A New Guitarfish of the Genus *Pseudobatos* (Batoidea: Rhinobatidae) with Key to the Guitarfishes of the Gulf of California

Kelsi M. Rutledge¹

A new guitarfish of the genus *Pseudobatos* is described based on 82 specimens obtained from the Gulf of California. Sixty-three morphometric measurements were taken on all specimens, and on ten specimens from each of three congeners. A principal component analysis and linear discriminant analysis were performed on these morphometric data for discrimination. The new species (~685 mm TL) is most similar to *Pseudobatos productus* but differs in having a narrower maximum disc width (30–35% vs. 36–38% TL), shorter distance from nostril to disc margin (2.8–4.0% vs. 4.2–5.2% TL), narrower disc width at anterior orbit (12–19% vs. 20–22% TL), and a narrower tip of snout width (3% vs. 4–6% TL). The species is also less densely scaled between the orbits and has less pronounced rostral thorns than *Pseudobatos productus*. A key to the guitarfishes of the Gulf of California is also provided.

Se describe una nueva especie de guitarra en el género *Pseudobatos* basado en 82 especímenes obtenidos del Golfo de California. Se tomaron sesenta y tres mediciones morfométricas en cada espécimen y en diez especímenes de cada uno de los tres congéneres. En estos datos morfométricos, se realizaron análisis de componentes principales y discriminante lineal para discriminación. Esta nueva especie (~685 mm TL) es más similar a *Pseudobatos productus*, pero se diferencia por tener un ancho máximo de disco más estrecho (30–35% vs. 36–38% TL), una distancia más corta desde la fosa nasal al margen del disco (2.8–4.0% vs. 4.2–5.2% TL), un ancho de disco más estrecho en la órbita anterior (12–19% vs. 20–22% TL) y el ancho de la punta de la nariz más estrecha (3% vs. 4–6% TL). Esta especie también tiene una escala menos densa entre las órbitas, y espinas rostrales menos pronunciadas, en comparación con *Pseudobatos productus*. Además, se provee una clave para las guitarras del Golfo de California.

HE genus *Pseudobatos* recently was recognized as a monophyletic group of amphi-American guitarfishes (Last et al., 2016a). This genus was found to be highly divergent from the rest of its family based on mitochondrial sequence data (Last et al., 2016a, 2016b) and comprises seven species, five of which are found in the eastern Pacific: *Pseudobatos glaucostigmus*, *P. leucorhynchus*, *P. planiceps*, *P. prahli*, and *P. productus*. Of these five, three are found in the Gulf of California:, *P. glaucostigmus*, *P. leucorhynchus*, and *P. productus*.

Ichthyologist Boyd Walker, UCLA, and colleagues caught 80 individuals of guitarfish during various collecting trips through the 1940s and 1950s in the Gulf of California (San Felipe to Loreto). In Walker's field notebooks, he recognized these specimens as a possible new species but never examined them for quantifiable differences.

Herein, a morphological analysis of these specimens is presented and a new species of *Pseudobatos* is described. The new species is distinguished from its sympatric congeners by several characters including: a narrower maximum disc width, shorter distance from nostril to disc margin, narrower disc width at anterior orbit, narrower tip of snout width, a light brown snout and body free of spots, very small or absent thorns around orbits and snout, and fewer scales between the orbits. A key to the guitarfishes of the Gulf of California is included.

MATERIALS AND METHODS

Morphometric measures follow those developed at a workshop on morphometric techniques developed for the family Rhinobatidae (Last et al., 2004, 2014, 2016a). Refinements were made to the existing convention (snout length, spiracle length, preoral length, mouth width, and pelvic-fin insertion to dorsal-fin origin), as outlined in Last et al. (2004). Measurements following Last (2004) of the nasal region were

also included as additional characters to define the nasal flaps. Dorsal-fin measurements follow the requiem shark drawn in Compagno (1984). "Tip of snout width" was created to distinguish snout shape between *P. buthi,* new species, and *P. productus,* and it is defined as: "horizontal distance across tip of snout measured directly behind nasal tassel." If nasal tassel was absent, distance was measured as the "narrowest region of snout." Lengths are presented as total length (TL) throughout.

Sixty-three morphometric characters were measured on all specimens using digital calipers (Table 1), and measurements were taken to the nearest 0.1 mm. Measurements were also taken on ten individuals of the sympatric P. glaucostigmus, P. leucorhynchus, and P. productus. In the case of a range extension, pictures of P. prahli and P. planiceps (found in South and Central America) were examined. Due to the distinctive coloration (numerous spots) and morphology (rostral cartilages and spiracle folds) of these two species, the case of a range extension was confidently dismissed (Robertson and Allen, 2015). Radiographs were also performed on nine specimens (SIO 15-477 [formerly UCLA W49-122]) at the Natural History Museum of Los Angeles County. Meristics were taken from radiographs, including vertebral counts and pectoral- and pelvic-fin radials of nine individuals (SIO 15-477 [formerly UCLA W49-122]; 4 females, 5 males). Institutional abbreviations follow Sabaj (2019).

To determine distinct morphological differences between the new species and the other three species occurring in the Gulf of California, a principal component analysis (PCA) and a linear discriminant analysis (LDA) were performed. The PCA was performed on the 63 morphometric characters used to distinguish guitarfishes (Last et al., 2004). An LDA was performed on the 63 morphometric characters to determine which measurements are most informative in distinguishing species. An additional LDA was performed on the characters

Department of Ecology and Evolutionary Biology, University of California Los Angeles, Los Angeles, California 90095; Email: kelsimarie7@g.ucla.edu.

Table 1. Morphometric measures as percentages of total length for the type specimens of P. buthi, new species (n = 80), and associated congeners (n = 10).

