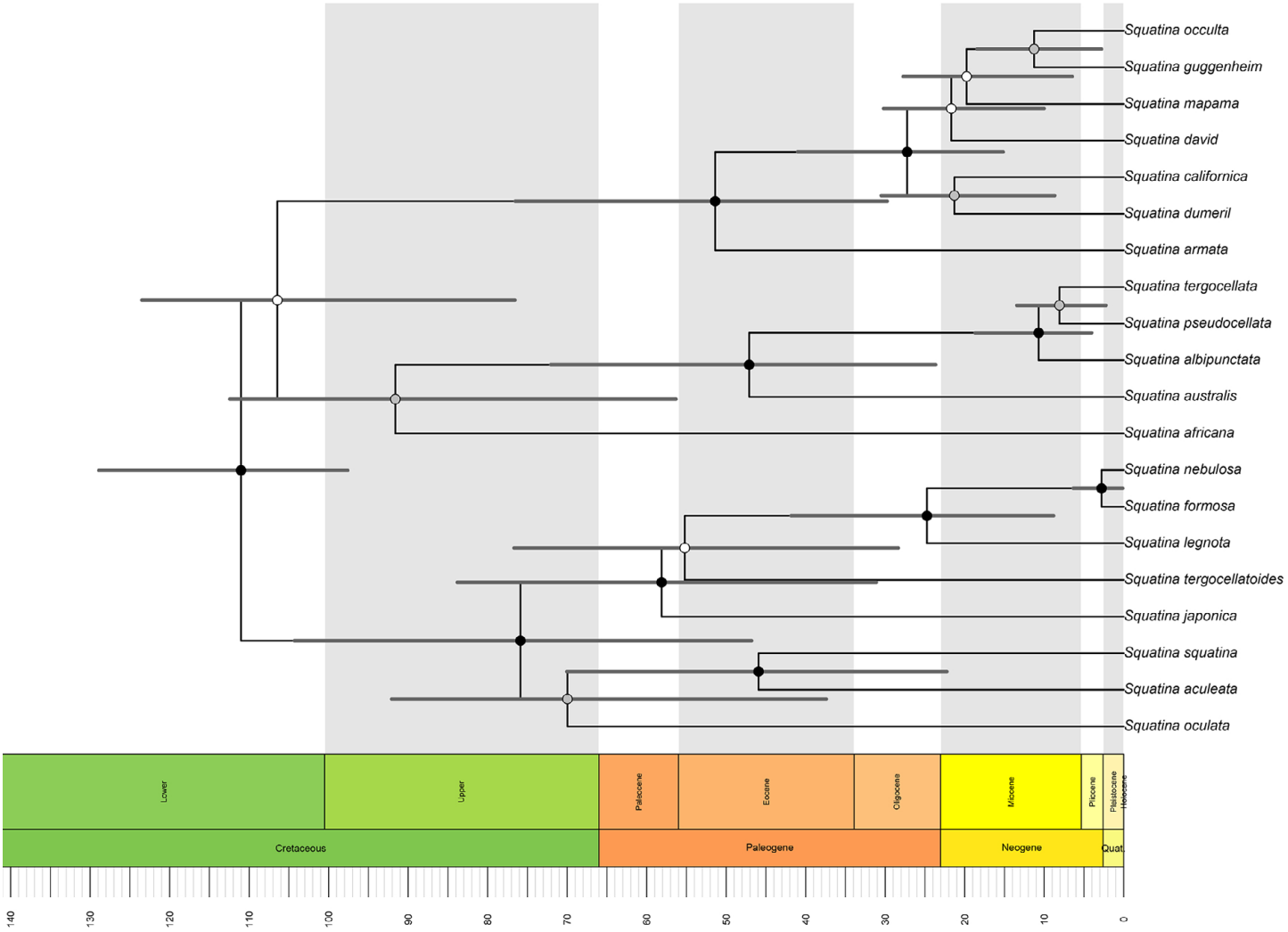


**Figure 10.** Time-calibrated phylogeny of the family Squatinidae and taxonomic relationships of *Squatina mapama*. Gray bars represent credibility intervals (95% highest posterior density) for the ages of the nodes. Circles on nodes depict support values, whereas black circles correspond to posterior probabilities higher than 0.95; grey circles are bonded to values between 0.95 and 0.90; white circles represent all those support values lower than 0.90.