Character				P. Dutni, new	shecies		P. productus	crus	σ.	glancostigmus	ugnius		r. ieucornynciius	vncnus	
mm (%) 4711 383.6 2159-6851 — 2169-4087 — 2385-4680 — 2065-5468 mm (%) 4710 383.6 2159-6851 1 2169-382 380-435 311 319-393 310 319-393 310 319-393 310	Character		Allotype	Paratype range			ınge			nge	×	SD	Range		SD
(%) 319 349 297-350 349 359 440 13 344 397-350 440 13 349 397-350 440 13 349 399-350 440 13 349 399-350 440 13 358-356 410 16 391-465 440 14 340 40	Total length (mm)	471.1	383.6	215.9–685.1	1	- 216.9	-408.7	-	- 238.5	-468	I	I	- 1	I	-
(%) 280 256-353 297 17 417-69 46 12 388-456 419 16 391-46 5 oder (%) 283 256-353 297 17 417-69 46 12 388-456 419 16 391-46 5 oder (%) 283 256-353 297 17 417-69 46 12 5 0.0 10 255-208 279 15 255-230 oder (%) 155 17 10 144-191 16 6 12 155-171 20 10 255-208 279 15 262-310 oder (%) 283 21 2 2 2 3 1 26-49 16 6 15 10 10 255-208 279 15 262-310 oder (%) 42 47 47 40-62 2 2 3 16-29 2 2 3 14-21 3 6 3 13-166 15 10 10 10 10 10 10 10 10 10 10 10 10 10	Disc width—maximum (%)	31.9	34.9	29.7-35.0	33.9 1.	4 35.8	3-38.2	36.4 1.	1 32.4	-35.6	34.1	1.0		34.3	8.
(%) 280 295 26-353 297 17 28-3-19 306 10 252-298 280 19 4 262-351 ode (%) 55 170 140-189 55 170	Disc length (%)	41.0	44.0	39.0-47.0	43.2 1.	7 41.7	-46.9	44.6 1.	2 38.8	-43.6	41.9	1.6	39.1–46.5	41.7	2.5
1,000, 1	Head length—dorsal (%)	28.0	30.5	25.6-33.3			-31.9		25.5	-29.8	28.0	1.4	26.2-31.1	27.8	1.6
ocker (%) 155 170 144-191 166 12 155-777 165 06 188-166 156 156 150 140-189 are	Head length—ventral (%)	28.3	29.7	26.2-33.5			31.5		25.2	-29.8	27.9	1.5	26.2-32.0	28.0	1.9
25 23 16-249 36 03 34-45 36 02 31-21 136 03 28-43 angle (%) 44 47 47 45 49 04 34-56 49 05 34-56 49 05 34-56 49 05 34-56 49 05 34-56 49 05 34-56 49 05 34-56 49 05 34-56 49 05 34-56 49 05 34-57 45 19 02 18-24 9 05 34-56 49 05 34-56 49 05 34-56 49 05 34-56 19 02 18-24 9 05 34-56 49 05 34-56 49 05 34-56 49 05 34-56 49 05 34-56 49 05 34-56 49 05 34-56 49 05 34-56 49 05 34-56 49 05 34-56 49 05 34-56 49 05 34-56 49 05 34-56 49 05 34-56 49 05 34-56 19 02 13 05-720 19 05 19 02 1	Snout length—presocket (%)	15.5	17.0	14.4–19.1			-17.7			-16.6	15.6	0.1	14.0-18.9	16.0	1.6
neght (%) 4 4 4 4 0-62	Orbit diameter (%)	3.5	3.1	2.6-4.4			4.3			-4.1	3.6	0.3	2.8-4.3	3.3 (7.4
44 47 40-62 49 64 39-52 45 04 39-51 42 49 47 40-62 49 60 34-56 45 04 39-51 58 62 56-70 62 03 62-71 67 02 41-61 88 13 153-20 18 16 18 16 18 16 18 19 18 19 18 19 18 19 18 19 18 18 19 18 19 18 19 18 19 18 19 18 19 18 19 18 19 18 19 18 19 18	Spiracle length (%)	2.2	2.3	1.6–2.9			3-2.8			-2.1	1.9	0.2	1.8–2.4	2.0	0.7
4.2 4.9 4.1-5.1 4.6 0.3 4.4-6.9 4.9 0.5 4.4-6.9 4.9 0.5 4.4-6.9 4.9 0.5 4.4-6.9 4.9 0.5 4.4-6.7 0.0 4.4-6.9 4.9 0.5 6.7.7 0.6 0.0 0.6 0.5 6.4-7.9 7.3 0.4 6.6 0.6 0.5 6.4-7.9 7.3 0.4 6.6 0.6 0.5 6.4-7.9 7.3 0.4 6.6 0.7 0.7 <td>Orbit and spiracle length (%)</td> <td>4.4</td> <td>4.7</td> <td>4.0-6.2</td> <td></td> <td></td> <td>-5.6</td> <td></td> <td></td> <td>-5.2</td> <td>4.5</td> <td>0.4</td> <td>3.9-5.1</td> <td></td> <td>7.4</td>	Orbit and spiracle length (%)	4.4	4.7	4.0-6.2			-5.6			-5.2	4.5	0.4	3.9-5.1		7.4
5.8 6.2 56-7.0 6.2 0.3 6.2-7.1 6.7 0.2 41-6.1 56 1.5 6.0-7.3 17.7 180 16-7.2 6.6 0.3 6.2-7.1 6.7 6.6 6.6 0.3 6.2-7.1 6.7 6.6 6.6 0.3 6.2-7.2 1.8 1.6 1.9 1.6 1.2 1.7 1.9 1.5-1.8 1.6 1.1 1.4 1.9 1.6 1.2 1.4 1.0 1.2 1.2 1.4 1.0 1.2 1.4 1.2 1.4 1.0 1.1 1.2 1.4 1.0 1.1 1.2 1.4 1.0 1.1 1.4 1.1 1.3 1.1 1.4 1.1 1.3 1.1 1.4 1.1 1.1 1.3 1.1 1.4 1.0 1.1 1.1 1.1 1.1 1.1 1.1 1.1 1.1 1.1 1.1 1.1 1.2 1.2 1.4 0.0 1.4 1.1 <	Interorbital width (%)	4.2	4.9	4.1–5.1			6.9			-4.5	4.4	0.1	4.3-4.9		0.2
177 190 164-220 189 1.3 173-202 192 08 161-198 180 13 163-201 146 56 56 7.9 6.0 6.47.9 7.3 0.4 6.0 6.0 6.47.9 7.3 0.4 6.0 6.0 1.0	Interspiracular width (%)	5.8	6.2	5.6-7.0	_		7.1			-6.1	5.6	7:	6.0-7.3	6.4 (7.4
62 68 56,79 66 67 64,79 73 04 60-68 65 63 62,77 40 159 13,1-180 156 11 145-190 158 10 129-154 146 09 150-172 40 13 35,4-49 13 35,4-49 44 00 22,1-23 18 02 11-115 11 16 01 11-115 13 01 11-117 14 02 14-20 15 01 11-115 13 01 11-115 13 01 11-115 14 01 11-115 13 01 11-115 13 01 11-115 13 01 11-115 13 01 11-115 13 01 11-115 13 01 11-115 13 01 11-115 13 01 11-115 13 01 11-115 13 01 11-115 13 01 11-115 13 01 11-115	Preoral length (%)	17.7	19.0	16.4–22.0			-20.5			-19.8	18.0	1.3	16.3-20.1	17.5	1.2
146 159 131-180 156 1.1 145-190 158 10 129-154 146 09 130-172 4,0 3.9 4,0 3 38-49 4,4 0.3 39-48 4,5 0.2 130-172 1,1 1,3 1,5-2.3 1,8 0.2 1,8-2.4 2,1 0.2 1,4-1.7 1.0 0.2 1,2-2.5 2,1 0.2 22-2.9 1.1 1,1-1.5 1.3 0.2 1,4-1.7 1.0 0.2 1,2-2.5 2,1 0.2 22-2.9 0.2 1,2-2.5 2,1 0.2 22-2.9 0.2 1,4-1.7 1.0 0.2 1,4-1.7 0.9 0.1 0.0 0.1 0.0 </td <td>Mouth width (%)</td> <td>6.2</td> <td>8.9</td> <td>5.6-7.9</td> <td>_</td> <td></td> <td>6.7-</td> <td>_</td> <td></td> <td>-6.8</td> <td>6.5</td> <td>0.3</td> <td>6.2-7.7</td> <td>6.7</td> <td>0.5</td>	Mouth width (%)	6.2	8.9	5.6-7.9	_		6.7-	_		-6.8	6.5	0.3	6.2-7.7	6.7	0.5
4.0 3.9 3.5-4.6 4.0 0.2 3.8-4.9 4.4 0.3 3.9-4.8 4.5 0.2 4.3-5.3 1.1 1.3 1.1-1.7 1.4 0.1 1.1-1.5 1.3 0.1 1.1-1.7 1.1 1.3 1.1-1.7 1.4 0.2 1.1-1.7 1.6 0.1 1.1-1.7 1.6 0.1 1.1-1.7 1.1 1.3 1.2-2.7 1.6 0.2 1.3-2.5 2.1 0.2 2.2-2.9 2.1 2.3 1.2 2.3 0.2 2.1-2.7 2.4 0.2 2.0-2.6 0.2 0.1 0.1 0.1 1.4-1.9 1.6 0.1 1.4-1.9 1.6 0.2 1.4-1.7 1.6 0.1 1.4-1.9 1.6 0.2 1.0-2.5 2.1 0.2 0.0 0.1 0.0 0.1 0.0 0.1 0.0-2.2 1.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2	Prenarial distance (%)	14.6	15.9	13.1-18.0			0.61-			-15.4	14.6	6.0	13.0-17.2	14.6	4.
1.1 1.3 1.1-1.7 1.4 0.1 1.1-1.5 1.3 0.1 1.1-1.5 1.3 0.1 1.1-1.5 1.3 0.1 1.1-1.5 1.3 0.1 1.1-1.5 1.3 0.1 1.1-1.5 1.3 0.1 1.1-1.5 1.3 0.1 1.1-1.5 1.3 0.1 1.1-1.5 1.3 0.1 1.1-1.5 1.3 0.1 1.1-1.5 1.3 0.1 1.1-1.5 1.3 0.1 1.2-2.9 1.2 1.2 2.2 2.2 2.2 2.2 2.2 2.0 2.0 1.4-1.7 1.6 0.2 1.4-1.7 1.6 0.2 1.4-1.7 1.6 0.2 1.4-1.7 1.6 0.2 1.4-1.7 1.6 0.2 1.4-1.7 1.6 0.2 1.4-1.7 1.6 0.2 1.6-1.7 1.6 0.2 1.6-1.7 1.6 0.2 1.6-1.1 1.6 0.2 1.6-1.1 1.6 0.2 1.6-1.1 1.6 0.2 1.6-1.1 1.6 0.2 1.6 0.2<	Nostril length (%)	4.0	3.9	3.5-4.6			6-4.9			-4.8	4.3	0.2	4.3-5.3		0.3
1.7 1.9 1.5-2.3 1.8 0.2 1.8-2.4 2.1 0.2 1.9-2.5 2.1 0.2 2.2-2.9 1.5 1.4 1.3-2.0 1.6 0.2 1.4-1.7 1.6 0.1 0.1 0.1 0.1 0.2 0.1 0.1 0.2 <td>Anterior aperture—width (%)</td> <td>1.1</td> <td>1.3</td> <td>1.1–1.7</td> <td></td> <td></td> <td>-1.5</td> <td></td> <td></td> <td>-1.5</td> <td>1.3</td> <td>0.1</td> <td>1.4-1.7</td> <td></td> <td>0.1</td>	Anterior aperture—width (%)	1.1	1.3	1.1–1.7			-1.5			-1.5	1.3	0.1	1.4-1.7		0.1
15 14 13-20 16 02 14-17 16 01 14-19 16 02 14-17 16 01 14-19 16 02 14-17 16 01 14-19 02-22 02-22 02 02-22 02 02 02-23 02 02-11 08 01 07-12 10 01 07-12 09 01 07-22 1.0 09 01 07-22 1.0 09 01 07-22 1.0 09 01 07-22 1.0 09 01 07-22 1.0 09 01 07-22 1.0 09 01 07-22 1.0 09 01 07-22 1.0 09 01 07-22 1.0 09 01 07-22 1.1 04 079-11 09 01 07-22 1.1 04 079-11 09 01 07-12 09 01 07-12 09 01 07-12 07 079-11 09	Anterior nasal flap—base length (%)	1.7	1.9	1.5–2.3			5-2.4			-2.5	2.1	0.2	2.2–2.9		0.2
2.1 2.3 19-2.7 2.3 2.1-2.7 2.4 0.2 20-2.6 2.3 0.2 20-3.2 0.5 0.9 0.5-1.1 0.8 0.1 0.7-1.2 0.9 0.1 0.6-0.1 0.8 0.2 0.4-0.9 1.8 1.6 1.0-2.2 1.6 0.3 1.5-1.8 1.6 0.1 0.7-1.2 9.7 9.9 9.0-11.7 10.2 0.6 99-11.4 10.8 0.4 0.6-1.0 0.7-1.2 0.9 0.7-1.2 0.9 0.7-1.2 0.9 0.7-1.2 0.9 0.7-1.2 0.9 0.7-1.2 0.9 0.7-1.2 0.9 0.7-1.2 0.9 0.7-1.2 0.9 0.7-1.1 0.0 0.7-1.2 0.9 0.7-1.1 0.0 0.7-1.2 0.9 0.7-1.2 0.9 0.7-1.1 0.9 0.7-1.2 0.9 0.7-1.1 0.0 0.7-1.2 0.9 0.7-1.2 0.0 0.7-1.1 0.0 0.7-1.1 0.0 0.7-1.1 0.0 0.7-1.1 0.0	Anterior nasal flap—width (%)	1.5	1.4	1.3-2.0			-2.0			-1.7	1.6	0.1	1.4–1.9	7	0.2
0.5 0.9 0.5-1.1 0.8 0.1 0.7-12 0.9 0.1 0.7-13 0.9 0.1 0.7-13 0.9 0.1 0.7-23 1.6 0.3 1.5-1.8 1.6 0.1 0.7-23 9.7 9.0 0.7-2.3 1.1 0.4 0.79-1.1 0.9 0.1 0.7-23 1.6 0.3 1.5-1.8 1.6 0.1 1.6-2.3 0.7 0.7-1.3 0.7 0.7-1.3 0.7 0.7-1.3 0.7 0.7-1.3 0.7 0.7-1.1 0.9 0.1 0.7-1.3 0.7 0.7-1.3 0.7 0.7-1.3 0.7 0.7-1.3 0.7 0.7-1.3 0.7 0.7-1.3 0.7 0.7-1.3 0.7 0.7-1.3 0.7 0.7-1.3 0.7-1.3 0.7 0.7-1.3 0.7-1.3 0.7 0.7-1.3 0.7 0.7-1.3 0.7 0.7-1.3 0.7 0.7-1.4 0.8 0.7-2.3 0.7 0.7-2.3 0.7 0.7-1.1 0.7 0.7 0.7-1.1 0.7 0.7-1.1 0.7	Posterolateral nasal flap—total length (%)	2.1	2.3	1.9–2.7	2.3 0.	2 2.1	-2.7			-2.6	2.3	0.2	2.0-3.2		0.4
1.8 1.6 1.0-2.2 1.7 0.2 1.0-2.2 1.6 0.3 1.5-1.8 1.6 0.1 1.6-2.3 0.9 1.0 0.7-1.3 0.9 0.1 0.7-2.3 1.1 0.4 0.79-1.1 0.9 0.1 0.7-2.3 1.1 0.4 0.79-1.1 0.9 0.1 0.7-1.2 0.9 0.1 0.7-2.3 1.1 0.4 0.79-1.1 0.9 0.1 0.7-2.3 1.1 0.4 0.7-2.5 3.2 0.2-3.5 3.2 0.2-3.5 4.4 4.0-6.3 4.8 0.4 4.6-6.4 5.3 0.4 4.2-5.2 4.8 0.3 3.0-1.3 <td< td=""><td>Posterolateral nasal flap—width (%)</td><td>0.5</td><td>0.9</td><td>0.5-1.1</td><td></td><td></td><td>′-1.2</td><td></td><td></td><td>-1:1</td><td>0.8</td><td>0.2</td><td>0.4-0.9</td><td>_</td><td>0.2</td></td<>	Posterolateral nasal flap—width (%)	0.5	0.9	0.5-1.1			′-1.2			-1:1	0.8	0.2	0.4-0.9	_	0.2
0.9 1.0 0.7-1.3 0.9 0.1 0.7-2.3 1.1 0.4 0.79-1.1 0.9 0.1 0.7-1.2 9.7 9.9 9.0-11.7 10.2 0.6 9.9-11.4 10.8 0.4 9.6-10.9 10.4 0.2 0.2	Posterior nasal flap—base length (%)	1.8	1.6	1.0-2.2)-2.2			-1.8	1.6	0.1	1.6–2.3		0.2
9.7 9.9 90-11.7 10.2 0.6 9.9-11.4 10.8 0.4 9.6-10.9 10.4 10.2-15.0 2.5 2.8 2.5-3.8 3.1 0.2 2.9-3.6 3.3 0.2 2.7-3.5 3.2 0.3 3.0-4.3 4.4 4.0-6.3 4.8 0.4 4.6-6.4 5.3 0.4 4.2-5.2 4.8 0.3 3.3-5.8 3.0-4.3 4.8 4.0-6.3 4.8 0.4 4.6-5.4 4.8 0.3 2.7-4.1 3.0 3.3-4.4 4.4 4.0-6.3 1.7 0.2 1.5-2.1 1.8 0.2 1.4-1.9 1.7 0.2 1.5-2.3 1.5 0.7 12.6-14.6 13.9 0.7 12.8-15.5 9.1 9.9 8.8-12.7 9.9 0.6 10.0-11.8 11.0 0.5 9.0-10.8 10.0 0.5 9.2-11.1 1.5 15.8 14.1-18.0 15.7 0.8 14.6-17.5 16.1 0.8 15.3-17.4 15.8 0.8 14.8-17.1 10.9 10.3 7.9-11.7 10.1 0.7 8.9-11.4 10.6 0.7 10.1-11.3 10.3 0.4 10.2-11.5 6.3 6.3 6.3-6.9 6.4 0.3 6.0-80 6.4 0.3 6.0-80 6.4 0.3 6.0-80 6.9 6.4 0.3 6.0-80 6.9 6.4 0.3 6.2-7.5 6.9 0.3 6.4-7.6 6.7 0.3 6.2-7.5 6.9 0.3 6.4-7.6 6.7 0.3 6.2-7.5 6.9 0.3 6.4-7.6 6.7 0.3 6.2-7.5 6.9 0.3 6.4-7.6 6.7 0.3 6.2-7.5 6.9 0.3 6.4-7.6 6.7 0.3 6.2-7.5 6.9 0.3 6.4-7.6 6.7 0.3 6.2-7.5 6.9 0.3 6.4-7.6 6.7 0.3 6.2-7.5 6.9 0.3 6.4-7.6 6.7 0.3 6.2-7.5 6.9 0.3 6.4-7.6 6.7 0.3 6.2-7.5 6.9 0.3 6.4-7.6 6.7 0.3 6.2-7.5 6.9 0.3 6.4-7.6 6.7 0.3 6.2-7.5 6.9 0.3 6.4-7.6 6.7 0.3 6.2-7.5 6.9 0.3 6.4-7.6 6.7 0.3 6.2-7.5 6.9 0.3 6.4-7.6 6.7 0.3 6.2-7.5 6.9 0.3 6.4-7.6 6.7 0.3 6.2-7.5 6.9 0.3 6.4-7.6 6.7 0.3 6.2-8.0 7.0 0.5 6.8-8.0 7.0 0.5 6.8-8.0 7.0 0.5 6.8-8.0 7.0 0.5 6.8-8.0 7.0 0.5 6.8-8.0 7.0 0.5 6.8-8.0 7.0 0.5 6.8-8.0 7.0 0.5 6.8-8.0 7.0 0.5 6.8-8.0 7.0 0.5 6.8-8.0 7.0 0.5 6.8-8.0 7.0 0.5 6.5-8.0 7.3 0.3 6.2-7.5 6.9 0.3 7.1-7.7 7.7 7.3 0.2 6.9-8.1 7.4 0.3 7.1-7.7 7.5 0.5 6.9-8.1 7.4 0.3 7.1-7.7 7.5 0.5 6.9-8.1 7.2 0.5 0.2 4.7-5.4 4.8 0.2 4.7-5.2 5.1 0.5 4.7-5.4 4.8 0.2 4.7-5.2 5.1 0.5 4.7-5.4 4.8 0.2 4.7-5.2 5.0 0.5 4.7-5.4 4.8 0.2 4.7-5.2 5.1 0.5 4.7-5.2 5.0 0.2 4.7-5.4 4.8 0.2 4.7-5.2 5.1 0.5 4.7-5.2 5.0 0.2 4.7-5.4 4.8 0.2 4.7-5.5 5.0 0.2 4.7-5.4 4.8 0.2 4.7-5.5 5.0 0.2 4.7-5.4 4.8 0.2 4.7-5.5 5.0 0.2 4.7-5.4 4.8 0.2 4.7-5.5 5.0 0.2 4.7-5.4 4.8 0.2 4.7-5.5 5.0 0.2 4.7-5.4 4.8 0.2 4.7-5.5 5.0 0.2 4.7-5.4 4.8 0.2 4.7-5.5 5.0 0.2 4.7-5.4 4.8 0.2 4.7-5.2 5.1 0.2 4.7-5.2 5.1 0.2 4.7-5.2 5.1 0.2 4.7-5.2 5.1 0.2 4.7-5.2 5.2 0.2 0.2 4.7-5.2 5.3 4.7-5.2 5.3	Posterior nasal flap—width (%)	6.0	1.0	0.7-1.3			/–2.3				6.0	0.1	0.7-1.2		0.7
2.5 2.8 2.5-3.8 3.1 0.2 2.9-3.6 3.5 0.2 2.7-3.5 3.2 0.3 3.0-4.3 4.4 4.0-6.5 4.8 0.4 4.6-6.4 5.3 0.4 4.2-5.2 4.8 0.3 2.5-4.1 3.7 0.4 4.6-6.4 5.3 0.4 4.2-5.2 4.8 0.3 2.5-4.1 3.7 0.4 4.6-6.4 5.3 0.4 4.2-5.2 4.8 0.3 2.5-4.1 3.5-5.8 3.3-5.8 1.6 1.9 1.6 1.0 1.6 1.7 1.0 1.7 0.2 1.5-2.1 1.8 0.2 2.7-3.5 3.2 0.3 3.2-3.8 1.6 1.9 1.4 1.6 0.7 1.26-14.6 1.3 0.7 1.28-15.2 1.5 1.4 1.0 0.2 1.2-11.6 1.0 1.1 0.7 1.4 1.0 0.7 1.1 1.0 0.7 1.1 0.0 0.2 1.1 1.0 1.2 1.2-1.	Distance across anterior nasal apertures (%)	9.7	6.6	9.0–11.7			9-11.4			-10.9	10.4	4.0	10.2-13.0		0.0
4.4 4.0-6.3 4.8 0.4 4.6-6.4 5.3 0.4 4.2-5.2 4.8 0.3 2.5-81 3.5-8 3.5-8.8 3.2 3.8 2.8-4.0 3.7 0.4 4.4-5.2 4.8 0.3 2.5-4.1 3.6 0.5 2.4-4.4 1.6 1.9 1.3-2.0 1.7 0.2 1.5-2.1 1.8 0.2 1.4-1.9 1.7 0.2 1.5-2.3 1.5 1.4 1.0 0.2 1.5-2.1 1.8 0.2 1.5-3.1 3.6 0.5 2.4-4.4 1.5 1.4 0.0 1.7 1.2 1.2 1.7 0.2 1.5-2.3 1.5 1.4 0.0 1.4 1.0 0.7 1.2 1.7 0.2 1.5-2.3 1.5 1.4 0.0 1.4 1.5 0.7 1.2 1.2 1.2 1.2 1.2 1.2 1.2 1.2 1.2 1.2 1.2 1.2 1.2 1.2 1.2	Internanal distance—minimum (%)	2.5	2.8	2.5–3.8			9-3.6			-3.5	3.2	0.3	3.0–4.3	_	0.5
5.2 5.8 2.8-4.0 3.7 0.4 4.4-5.2 4.8 0.5 2.5-4.1 3.6 0.5 2.4-4.4 1.6 1.9 1.3-2.0 1.7 0.2 1.5-2.1 1.8 0.2 1.4-1.9 1.7 0.2 1.5-2.3 13.0 1.3 1.6-1.6.6 14.1 0.9 14.1-16.7 15.5 0.7 12.6-14.6 13.9 0.7 12.8-15.5 15.0 1.6 1.7 0.5 10.0-11.8 11.0 0.5 9.2-11.1 12.8-15.5 15.6 1.5 1.4 1.6 0.7 10.1-17.4 15.8 0.8 14.8-17.1 10.8 0.9 10.2-11.1 10.6 0.8 10.2-11.1 10.6 0.7 10.1-11.2 10.2-11.1 10.2-11.1 10.2-11.1 10.2-11.1 10.2-11.1 10.2-11.1 10.2-11.1 10.2-11.1 10.2-11.1 10.2-11.1 10.2-11.1 10.2-11.1 10.2-11.1 10.2-11.1 10.2-11.1 10.2-11.1 10.2-11.1 10.2-11.1 10.2-11.2 <	Distance between anterior nasal flaps (%)	4.4	4.4	4.0–6.3			6.4			-5.2	8.4	0.3	3.3–5.8	_	7.0
1.6 1.9 1.5-2.0 1.7 0.2 1.5-2.1 1.8 0.2 1.4-1.9 1.7 0.2 1.5-2.3 13.0 14.3 11.6-16.6 14.1 0.9 14.1-16.7 15.5 0.7 12.6-14.6 13.9 0.7 12.8-15.5 9.1 14.5 15.6 17 0.5 90-10.8 10.0 0.5 92-11.1 15.6 15.8 15.4 16.1 0.8 15.3-17.4 15.8 0.8 14.8-17.1 10.9 10.3 16.1 0.8 15.3-17.4 15.8 0.8 14.8-17.1 10.9 10.3 16.1 0.8 15.3-17.4 15.8 0.8 14.8-17.1 10.9 10.3 14.6-17.5 16.1 0.8 15.3-17.4 15.8 0.8 10.2 11.8-17.1 10.9 10.3 14.6-17.5 16.1 0.8 15.3-17.4 15.8 0.8 10.2 10.11.1 10.9 10.3 10.4 10.5 <	Distance from nostril to disc margin (%)	3.2	2.8	2.8–4.0			5.2			-4.1	3.6	0.5	2.4-4.4	3.3	9.0
13.0 14.3 11.6-16.6 14.1 0.9 14.1-16.7 15.5 0.7 12.6-14.6 13.9 0.7 12.8-15.5 9.1 9.9 8.8-12.7 9.9 0.6 10.0-11.8 11.0 0.5 90-10.8 10.0 0.5 92-11.1 15.6 15.8 14.1-18.0 15.7 0.8 14.6-17.5 16.1 0.8 15.3-17.4 15.8 0.8 14.8-17.1 10.9 10.3 7.9-11.7 10.1 0.7 8.9-11.4 10.6 0.7 10.1-11.3 10.3 0.4 10.2-11.5 6.3 6.3 6.3 6.0-6.9 6.4 0.5 6.0-8.0 6.0-8.0 6.0-8.0 6.0-8.0 8.0 9.2 5.9-10.6 8.5 0.8 7.0-9.6 8.4 0.7 8.1-10.5 8.6 0.7 7.2-10.1 8.0 5.9-10.6 8.5 0.8 7.0-9.6 8.4 0.7 8.1-10.5 8.6 0.7 0.1-10.5 8.6 0.7 0.1-10.5 8.6 0.7 0.1-10.5 8.6 0.7 0.1 0.1 <t< td=""><td>Third gill opening—width (%)</td><td>1.6</td><td>0.1</td><td>1.3-2.0</td><td></td><td></td><td>2.1</td><td></td><td></td><td>-1.9</td><td>1.7</td><td>0.2</td><td>1.5–2.3</td><td>0.8</td><td>0.3</td></t<>	Third gill opening—width (%)	1.6	0.1	1.3-2.0			2.1			-1.9	1.7	0.2	1.5–2.3	0.8	0.3
9.1 9.9 8.8–12.7 9.9 0.6 10.0–11.8 11.0 0.5 9.0–10.8 10.0 0.5 9.2–11.1 15.6 15.8 14.1–18.0 15.7 0.8 14.6–17.5 16.1 0.8 15.3–17.4 15.8 0.8 14.8–17.1 10.9 10.3 7.9–11.7 10.1 0.7 8.9–11.4 10.6 0.7 10.1–11.3 10.3 0.4 10.2–11.5 6.3 6.3 4.9–7.4 6.3 0.4 6.2–7.3 6.8 0.3 6.0–6.9 6.4 0.3 6.0–8.0 8.0 8.0 9.2 5.9–10.6 8.5 0.8 7.0–9.6 8.4 0.7 8.1–10.5 8.6 0.7 7.2–10.1 8.6 7.9 5.8–10.7 7.5 0.9 5.7–9.0 7.8 0.9 6.9–8.2 7.2 0.5 6.4–9.8 6.9 6.9 6.9 6.9 6.9 0.3 6.4–7.6 6.7 0.3 6.7–7.4 9.2 9.1 8.2–10.6 9.3 0.5 7.7–10.1 9.1 0.5 8.9–10.0 9.0 0.4 4.1–10.5 7.2 6.6 5.4–8.7 7.0 0.6 5.8–8.4 6.8 0.6 6.8–8.6 7.0 0.5 6.8–8.0 4.6 5.4–8.7 7.0 0.6 5.8–8.4 6.8 0.6 6.8–8.6 7.0 0.5 6.8–8.0 4.6 5.9–5.9 4.5 0.3 4.0–4.7 4.4 0.2 4.0–4.7 4.5 0.2 3.5–7.4 4.5 0.3 6.5–8.0 7.3 0.3 6.9–8.1 7.4 0.3 7.1–7.7 7.3 0.2 6.9–8.1 7.4 0.3 7.1–7.7 7.3 0.2 6.9–8.1 7.4 0.3 7.1–7.7 7.3 0.2 6.9–8.1 7.4 0.3 7.1–7.7 7.3 0.2 6.9–8.1 7.1 7.6 6.5–8.0 7.3 0.3 6.9–8.1 7.4 0.3 7.1–7.7 7.3 0.5 6.3–8.3 7.2 7.0 0.3 6.3–8.3 7.1–7.7 7.3 0.3 6.3–8.3 7.1–7.7 7.3 0.3 6.3–8.3 7.1–7.7 7.3 0.2 6.3–8.3 7.2 7.1 7.2 7.3 0.3 6.3–8.3 7.1–7.7 7.3 0.3 6.3–8.3 7.1–7.7 7.3 0.3 6.3–8.3 7.1–7.7 7.3 0.3 6.3–8.3 7.1–7.7 7.3 0.3 6.3–8.3 7.1–7.7 7.3 0.3 6.3–8.3 7.1–7.7 7.3 0.3 6.3–8.3 7.1–7.7 7.3 0.3 0.3 6.3–8.3 7.1–7.7 7.3 0.3 0.3 6.3–8.3 7.1–7.7 7.3 0.3 0.3 6.3–8.3 7.1–7.7 7.3 0.3 0.3 6.3–8.3 7.1–7.7 7.3 0.3 0.3 6.3–8.3 7.1–7.7 7.3 0.3 0.3 6.3–8.3 7.1–7.7 7.3 0.3 0.3 6.3–8.3 7.1–7.7 7.3 0.3 0.3 6.3–8.3 7.1–7.7 7.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0	Distance between first gill openings (%)	13.0	14.3	11.6–16.6			-16.7			-14.6	13.9	0.7	12.8–15.5	13.7 (9.9
15.6 15.8 14.1-18.0 15.7 0.8 14.6-17.5 16.1 0.8 15.5-17.4 15.8 0.8 14.8-17.1 10.9 10.3 7.9-11.7 10.1 0.7 8.9-11.4 10.6 0.7 10.1-11.3 10.3 0.4 10.2-11.5 6.3 6.4-6.9 6.4 0.3 6.0-8.0 6.4 0.3 6.0-8.0 6.3 6.	Distance between fifth gill openings (%)	ب ا ت	ນ ເ ວັດ	8.8-12.7		•) - [.3 1 .3			-10.8	0.01	0.5	9.2-11.1	ω. i ω. i	9.6
10.3 10.3 7.9-11.7 10.1 0.7 8.9-11.4 10.6 0.7 10.1-11.5 10.3 0.4 10.2-11.5 6.3 6.3 6.3 0.4 6.2-7.3 6.8 0.3 6.0-6.9 6.4 0.3 6.0-8.0 8.0 9.2 5.9-10.6 8.5 0.8 7.0-9.6 8.4 0.7 8.1-10.5 8.6 0.7 7.2-10.1 8.6 7.9 5.9-10.6 8.5 0.9 5.7-9.0 7.8 0.9 6.9-8.2 7.2 0.5 6.4-9.8 8.9 6.9 6.9 0.3 6.4-7.6 6.7 7.2-10.1 9.1 0.5 6.4-9.8 6.7-7.4 9.2 9.1 8.2-10.6 9.3 0.5 7.7-10.1 9.1 0.5 8.9-10.0 9.0 0.4 4.1-10.5 7.2 6.6 5.4-8.7 7.0 0.6 5.8-8.4 6.8 0.6 6.8-8.6 7.0 0.5 6.8-8.0 4.6 5.9-5.9 4.5 0.3 4.0-4.7 4.4 0.2 4.0-4.7 4.4 0.2	Pelvic Tin—length (%)	15.6	7.0	14.1–18.0		_	J-1/.5			17.4		χ. ·	14.8-17.1	15.9	Σ. α
8.0 9.2 5.9–10.6 8.5 0.8 7.0–9.6 8.4 0.7 81–10.5 8.6 0.7 7.2–10.1 8.6 0.7 7.2–10.1 8.6 0.7 7.2–10.1 8.6 0.7 7.2–10.1 8.6 0.7 7.2–10.1 8.6 0.7 7.2–10.1 8.2–10.6 8.5 0.8 7.0–9.6 8.4 0.7 81–10.5 8.6 0.7 7.2–10.1 8.2–10.6 9.3 0.5 7.7–10.1 9.1 0.5 8.9–10.0 9.0 0.4 4.1–10.5 7.2 0.5 6.4–9.8 6.9 0.3 6.4–7.6 6.7 0.3 6.7–7.4 4.6 9.2 0.3 6.4–7.6 6.7 0.3 6.7–7.4 4.9 0.2 7.7–10.1 9.1 0.5 8.9–10.0 9.0 0.4 4.1–10.5 7.2 0.6 5.8–8.4 6.8 0.6 6.8–8.6 7.0 0.5 6.8–8.0 4.6 3.9–5.9 4.5 0.3 4.0–4.7 4.4 0.2 4.0–4.7 4.5 0.2 3.5–7.4 4.5 0.3 2.1–2.8 2.4 0.3 2.1–2.8 2.4 0.3 2.1–2.8 2.4 0.3 2.1–2.8 2.4 0.3 2.1–2.8 2.4 0.3 2.1–2.8 2.4 0.3 2.1–2.1 7.1 7.6 6.5–8.0 7.3 0.3 6.9–8.1 7.4 0.3 7.1–7.7 7.3 0.2 6.9–8.1 8.7 9.3 4.5–10.3 9.1 0.8 8.4–9.9 9.3 0.3 8.7–10.0 9.0 0.4 7.9–11.7 7.2 7.0 4.7–8.3 6.9 0.6 6.3–7.4 7.0 0.3 5.6–7.9 6.7 0.6 6.3–8.3 5.2 5.3 4.6–7.5 5.3 4.6–7.5 5.1 0.5 4.7–5.3 5.0 0.2 4.7–5.4 4.8 0.2 4.3–5.2	Pelvic fin—anterior margin length (%)		10.5	/.9-11./			7 7 7			5.11.5	5.01	4.0	0.2-11.5	0.1	4.0
8.6 7.9 5.2 10.0 0.0 5.7-9.0 7.8 0.9 6.9-8.2 7.2 0.5 6.4-9.8 8.6 6.9 0.3 6.4-7.6 6.7 0.3 6.2-7.5 6.9 0.3 6.4-7.6 6.7 0.3 6.4-9.8 6.7-7.4 6.9 0.3 6.4-7.6 6.7 0.3 6.7-7.4 6.9 0.3 6.4-7.6 6.7 0.3 6.7-7.4 6.9 0.3 6.4-7.6 6.7 0.3 6.7-7.4 6.9 0.3 6.4-7.6 6.7 0.3 6.7-7.4 6.9 0.3 6.4-7.6 6.7 0.3 6.7-7.4 6.9 0.3 6.4-9.8 6.8 0.6 6.8-8.6 7.0 0.5 6.8-8.0 4.1-10.5 6.8-8.0 7.0 0.5 6.8-8.0 7.0 0.5 6.8-8.0 7.0 0.5 6.8-8.0 7.0 0.5 6.8-8.0 7.0 0.5 6.8-8.0 7.0 0.5 6.8-8.0 7.0 0.5 6.8-8.0 7.1 7.6 6.5-8.0 7.3 0.3 6.9-8.1 7.4 0.3 7.1-7.7 7.3 0.2 6.9-8.1 7.4 0.3 7.1-7.7 7.3 0.2 6.9-8.1 7.4 0.3 7.1-7.7 7.3 0.2 6.9-8.1 7.4 0.3 7.1-7.7 7.3 0.2 6.9-8.1 7.2 7.0 4.7-8.3 6.9 0.6 6.3-7.4 7.0 0.3 5.6-7.9 6.7 0.6 6.3-8.3 5.2 5.3 4.6-7.5 5.1 0.5 4.7-5.3 5.0 0.2 4.7-5.4 4.8 0.2 4.3-5.2	Pelvic fin—base length (%)	n ⊂	0.0	4.9-17.4 7.9-10.6			5.7			0.9 10 万	ο α τ. α))))	7.2–10.1	ς α	ρα
6.9 6.9 6.9 6.4-7.9 7.0 0.3 6.2-7.5 6.9 0.3 6.4-7.6 6.7 0.3 6.7-7.4 6.9 0.3 6.4-7.6 6.7 0.3 6.7-7.4 6.9 0.3 6.4-7.6 6.7 0.3 6.7-7.4 6.9 0.3 6.4-7.6 6.7 0.3 6.7-7.4 6.9 0.3 6.4-7.6 6.7 0.3 6.7-7.4 6.9 0.3 6.4-7.6 6.7 0.3 6.7-7.4 6.9 0.3 6.4-7.6 6.7 0.3 6.7-7.4 6.9 0.3 6.8-8.6 7.0 0.4 4.1-10.5 6.8-8.0 7.0 0.6 5.8-8.4 6.8 0.6 6.8-8.6 7.0 0.5 6.8-8.0 7.0 0.5 6.8-8.0 7.0 0.5 6.8-8.0 7.0 0.5 6.9-8.1 7.4 0.2 7.1-2.8 2.4 0.3 2.1-2.8 2.4 0.3 2.1-3.1 7.1 7.6 6.5-8.0 7.3 0.3 6.9-8.1 7.4 0.3 7.1-7.7 7.3 0.2 6.9-8.1 7.4 0.3 7.1-7.7 7.3 0.2 6.9-8.1 7.4 0.3 7.1-7.7 7.3 0.2 6.9-8.1 7.2 7.0 4.7-8.3 6.9 0.6 6.3-7.4 7.0 0.3 5.6-7.9 6.7 0.6 6.3-8.3 5.2 5.3 4.6-7.5 5.1 0.5 4.7-5.3 5.0 0.2 4.7-5.4 4.8 0.2 4.3-5.2	Pelvic fin—inner margin length (%)) w	7.0	5.8-10.7			0.6-				7.0	, C	6.4-9.8	. c	2 -
9.2 9.1 8.2–10.6 9.3 0.5 7.7–10.1 9.1 0.5 8.9–10.0 9.0 0.4 4.1–10.5 7.7–10.1 9.1 0.5 6.8–8.6 7.0 0.5 6.8–8.0 4.1–10.5 7.7–10.1 9.1 0.5 8.9–10.0 9.0 0.4 4.1–10.5 6.8–8.0 4.6 4.6 5.9–5.9 4.5 0.3 4.0–4.7 4.4 0.2 4.0–4.7 4.5 0.2 5.5–7.4 4.5 0.2 2.0–3.0 2.4 0.3 2.1–2.8 2.4 0.3 2.1–3.1 7.1 7.6 6.5–8.0 7.3 0.3 6.9–8.1 7.4 0.3 7.1–7.7 7.3 0.2 6.9–8.1 8.7 9.3 4.5–10.3 9.1 0.8 8.4–9.9 9.3 0.3 8.7–10.0 9.0 0.4 7.9–11.7 7.2 7.0 4.7–8.3 6.9 0.6 6.3–7.4 7.0 0.3 5.6–7.9 6.7 0.6 6.3–8.3 5.2 5.3 4.6–7.5 5.1 0.5 4.7–5.3 5.0 0.2 4.7–5.4 4.8 0.2 4.3–5.2	First dorsal fin—length (%)	0 0	6.9	6.4–7.9			7.5			-7.6 -7.6	6.7	0.3	6.7-7.4	6.9	2
7.2 6.6 5.4-8.7 7.0 0.6 5.8-8.4 6.8 0.6 6.8-8.6 7.0 0.5 6.8-8.0 4.6 4.6 3.9-5.9 4.5 0.3 4.0-4.7 4.4 0.2 4.0-4.7 4.5 0.2 3.5-7.4 2.3 2.2 1.9-2.8 2.4 0.2 2.0-3.0 2.4 0.3 2.1-2.8 2.4 0.3 2.1-3.1 7.1 7.6 6.5-8.0 7.3 0.3 6.9-8.1 7.4 0.3 7.1-7.7 7.3 0.2 6.9-8.1 8.7 9.3 4.5-10.3 9.1 0.8 8.4-9.9 9.3 0.3 8.7-10.0 9.0 0.4 7.9-11.7 7.2 7.0 4.7-8.3 6.9 0.6 6.3-7.4 7.0 0.3 5.6-7.9 6.7 0.6 6.3-8.3 5.2 5.3 4.6-7.5 5.0 0.2 4.7-5.4 4.8 0.2 4.3-5.2	First dorsal fin—anterior margin length (%)	9.2	9.1	8.2-10.6			/-10.1			-10.0	9.0	0.4	4.1–10.5	9.5	8.
4.6 4.6 5.9-5.9 4.5 0.3 4.0-4.7 4.4 0.2 4.0-4.7 4.5 0.2 5.7.4 2.3 2.2 1.9-2.8 2.4 0.2 2.0-3.0 2.4 0.3 2.1-2.8 2.4 0.3 2.1-3.1 7.1 7.6 6.5-8.0 7.3 0.3 6.9-8.1 7.4 0.3 7.1-7.7 7.3 0.2 6.9-8.1 8.7 9.3 4.5-10.3 9.1 0.8 8.4-9.9 9.3 0.3 8.7-10.0 9.0 0.4 7.9-11.7 7.2 7.0 4.7-8.3 6.9 0.6 6.3-7.4 7.0 0.3 5.6-7.9 6.7 0.6 6.3-8.3 5.2 5.3 4.6-7.5 5.1 0.5 4.7-5.4 4.8 0.2 4.3-5.2	First dorsal fin—height (%)	7.2	9.9	5.4-8.7			3-8.4			-8.6	7.0	0.5	6.8-8.0	7.5 (7.4
2.3 2.2 1.9-2.8 2.4 0.2 2.0-3.0 2.4 0.3 2.1-2.8 2.4 0.3 2.1-2.8 2.4 0.3 2.1-2.8 2.4 0.3 2.1-2.8 2.4 0.3 2.1-2.8 2.4 0.3 2.1-2.8 2.4 0.2 6.9-8.1 7.1 7.6 6.5-8.0 7.3 0.3 6.9-8.1 7.4 0.3 7.1-7.7 7.3 0.2 6.9-8.1 8.7 9.3 4.5-10.3 9.1 0.8 8.4-9.9 9.3 0.3 8.7-10.0 9.0 0.4 7.9-7.9 7.2 7.0 4.7-8.3 6.9 0.6 6.3-7.4 7.0 0.3 5.6-7.9 6.7 0.6 6.3-7.4 5.2 5.3 4.6-7.5 5.1 0.5 4.7-5.3 5.0 0.2 4.7-5.4 4.8 0.2 4.3-	First dorsal fin—base length (%)	4.6	4.6	3.9–5.9			7.4-0			-4.7	4.5	0.2	3.5-7.4	4.5	Ξ:
7.1 7.6 6.5-8.0 7.3 0.3 6.9-8.1 7.4 0.3 7.1-7.7 7.3 0.2 6.9-8.7 9.3 0.3 8.7-10.0 9.0 0.4 7.9-8.7 7.0 0.3 8.7-10.0 9.0 0.4 7.9-8.7 6.9 0.6 6.3-7.4 7.0 0.3 5.6-7.9 6.7 0.6 6.3-5.3 4.6-7.5 5.1 0.5 4.7-5.3 5.0 0.2 4.7-5.4 4.8 0.2 4.3-8.3	First dorsal fin—inner margin length (%)	2.3	2.2	1.9–2.8			0-2.0			-2.8	2.4	0.3	2.1–3.1	2.6 (0.3
8.7 9.3 4.5–10.3 9.1 0.8 8.4–9.9 9.3 0.3 8.7–10.0 9.0 0.4 7.9– 7.2 7.0 4.7–8.3 6.9 0.6 6.3–7.4 7.0 0.3 5.6–7.9 6.7 0.6 6.3– 5.2 5.3 4.6–7.5 5.1 0.5 4.7–5.3 5.0 0.2 4.7–5.4 4.8 0.2 4.3–	Second dorsal fin—length (%)	7.1	7.6	6.5-8.0	7.3 0.	5 6.9	0-8.1			-7.7	7.3	0.2		7.5 (7.4
7.2 7.0 4.7–8.3 6.9 0.6 6.3–7.4 7.0 0.3 5.6–7.9 6.7 0.6 6.3–5.2 5.3 4.6–7.5 5.1 0.5 4.7–5.3 5.0 0.2 4.7–5.4 4.8 0.2 4.3–	Second dorsal fin—anterior margin length (%)	8.7	9.3	4.5-10.3	9.1 0.	8 8.4	6.6-			-10.0	0.6	0.4	7.9-11.7	6.6	
5.2 5.3 4.6-7.5 5.1 0.5 4.7-5.3 5.0 0.2 4.7-5.4 4.8 0.2 4.3-	Second dorsal fin—height (%)	7.2	7.0	4.7-8.3	6.9	6.3		7.0 0.		-7.9	6.7	9.0	6.3-8.3	7.5 (7.7
	Second dorsal fin—base length (%)	5.2	5.3	4.6-7.5	5.1 0.	5 4.7	/–5.3	5.0 0.		-5.4	4.8	0.2	4.3-5.2	4.9	0.3