Additional differences in morphometrics further distinguish *S. mapama* from *S. david*. Acero et al. (2016) in their description of *S. david*, included measurements from immature paratypes (one male and two females, <500 mm), which allow us to better compare our similarly sized immature *S. mapama* specimens. *S. mapama* has a greater pectoral-fin span (52.0–58.1% TL) than *S. david* (44.2–45.3% TL); a wider pelvic-fin span (30.7% TL) vs, 12.9–13.5% TL; a shorter pre-pectoral-fin length (19.4–19.8% TL) vs. 20.8–21.6% TL; a greater trunk width (18.1–19.5% TL) vs. 13.5–15.7% TL; a shorter head length (16.5–17.5% TL) vs. 20.2–23.2% TL; a greater spiracle length (2.2–2.3% TL) vs. 0.9–1.2% TL; a slightly narrower eye-to-spiracle length (1.6–2.2% TL) vs. 2.3–3.3% TL; a narrower mouth (10.5–12.1% TL) vs. 13.1–13.4% TL; a wider nostril (1.6–2.3% TL) vs. 0.7–0.9% TL; a shorter snout-to-pectoral distance (19.4–19.8% of TL) vs. 20.8–21.6% TL; a wider dorsal-to-caudal space (8.0–8.3% TL) vs. 6.9-7.2% TL; and, finally, considerably longer pectoral-fin inner margins (17.5–18.3% TL) vs. 6.7–8.2% TL.

**Remarks.** The paratype specimen of *Squatina mapama* was previously figured as *S. david* in Vaz & Carvalho, 2018 (144–159, Fig. 10b), but we establish it here as the new species *S. mapama*.

The R/V *Miguel Oliver* expedition did capture a single immature female specimen of *S. david* (Fig. 9: USNM 400759) from a depth of 252–289 m off the western Caribbean coast of Panama (9.27°, -81.69°; Fig. 8). This represents the westernmost extension of the range of *S. david*, as the previous known western limit of *S. david* was off central Colombia at Bocas de Ceniza (Acero et al. 2016), 750 km east of locality MOC11-31. From these limited collections the ranges of *S. mapama* and *S. david* overlap by at least 500 km.

If there are any doubts about morphological and meristic traits establishing *S. mapama* as a valid new species, molecular analyses reveal *S. mapama* to be genetically distinct from *S. david* and all other northwestern Atlantic *Squatina* species. Our phylogenetic reconstruction with the 19 included *Squatina* species (Fig. 10) yielded the same topological results as those of Stelbrink et al. (2010) and Acero et al. (2016). In the new phylogenetic construction presented here, *S. mapama* is nested in the same clade as both *S. david* and the southwestern Atlantic species *Squatina occulta* and *Squatina guggenheim* Marini, 1936. However, weak support of branches within that clade precludes a conclusion as to whether *S. mapama* is sister to *S. david* or to the branch containing *S. occulta* and S. *guggenheim*.

Based on the available sequences of mtDNA COI, the genetic divergence between *S. mapama* and the other *Squatina* species ranges from 1.01% from *S. occulta* (minimum interspecific distance or nearest-neighbor distance; mean distance =1.1%) up to 10.98% (mean distance =10.78%) from *Squatina japonica* Bleeker, 1858. The nearest-neighbor divergence between *S. mapama* and the sympatric *S. david* is 1.79% (mean distance =1.81%). For the entire genus, the mean distance among individuals within a species (0.1–0.3%) is far less than the mean genetic distance between species (7.52%). However, the "barcode gap" within the genus, i.e. the difference between the maximum intraspecific distance and the minimum interspecific distance, is not achieved, with the maximum intraspecific distance (1.15%) overlapping the minimum interspecific distance (only 0.37% between S. *guggenheim* and *S. occulta*). The mean intraspecific distance is consistent with that (0.39%) presented by Ward et al. (2005) for Australian sharks and rays. The degree of COI divergence and species differentiation has been previously assessed for other marine fishes, the average divergence within and among species (and higher taxa) varies a lot from group to group. For example, Ward et al. (2005) reported a mean difference between species within a genus of 9.93% (vs. 7.52% for *Squatina*) but a range of 0 to 20.63% (with 0 for species pairs that share haplotypes and may prove to be the same species and the maximum for genera that may be broad and paraphyletic).

The fact that *S. mapama* is more divergent from *S. david* than from the two congeners from Argentina and Brazil (*S. guggenheim* and S. *occulta*), along with the uncertainty of its phylogenetic placement in between these lineages, supports the validity of this new species. The alternative that three of the four species are invalid due to paraphyly (since *S. mapama* is nested in between them), leaving all populations synonymized as S. *guggenheim* (the oldest name and thus having priority) is difficult to justify. It would result in a species with heterogeneity in phenotype as well as genotype: Cañedo-Apolaya et al. (2021) used four different MOTU-delimitation analyses and those were consistent with four *Squatina* species. Furthermore, the potential presence of additional species lineages between the four branches in the neighbor-joining tree in BOLD would also suggest paraphyly, making anything other than a full separation of species in the complex unworkable.