Table 1. Continued.

			P. buthi, new species	w specie	s	P. pro	P. productus		P. glaucostigmus	ostigmu	S	P. leucorhynchus	hynchu	S
Character	Holotype	Allotype	Paratype range	×	SD	Range	×	SD	Range	×	SD	Range	×	SD
Second dorsal fin—inner margin length (%)	2.1	2.1	1.7–2.6	2.2	0.2	1.8–2.6	2.2	0.3	1.8–2.4	2.2	0.2	1.8-3.1	2.4	0.4
Caudal fin-dorsal margin (%)	9.8	8.2	8.2-14.2	11.0	1.4	8.8-11.9	10.2	6.0	8.6-10.6	9.3	9.0	9.0-11.5	10.8	0.7
Caudal fin—preventral margin (%)	7.7	6.6	6.7-10.3	8.9	0.8	8.8-11.3	10.0	0.7	7.2-10.0	9.0	1.1	7.3-10.8	8.3	1.0
Snout to first dorsal-fin origin (%)	56.4	58.4	53.7-61.2	58.0	1.5	57.3-61.1	59.5	1.3	55.2-59.7	57.3	1.5	56.1-61.9	58.0	1.7
Snout to second dorsal-fin origin (%)	72.7	73.7	69.2-77.8	73.6	1.6	70.9–76.5	74.3	1.4	70.1–74.2	72.4	1.5	66.6-76.3	72.3	2.8
Snout to upper caudal-fin origin (%)	87.7	93.9	83.3–93.9	89.5	2.2	85.5-93.0	90.3	2.1	88.8-92.3	89.5	1.1	82.5-93.8	89.2	2.8
Snout to lower caudal-fin origin (%)	83.4	89.2	81.7-91.0	86.8	1.9	83.1–89.9	87.1	1.9	84.2-88.3	86.0	1.3	84.1–91.6	86.8	2.1
Snout to pelvic-fin origin (%)	37.7	39.0	33.5-42.7	39.1	1.7	37.7-41.6	39.9	1.0	34.7-38.8	37.2	1.4	35.2-41.5	37.3	2.0
Snout to anterior vent (%)	41.4	44.1	37.9-46.6	42.8	1.6	40.6-46.0	43.8	1.5	38.9-42.8	41.1	1.3	39.2-44.6	41.0	1.8
Pelvic-fin insertion to dorsal-fin origin (%)	22.9	12.4	9.4-13.4	11.4	0.1	10.2-14.4	11.9	1.1	11.9-15.5	12.5	1.3	12.3-16.0	14.2	1.3
Interdorsal distance (%)	12.1	11.3	9.6 - 13.1	11.4	0.7	9.9-11.5	10.9	0.4	10.8-13.4	11.4	0.8	9.9-12.4	11.2	8.0
Caudal peduncle length—dorsal (%)	10.2	13.5	8.4-13.8	11.3	1.2	9.8-13.4	12.0	0.8	10.9-13.2	11.8	0.8	10.8-13.8	12.2	1.1
Body width—pelvic insertion (tail) (%)	10.5	6.6	5.2-13.9	10.7	1.8	8.3-14.4	10.5	2.0	9.8-12.1	9.8	0.8	10.3-11.6	10.8	0.5
Disc width—anterior orbit (%)	16.6	18.7	12.4-19.2	16.3	1.7	20.2-22.0	21.6	1.0	14.8-18.6	17.3	1.2	14.1–20.1	17.1	2.0
Body width—first dorsal-fin origin (%)	8.9	8.7	4.6 - 10.3	8.5	0.8	6.4-8.8	7.8	9.0	7.9-10.3	8.3	1.0	8.3-10.4	9.1	9.0
Body width—second dorsal-fin origin (%)	4.8	4.8	2.8-5.8	4.7	0.5	3.7-5.1	4.4	0.4	4.3-5.8	4.5	0.5	4.4-5.5	4.9	0.3
Body depth—maximum (%)	5.8	6.5	5.3-7.5	6.2	0.5	5.3-8.7	7.0	6.0	5.1-6.2	5.8	0.3	5.1-5.8	5.5	0.3
Body depth—pelvic-fin insertion (%)	5.2	5.9	4.24	5.6	9.0	5.1-8.1	6.5	6.0	5.0-6.1	5.5	0.4	4.5-5.8	5.2	9.4
Body depth—first dorsal-fin origin (%)	4.5	4.3	2.8–6.2	4.4	0.5	3.8-4.8	4.2	0.3	3.9-4.7	4.1	0.3	4.3-5.1	4.7	0.3
Body depth—second dorsal-fin origin (%)	2.8	2.7	2.3-3.4	2.7	0.2	2.4-3.2	2.8	0.2	2.6-3.2	2.7	0.2	2.8-3.2	3.0	0.1

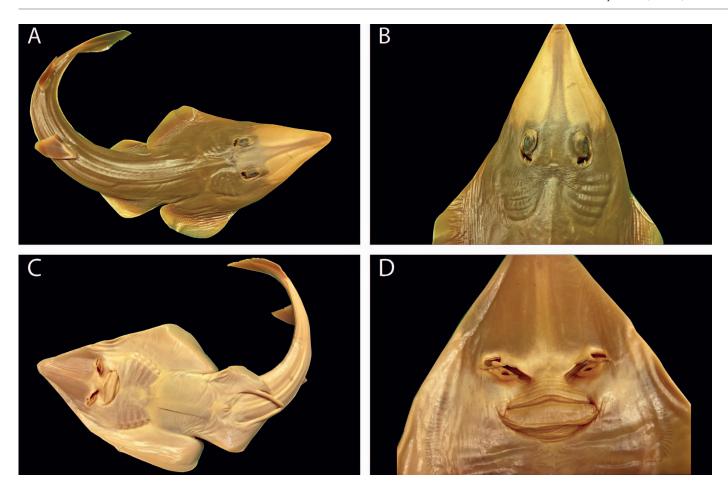


Fig. 1. Holotype of *P. buthi*, new species (SIO 15-405 [formerly UCLA W50-189], 471.1 TL male). (A) Dorsal view, (B) dorsal view of snout, (C) ventral view, (D) ventral oronasal morphology.

relating only to nasal morphology. All analyses were performed using the computational packages factoextra (Kassambara and Mundt, 2017), MASS (Venables and Ripley, 2002), devtools (Wickham et al., 2018), and flipMultivariates in R v. 3.3.3 (R Core Team, 2017). Plots were created using the R function, ggplot2, and ggbiplot (Wickham, 2009).