TABLE 3

Accession numbers for *Squatina* and comparison sequences from Genbank used for the time-calibrated phylogeny

| Species | COI Genbank accession number | 16 S Genbank accession number | Species | COI Genbank accession number | 16 S Genbank accession number |
|---|---|---|---|---|---|
| *Squalus cubensis* | FN431670 | FN431789 | *S. formosa* | FN431741 | FN431860 |
| *Squatina aculeata* | FN431671 | FN431790 | *S. guggenheim* | FN431746 | FN431865 |
| *S. africana* | FN431673 | FN431792 | *S. japonica* | FN431750 | FN431869 |
| *S. albipunctata* | FN431689 | FN431809 | *S. legnota* | FN431751 | FN431870 |
| *S. armata* | FN431694 | FN431814 | *S. mapama* | MT048390 | pending |
| *S. australis* | FN431697 | FN431817 | *S. mapama* | MT048391 | pending |
| *S. californica* | FN431729 | FN431849 | *S. occulta* | FN431752 | FN431871 |
| *S. californica* | FN431703 | FN431823 | *S. oculata* | FN431754 | FN431873 |
| *S. david* | KX162720 | KX162723 | *S. pseudocellata* | FN431755 | FN431874 |
| *S. david* | KX162719 | KX162722 | *S. squatina* | FN431760 | FN431879 |
| *S. david* | KX162721 | KX162724 | *S. tergocellata* | FN431763 | FN431882 |
| *S. dumeril* | FN431734 | FN431853 | *S. tergocellatoides* | FN431766 | FN431885 |
| *S. dumeril* | FN431739 | FN431858 | | | |

We also note that the sequences of *S. dumeril* used in this phylogenetic reconstruction came from individuals collected on both the Atlantic and Gulf of Mexico coasts of the USA, and there are no differences between the sequences of fish in those two areas, indicating that they constitute a single panmictic population. Unfortunately, molecular data are not yet available for the two putative species thought to be endemic to the Gulf of Mexico (*S. mexicana* and *S. heteroptera*), which could help settle the debate about their validity [see Ebert et al. (2013), Vaz & Carvalho (2013, 2018), and Fricke et al. (2019)], while also refining the phylogenetic reconstruction of the genus and strengthening the temporal evolutionary scenarios.

Our time-calibrated phylogeny recovered much older ages than those presented in Acero et al. (2016), placing the 95 HPD credible interval of the time of divergence of *S. mapama* from other members of its clade between 28 and 8 mya, somewhere between the late Oligocene to the late Miocene periods (Fig. 10). The fossil record generally supports this scenario. Earliest records of *Squatina* from the southern Atlantic are from the Eocene of the Antarctic Peninsula (Long 1992, Engelbrecht et al. 2017), from the Miocene of southeastern Argentina (Arratia & Cione 1996, Cabrera et al. 2012), late Miocene to early Pliocene of the Caribbean (northeastern Venezuela, Aguilera & de Aguilera 2001), and the northeastern Gulf of Mexico (southwestern Florida) in the Miocene and Pliocene (Pérez & Marks 2017). While *Squatina* teeth do not show species-specific features and thus cannot show speciation or changes in lineages over time (Cappetta 2012, Englebrecht et al. 2017), the long fossil presence of *Squatina* in this region supports the overall temporal and biogeographical framework presented by the genetic data.

**Comparative material.** *Squatina david*: USNM 400759, immature female, 503 mm TL, Panama, Caribbean coast, Comarca de Ngobe-Bugle, off Bocas del Toro, 9.27˚, -81.69˚, 252–289 m, trawl, station MOC11-31, D.R. Robertson & C. Castillo, 12 January 2011.

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FIS/15/04/2011(91) Vol. VIII, of 31 January 2011 from the Belize Fisheries Department. For organizing loans, handling of specimens, and research facilities we thank D. Catania, J. Fong, and M. Hoang of the Department of Ichthyology at the California Academy of Sciences, and C. Baldwin, D. Pitassy, and J. Williams at the Section of Fishes, National Museum of Natural History, Smithsonian. H.B. Constable of the University of California, Riverside, provided assistance with figures and comments on the manuscript. Two anonymous referees provided useful reviews of the manuscript.

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