Examined material of *Pseudobatos* is deposited in the following institutions: University of California Los Angeles Ichthyology Research Collection, Los Angeles (UCLA);

Natural History Museum of Los Angeles County (LACM); Scripps Institution of Oceanography, San Diego (SIO).

Pseudobatos buthi, new species

urn:lsid:zoobank.org:act:C6987710-540F-4F3F-8BF3-48DB119306A4 Spadenose Guitarfish, Guitarra Pala Figures 1, 2, 3, 4, 5; Table 1

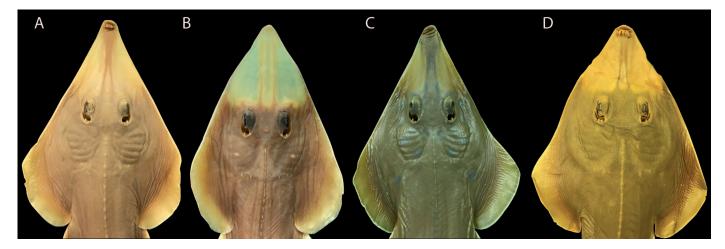


Fig. 2. All four species of guitarfishes from the Gulf of California, shown from end of disc to snout. (A) *P. buthi*, new species (allotype, SIO 15-477 [formerly UCLA W49-122], 383.6 mm TL). (B) *P. leucorhynchus* (UCLA W53-317, 262.7 mm TL). (C) *P. glaucostigmus* (UCLA W56-117, 319.4 mm TL). (D) *P. productus* (UCLA W50-128, 364.5 mm TL).

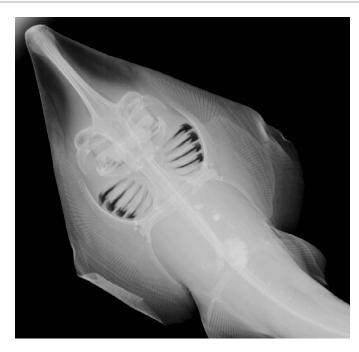


Fig. 3. Radiograph of the chondrocranium and beginning of vertebral column of *P. buthi*, new species, paratype (SIO 15-477 [formerly UCLA W49-122]).

Holotype.—SIO 15-405 (formerly UCLA W50-189), adult male, 471.1 mm TL, Gulf of California, San Felipe, Mexico, 2 m deep, very fine, dark sand, clear salt water, low incoming tide, 45–135 m offshore, temp. 19–20°C, 30 m beach seine, 24 November 1950.

Allotype.—SIO 15-477 (formerly UCLA W49-122), adult female, 383.6 mm TL, Gulf of California, San Felipe, Mexico, 1.1 m deep, muddy sand, turbid salt water, 76 m offshore, temp. 24°C, 30 m beach seine, 25 March 1949.

Paratypes.—(80 specimens) LACM 9302-14, female, 555.1 mm TL, Gulf of California, Sonora; LACM 9444-8, 5 males, 215.9-333.1 mm TL, female, 269.2 mm TL, Gulf of California, Punta Majora and Punta Eusenada Blanca; LACM 48221-10, female, 646.7 mm TL, Gulf of California, Sonora; LACM 48225-6, female, 550.1 mm TL, Gulf of California, Sonora; LACM 48242-2, 2 females, 578.9-685.1 mm TL, Gulf of California, Sonora; LACM 48666-23 (formerly UCLA W52-45), 4 females, 288.6-358.8 mm TL, Gulf of California, south of San Felipe, 6 males, 275.2-324.7 mm TL, Gulf of California, off Punta San Fermin; SIO 08-186 (formerly UCLA W50-67), male, 543.1 mm TL, Gulf of California, Sonora Puerto Libertad; SIO 13-237 (formerly UCLA W54-366), female, 278.2 mm TL, male, 252.8 mm TL, Gulf of California, Punta Diggs; SIO 15-81 (formerly UCLA W50-57), 3 females, 326.6-585.3 mm TL, 8 males, 297.4-516.5 mm TL, Gulf of California, Sonora Bahia Kino [only 10 specimens reported in field notes]; SIO 15-89 (formerly UCLA W50-61), 3 females, 244.4-315.9 mm TL, male, 286.5 mm TL, Gulf of California, Sonora Puerto Libertad; SIO 15-324 (formerly UCLA W55-2), female, 358.7 mm TL, Gulf of California, Punta Diggs; SIO 15-370 (formerly UCLA W52-16), female, 417.4 mm TL, Gulf of California, Sonora Estero Soblado; SIO 15-405 (formerly UCLA W50-189), 2 males, 490.6-501.9 mm TL, Gulf of California, San Felipe [an additional specimen was chosen as holotype]; SIO 15-406 (formerly UCLA W50-190), female, 386.2 mm TL, male, 388.3 mm TL, Gulf of California, San

Felipe; SIO 15-442 (formerly UCLA W49-126), male, 342.0 mm TL, Gulf of California, San Felipe; SIO 15-454 (formerly UCLA W49-55), male, 320.9 mm TL, female, 277.3 mm TL, Gulf of California, Sonora; SIO 15-477 (formerly UCLA W49-122), 6 females, 251.6-402.1 mm TL, 7 males, 337.1-414.7 mm TL, Gulf of California, San Felipe [an additional specimen was chosen as allotype]; SIO 15-646 (formerly UCLA W49-119), male, 382.7 mm TL, Gulf of California, San Felipe; SIO 15-1075 (formerly UCLA W49-91), female, 293.3 mm TL, male, 295.9 mm TL, Gulf of California, San Felipe; SIO 15-1174 (formerly UCLA W56-28), male, 306.9 mm TL, female, 304.8 mm TL, Gulf of California, Sonora Punta Lubos; SIO 15-1232 (formerly UCLA W54-367), male, 264.3 mm TL, Gulf of California, Playahas Almejas; SIO 15-1630 (formerly UCLA W57-155), female, 376.4 mm TL, Gulf of California, San Felipe; SIO 15-1666 (formerly UCLA W55-1), female, 356.5 mm TL, Gulf of California, San Felipe; SIO 15-2606 (formerly UCLA W55-200), female, 362.8 mm TL, Gulf of California, San Felipe; SIO 15-2711 (formerly UCLA W56-73), 3 females, 535.7-599.6 mm TL, 2 males, 412.3-599.4 mm TL, Gulf of California, Sonora Bocochibampo; SIO 47-59 (formerly UCLA W49-423), 2 females, 389.6-392.6 mm TL, male, 379.9 mm TL, Gulf of California, San Felipe; SIO 61-82, female, 400 mm TL, Gulf of California, San Felipe; SIO 61-183, male, 460.2 mm TL, Gulf of California, San Felipe.

Diagnosis.—Pseudobatos buthi is distinguished from P. glaucostigmus (Fig. 2A) in having a nasal tassel, uniform coloration, a slightly narrower maximum disc width and disc width at anterior orbit, longer head, longer snout, shorter anterior nasal flap, smaller nostril length, and a smaller body width at first dorsal-fin origin.

Pseudobatos buthi is distinguished from P. leucorhynchus (Fig. 2B) in having a nasal tassel, brown rostrum, shorter distance from snout to first dorsal-fin origin, shorter distance from snout to lower caudal-fin origin, slightly narrower disc width at anterior orbit, a narrower body at first dorsal-fin origin, shorter anterior nasal flap base length, and shorter nostril length.

Pseudobatos buthi (Fig. 2C) is most similar to *P. productus* (Fig. 2D) but differs in having a narrower disc width (30–35% vs. 36–38% TL range), shorter distance from nostril to disc margin (2.8–4.0% vs. 4.2–5.2% TL range), narrower disc width at anterior orbit (12–19% vs. 20–22% TL range), narrower tip of snout width (3% vs. 4–6% TL average), and no prominent thorns as a juvenile (see remarks).

Description.—Disc wedge-shaped, anterior margin straight, angle anterior to eyes about 60°. Outer corner of pectoral-fin area mostly rounded, length 1.28 times width in holotype; 1.17 in smaller immature paratypes (Table 1). Pelvic fins relatively short, length at base about 0.93 of inner margin; total length 1.95 times their base length, 1.43 times their width; anterior margin weakly convex, apex broadly rounded, posterior margin almost straight. Tail slender; in crosssection very depressed, rounded dorsally; tail length from anterior cloaca 1.41 times precloacal length, 1.42 times disc length, 5.57 times body width at pelvic-fin insertions; tail width 2.02 times depth at pelvic-fin insertions, 2.37 at first dorsal-fin origin, 3.77 at second dorsal-fin origin. Dermal fold lateral on tail, originating slightly anterior to free rear tip of pelvic fin, reaching just behind ventral caudal-fin origin; fold moderately narrow, maximum width in interdorsal space about 2.28 times width of posterior nasal flap.

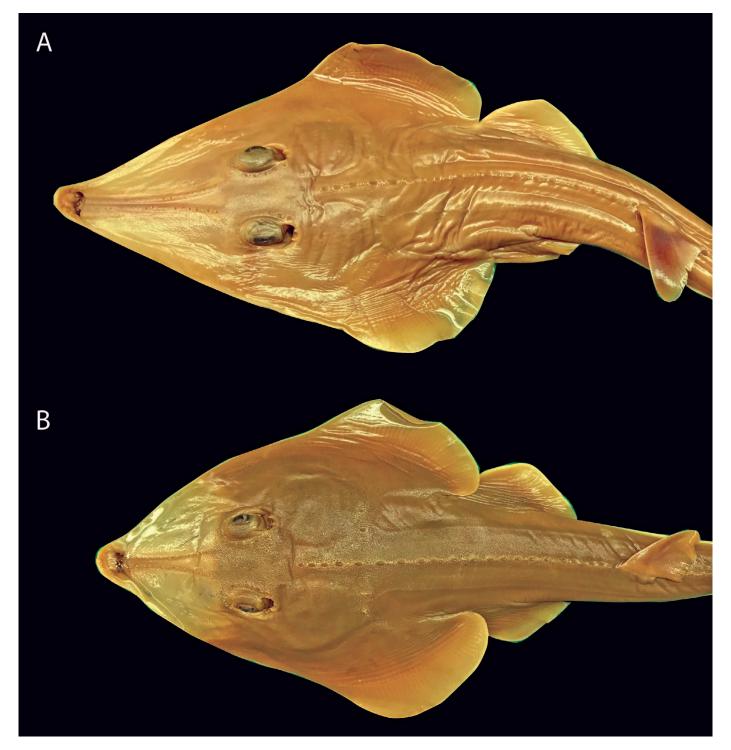


Fig. 4. (A) Juvenile *P. buthi*, new species (LACM 48666-23 [formerly UCLA W52-45]), and (B) juvenile *P. productus* (UCLA W49-375). Snout length, disc shape, nasal tassel, and density of scales between orbits are very distinct between immature specimens of *P. buthi*, new species, and *P. productus* (<400 mm TL).

Dorsal fins short, relatively upright; apices acutely rounded rather than angular; anterior margins weakly convex; posterior margins almost straight to weakly concave; free rear tips forming right angle; first dorsal fin just barely taller than second, length of first 1.03 times its height, base length 2.05 times inner margin length; second dorsal-fin length 1.01 times its height, base length 2.50 times inner margin length. First dorsal fin relatively close to pelvic-fin insertion, interspace 1.89 times interdorsal distance; interdorsal space relatively short, 1.79 times second dorsal-fin height, 2.60

times base of first dorsal fin, 1.18 times interspace between second dorsal-fin insertion and upper origin of caudal fin (caudal-peduncle length). Caudal fin small, dorsal caudal margin 1.26 times preventral margin length.

Head moderately to very long, ventral length 28.25% (26.2–33.5%) TL; snout moderately long and pointed; preoral snout length long 19% (16.4–22%), 2.85 times mouth width in holotype but up to 3.5 times mouth width in paratypes, 7.09 (6.61–8.87) times internarial distance, 1.79 (1.66–2.23) times dorsal caudal-fin margin, 5.44 (5.07–6.81) times distance from

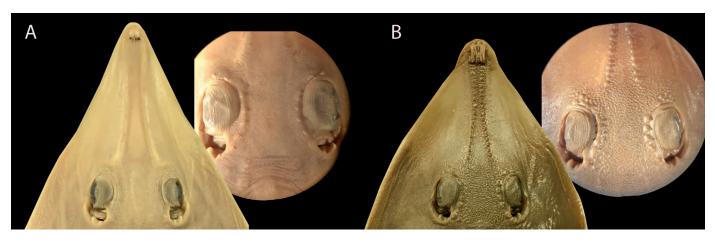


Fig. 5. View under dissecting microscope of interorbital region of (A) juvenile *P. buthi*, new species (SIO 13-237 [formerly UCLA W54-366]), and (B) juvenile *P. productus* (UCLA W49-375). Juveniles of *P. productus* display larger scales and more prominent thorns around orbits and down rostrum.

nostril to margin of disc; presocket snout length 2.69 (2.49–3.35) times interspiracular width, 4.49 (4.16–5.52) times orbit diameter; interorbital space almost flat, rather narrow; eyes moderately small, slightly elevated, orbit diameter 1.59 (1.51–1.87) times spiracle length, 1.21 (1.15–1.36) times interorbital width. Spiracle lunate, moderately large; two weakly compressed spiracular folds on posterior margin, innermost fold half or less length of outer fold; distance between bases of folds equal to length of inner fold.

Nostril length relatively small (3.5–4.6% TL), oblique, nasal flaps well developed; anterior aperture suboval, width well exceeding length; nostril length 3.69 times anterior aperture width, 2.19 times anterior nasal-flap base length, 1.23 times distance from nostril to disc margin, 1.61 times internarial width. Anterior nasal flap narrow with long, bluntly pointed process that curves posteriorly; flap base 1.29 times its width at process, 1.59 times anterior aperture width; inserted well into internarial space, not at nostril margin, distance between their insertions 4.37 in distance between lateral margins of anterior apertures, 2.5 in internarial width; process of flap almost as long as it is wide at its base, overlapping posterolateral nasal flap and determining hind margin of anterior aperture. Posterolateral nasal flap lobelike, width uniform, length 3.88 times width; originating at lateral extremity of anterior nasal aperture, extending posteriorly as free fold (below anterior fold and above posterior fold along lateral margin of nostril) to about level of insertion of anterior nasal flap. Posterior nasal flap strongly lobe-like, base length 2.05 times its width, not reaching end of nostril, inserted well forward of posterior tip; width smaller than anterior aperture width, 1.68 times posterolateral nasal-flap width. Nasal lamellae 43.

Mouth width large, width 1.56 times nostril length, 6.73 (7.33–7.78) in precloacal length; positioned below hind margin of orbit. Upper jaw almost horizontal, upper lip slightly concave; lower lip pronounced, separated from oral groove by ridges of strongly corrugated skin; weak lateral grooves around corners of mouth. Teeth small, blunt, crowns rhomboidal with weak, pointed posterior cusps; teeth quincuncial; upper and lower jaw teeth similar in shape and size; first upper tooth row 59.

Gill openings weakly s-shaped; length of third gill slit 1.3–2.0% TL, 8.8–12.7% TL in distance between fifth gill slits; distance between first gill slits 1.43 times distance between fifth gill slits; distance between fifth gill slits 3.67 times

internarial distance, 1.46 times mouth width, 3.10 (2.87–3.67) times in ventral head length.

Adult clasper length 12–19% TL. Clasper very elongate, slender, calcified, extending well beyond pelvic fin when fully developed. Clasper slightly flattened, oval in cross section. Clasper groove long, extending 90% of total clasper length. Rhipidion short, spur often displayed when claspers extend well beyond pelvic fin. Claspers slightly shorter in holotype than in other adults, inner length of right clasper about 12% TL; tip acute.

Dermal denticles minute, close-set, covering entire body; small or absent thornlets on rostral ridges, around orbits and spiracles, on each shoulder and in a median row between dorsal fins. Tip of snout with or without nasal tassel. Holotype without nasal tassel; however, nasal tassel present on allotype and other paratypes. Thorns and nasal tassel absent or less pronounced on larger specimens. Ventral surface uniformly covered in minute denticles.

Vertebral column with 174 (171–182) total centra; 13 (12–13) synarcual centra, 26 (25–27) monospondylous centra, 96 (90–100) diplospondylous precaudal centra, 39 (30–49) diplospondylous caudal centra (Fig. 3). Total synarcual segments 7.5% (6.8–7.5%); monospondylous centra 15.0% (14.1–15.3%); diplospondylous precaudal centra 55% (50.8–56.5%), and diplospondylous caudal centra 22.5% (17.2–28.2%) of total centrum count. Total pectoral radials 56 (53–59): 25 (24–27) propterygials, 8 (6–9) mesopterygials, 1 neopterygial, 22 (20–24) metapterygials. Total pelvic radials 22 (18–22).

Coloration of preserved specimens.—Dorsal surface brownish gray, free of spots, snout lighter in coloration. Ventral surface evenly pale or with dark marking on snout tip.

Size.—To at least 685.1 mm TL, smallest adult 480 mm TL.

Distribution.—Shallow coastal regions of the Gulf of California (Fig. 6) to at least two meters depth.

Etymology.—Named in honor of my mentor, UCLA ichthyologist Donald Buth, who provided me with the opportunity to describe this new species and whose support and guidance has been instrumental in my scientific career.

Additional comparisons.—In addition to the distinguishing characters above, *P. buthi* (with some overlap) has a slightly longer snout length (19% vs. 17% TL average), wider interorbital width (4.1–6.2% vs. 3.4–5.6% TL range), thicker

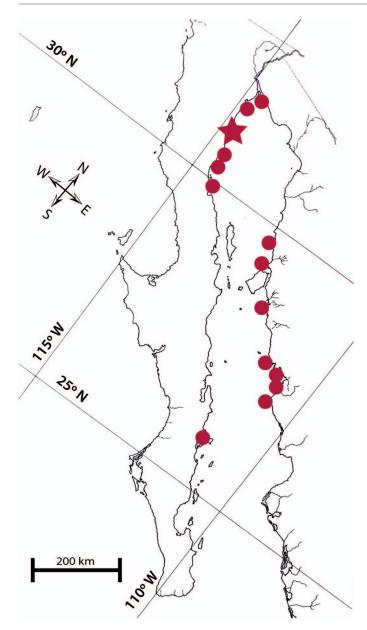


Fig. 6. The distribution of *P. buthi*, new species, caught by Boyd Walker and colleagues on collecting trips in the 1940s and 1950s. Each red dot represents a different sampling locality. The red star represents the type locality of the holotype.

posterior nasal flap width (1.3% vs. 2.3% TL average), shorter nostril length (4.0% vs. 4.5% TL average), slightly shorter anterior nasal flap base length (1.8% vs. 2.1% TL average), slightly thinner posterior nasal flap width (0.9% vs. 1.1% TL average), slightly shorter distance between anterior nasal flaps (4.7% vs. 5.4% TL average), shorter distance between first gill openings (11.6% vs. 14.1% TL average), shorter distance between fifth gill openings (8.8% vs. 10.0% TL average), shorter snout to first dorsal-fin origin (53% vs. 57% TL average), shorter snout to pelvic-fin origin (33.0% vs. 37.7% TL average), shorter snout to anterior vent length (38% vs. 41% TL average), thinner tail (5.2% vs. 8.3% TL average), smaller body width at first dorsal-fin origin (4.6% vs. 6.4% TL average), smaller maximum body depth (7.5% vs. 8.7% TL average), and a smaller body depth at pelvic-fin insertion (4–7% vs. 5–8% TL range).

Additionally, *P. leucorhynchus* is distinguished from *P. productus* in having a white rostrum, no nasal tassel, longer

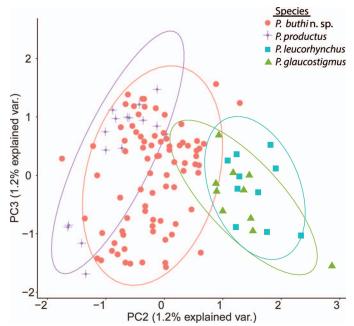


Fig. 7. PCA of three known species of guitarfishes found in the Gulf of California (*P. glaucostigmus, P. leucorhynchus, P. productus*) and *P. buthi,* new species, based on 63 morphometric characters used to classify species of guitarfish. PC1 was largely characterized by measurements relating to body size. Plotted here are PC2 vs. PC3 with 95% confidence ellipses, which are characterized by interspiracular width, posterolateral nasal flap width, anterior nasal flap base length, and posterior nasal flap base length.

nostril length, larger anterior nasal flap base length, smaller posterior nasal flap width, a narrower disc width, and a shorter distance from orbit to disc margin. *Pseudobatos glaucostigmus* is distinguished from *P. productus* in having prominent blue spots seen live and fixed behind and around the orbits on the dorsal surface, no nasal tassel, longer nostril length, larger anterior nasal flap base length, smaller posterior nasal flap width, narrow maximum disc width, smaller disc length, smaller interspiracular width, shorter prenarial distance, shorter distance from nostril to disc margin, shorter distances between gill openings, narrower disc width at anterior orbit, and a thicker body width at first dorsal-fin origin.

Remarks.—Pseudobatos buthi also has a less prominent scale patch between orbits and a less thorny rostrum, with very small or absent rostral and orbital thorns when compared to P. productus. This character remains fairly consistent throughout their growth. Pseudobatos productus, however, shows much more dramatic changes in this character with ontogeny. Therefore, juvenile specimens of P. buthi and P. productus are easier to visually distinguish than adults. Pseudobatos productus displays a densely scaled interorbital region with prominent rostral thorns at sizes smaller than 400 mm TL (Figs. 4, 5). At larger sizes, the thorns and scales of P. productus become worn down or less prominent, which more closely resembles *P. buthi*. Therefore, this trait is only informative for juvenile guitarfishes, and other discrete morphological characters mentioned here should be used for distinguishing adults.

Statistical analysis.—The PCA resulted in 95% confidence ellipses with some overlap between all four species of guitarfishes examined (Fig. 7). Pseudobatos leucorhynchus overlapped heavily with P. glaucostigmus. Pseudobatos produc-

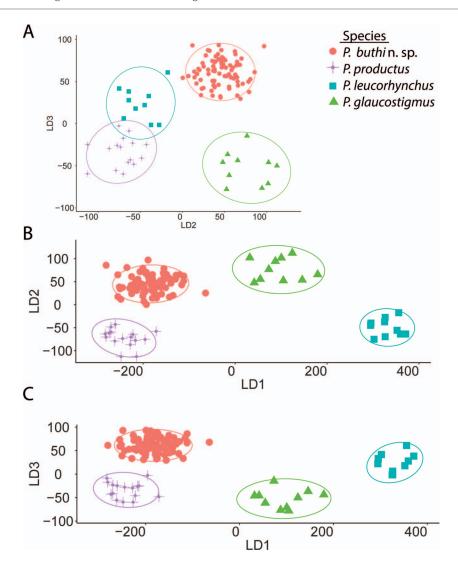


Fig. 8. LDA with 95% confidence ellipses of three known species of guitarfish found in the Gulf of California (P. glaucostigmus, P. leucorhynchus, P. productus) and P. buthi, new species, based on 63 morphometric characters. LD1 primarily loaded with head length, snout length, and nostril length. LD2 primarily loaded with total length, head length, snout length, and prenarial distance. LD3 primarily loaded with snout length and distance across anterior nasal apertures. Plotted here are (A) LD2 vs. LD3 (B) LD1 vs. LD2 and (C) LD1 vs. LD3.

tus overlapped heavily with P. buthi. Other non-continuous variables such as snout color, spots, and rostral cartilages may be better characters to distinguish these species. While Last's (2004) 63 characters are useful in distinguishing among genera, the results of this PCA suggest they are not as informative within this genus. A scree plot of the PC variance found that the first PC described the majority of the variance $(\sim 97\%)$, which mainly loaded with body size. PC1 primarily loaded with body size characters such as total length, disc width, and disc length, etc. The other principal components were the ones of interest and mostly loaded with characters relating to subtle differences in nasal morphology. PC2 loaded positively with anterior nasal flap base length and posterior nasal flap base length (Table 2). PC3 loaded positively with interspiracular width and posterolateral nasal flap width. Pseudobatos buthi generally has shorter anterior and posterior nasal flap base lengths than P. leucorhynchus and P. glaucostigmus. Sex was also compared to determine if grouping was influenced by dimorphism. However, sex was found not have a clear intraspecific grouping pattern.

The LDA performed on all 63 measurements found that the characters relating to body size and nasal structure best distinguish these species (Fig. 8). LD1 primarily loaded with head length, snout length, and nostril length. LD2 primarily loaded with total length, head length, snout length, and prenarial distance. LD3 primarily loaded with snout length and distance across anterior nasal apertures (Table 3).

Pseudobatos buthi loaded positively with a longer snout length and head length than *P. productus*. The LDA performed on characters relating to nasal morphology displayed some overlap but was fairly distinguishable across species (Fig. 9). LD1 primarily loaded with anterior nasal flap base length and distance from nostril to disc margin. LD2 primarily loaded with nostril length, anterior aperture width, and anterior nasal flap base length. LD3 primarily loaded with posterolateral nasal flap width (Table 4).

DISCUSSION

Guitarfishes are difficult to distinguish within genera, and diagnostic characters are often not easily recognizable to the untrained eye. As described by Last et al. (2016a), members of the genus *Pseudobatos* are distinct from all other rhinobatids in their nasal morphology. This group is distinguished by having narrow, elongate posterior apertures, bilobed anterior nasal flaps, broad posterolateral nasal flaps, and various other morphological differences. The results of the statistical analysis in this study suggest subtle differences in nasal morphology between species within this genus. In an effort to aid in the identification process, a key to the guitarfishes of the Gulf of California was created.

Pseudobatos buthi is most similar to P. productus but with a narrower snout, narrower disc width, shorter distance from nostril to disc margin, and a narrower disc width at anterior

Table 2. Principal component analysis loadings for the type specimens of *P. buthi*, new species (n = 82), and associated congeners (n = 10).

Character	PC1	PC2	PC3	PC4
Total length	-0.13239	0.026866	-0.02794	0.039827
Disc width—maximum	-0.13225	-0.00327	-0.00095	-0.03439
Disc length	-0.1325	-0.03515	0.026046	0.070123
Head length—dorsal	-0.13132	-0.08564	0.011893	0.127984
Head length—ventral	-0.13135	-0.06047	0.011303	0.13142
Snout length—presocket	-0.13037	-0.02445	0.05484	0.169
Orbit diameter	-0.12519	-0.06218	-0.11635	0.030873
Spiracle length	-0.11726	-0.26872	-0.01072	0.223814
Orbit and spiracle length Interorbital width	-0.12564	-0.10301	-0.06837	0.198134
Interorbital width Interspiracular width	-0.12947 -0.11043	-0.05884 -0.199	0.018036 0.139892	0.035862 -0.00481
Preoral length	-0.11045 -0.1302	-0.199 -0.05586	0.139692	0.169377
Mouth width	-0.13092	-0.01798	0.044763	0.010205
Prenarial distance	-0.1299	-0.07634	0.02954	0.170752
Nostril length	-0.12924	0.164064	0.014316	-0.13013
Anterior aperture—width	-0.12632	0.084277	0.03654	0.04699
Anterior nasal flap—base length	-0.11853	0.33188	-0.02639	-0.31314
Anterior nasal flap—width	-0.12276	0.141571	0.019189	0.052364
Posterolateral nasal flap—total length	-0.12661	0.122397	-0.02317	-0.03228
Posterolateral nasal flap—width	-0.09812	-0.14895	0.325078	0.095373
Posterior nasal flap—base length	-0.11798	0.227444	0.063725	0.16352
Posterior nasal flap—width	-0.11302	-0.06955	-0.09622	-0.30192
Distance across anterior nasal apertures	-0.13193	0.062901	0.011247	-0.01138
Internarial distance—minimum	-0.12762	0.099777	0.017782	0.002531
Distance between anterior nasal flaps	-0.12812	-0.1	0.017247	-0.04034
Distance from nostril to disc margin Third gill opening—width	-0.11158 -0.1229	-0.45583 0.038582	0.194793 0.173989	-0.27437 -0.13232
Distance between first gill openings	-0.1229 -0.13019	-0.1005	0.173969	-0.13232 -0.02273
Distance between fifth gill openings	-0.13019 -0.12867	-0.1003 -0.05538	0.104684	-0.05961
Pelvic fin—length	-0.13187	0.03336	-0.01439	-0.03922
Pelvic fin—anterior margin length	-0.12894	0.133565	0.017079	-0.08945
Pelvic fin—width	-0.12931	0.031755	0.020565	-0.14443
Pelvic fin—base length	-0.12676	0.004028	0.037445	0.065727
Pelvic fin—inner margin length	-0.12619	0.0659	-0.04603	-0.09481
First dorsal fin—length	-0.13131	0.035143	-0.03432	0.091233
First dorsal fin—anterior margin length	-0.1257	0.054487	0.008466	0.080898
First dorsal fin—height	-0.12749	0.167771	0.032533	0.008586
First dorsal fin—base length	-0.12888	0.008847	0.012294	0.051145
First dorsal fin—inner margin length	-0.12483	0.110758	0.092937	0.013345
Second dorsal fin antorior margin langth	-0.13169	0.067773	-0.00521	0.027814
Second dorsal fin—anterior margin length Second dorsal fin—height	-0.1236 -0.12797	0.135951 0.135599	0.072172 0.056425	-0.05392
Second dorsal fin—base length	-0.12769	0.037115	0.028873	0.134635
Second dorsal fin—inner margin length	-0.12316	0.095847	0.044785	-0.0986
Caudal fin—dorsal margin	-0.12359	-0.11253	-0.01008	0.227169
Caudal fin—preventral margin	-0.12319	-0.10933	0.134301	-0.13281
Snout to first dorsal-fin origin	-0.1325	0.004143	-0.00772	0.041237
Snout to second dorsal-fin origin	-0.13226	-0.00113	-0.01341	0.056393
Snout to upper caudal-fin origin	-0.13188	0.032353	-0.02568	0.011447
Snout to lower caudal-fin origin	-0.13207	0.030423	-0.0065	0.053791
Snout to pelvic-fin origin	-0.13171	-0.04745	-0.0049	0.108734
Snout to anterior vent	-0.13227	-0.03725	0.02129	0.093155
Pelvic-fin insertion to dorsal-fin origin	-0.10065	-0.09644	-0.66456	0.020775
Interdorsal distance	-0.13023	0.021138	-0.05695	0.046331
Caudal peduncle length—dorsal	-0.12319	0.151378	0.006967	-0.165
Body width—pelvic insertion Disc width—antorior orbit	-0.11099 0.11076	-0.13202 0.15977	-0.47196 0.02108	-0.04071
Disc width—anterior orbit Body width—first dorsal-fin origin	-0.11936 -0.12675	-0.15873 0.085209	-0.02108 -0.14064	-0.33216
Body width—lifst dorsal-fin origin Body width—second dorsal-fin origin	-0.12675 -0.12545	0.085209	-0.14064 -0.10255	0.054568 0.016953
Body depth—maximum	-0.12593	-0.23349	-0.10233 -0.02813	-0.12552
Body depth—maximum Body depth—pelvic-fin insertion	-0.12393 -0.12429	-0.19385	-0.02613 -0.04872	-0.12332 -0.26215
Body depth—first dorsal-fin origin	-0.12939	0.046967	0.003443	-0.05946
Body depth—second dorsal-fin origin	-0.13017	0.066681	-0.00898	-0.09165

Table 3. Linear discriminant analysis loadings for the type specimens of *P. buthi*, new species (n = 82), and associated congeners (n = 10).

Character	LD1	LD2	LD3
Total length	4.858903	15.9223	-11.0439
Disc width—maximum	7.863489	-7.59682	-6.83492
Disc length	-2.40725	3.556414	8.726322
Head length—dorsal	-29.2724	15.05479	12.21219
Head length—ventral	13.5079	-5.20575	-3.72243
Snout length—presocket	12.71704	19.88865	30.72412
Orbit diameter	-4.8241	4.086152	0.137235
Spiracle length	-3.61647	-1.54741	1.948214
Orbit and spiracle length	7.450662	4.386397	-2.35745
Interorbital width	2.855587	-8.07551	0.354597
Interspiracular width	-0.82843	-2.98787	-0.11008
Preoral length Mouth width	-3.45617 0.514224	4.974175	2.192965
Prenarial distance	0.514224 3.729232	-11.4955 -17.7634	-0.2937 -6.53519
Nostril length	12.93351	-10.1262	-15.3214
Anterior aperture—width	1.572226	6.859619	4.019028
Anterior nasal flap—base length	5.305516	-4.85196	-2.29457
Anterior nasal flap—width	5.109127	-0.15676	1.327304
Posterolateral nasal flap—total length	2.347165	-0.09273	-5.84586
Posterolateral nasal flap—width	-1.39757	3.206691	-0.1561
Posterior nasal flap—base length	0.021543	-0.63299	-0.65156
Posterior nasal flap—width	-5.75841	-0.22534	-1.04773
Distance across anterior nasal apertures	3.498171	2.006427	23.44751
Internarial distance-minimum	11.50308	-5.51124	-1.05387
Distance between anterior nasal flaps	0.633491	-2.74757	-8.47774
Distance from nostril to disc margin	-2.9069	-7.04802	-0.76966
Third gill opening—width	-2.93382	2.639307	1.083988
Distance between first gill openings	4.815572	-4.34054	6.654237
Distance between fifth gill openings	-8.50534	4.617809	-6.36695
Pelvic fin—length	-9.6388	3.048734	-9.74113
Pelvic fin—anterior margin length Pelvic fin—width	1.635562 0.13296	-5.20411 0.468594	-2.43646 -0.04515
Pelvic fin—base length	4.206957	5.32686	-0.04313 -1.78691
Pelvic fin—inner margin length	-0.60856	3.415336	0.770041
First dorsal fin—length	-4.67928	1.736064	4.87832
First dorsal fin—anterior margin length	-1.45407	0.332479	-1.95653
First dorsal fin—height	4.046323	4.808077	-0.31592
First dorsal fin—base length	-4.25677	0.516221	1.446707
First dorsal fin—inner margin length	-0.31312	-1.20991	-2.64335
Second dorsal fin—length	8.497701	6.854216	4.420745
Second dorsal fin—anterior margin length	-3.18125	-2.93778	-1.79749
Second dorsal fin—height	-1.26318	-4.22985	-2.03007
Second dorsal fin—base length	-0.16403	-1.87591	-1.4887
Second dorsal fin—inner margin length	5.877566	0.942038	3.27344
Caudal fin—dorsal margin	-1.5373	-4.1136	2.637808
Caudal fin—preventral margin	-6.09243	5.211237	3.371257
Snout to first dorsal-fin origin	25.14575 -5.23758	-10.2823	3.122446
Snout to second dorsal-fin origin Snout to upper caudal-fin origin	-5.23758 5.188756	9.476436 3.601299	3.825798 16.01214
Snout to lower caudal-fin origin	-11.0795	-3.6531	-13.3915
Snout to pelvic-fin origin	-6.23228	-1.39842	8.811564
Snout to anterior vent	-31.0087	-12.5804	-23.4553
Pelvic-fin insertion to dorsal-fin origin	-0.24804	-1.21401	1.600285
Interdorsal distance	-0.40689	2.991672	-4.21485
Caudal peduncle length—dorsal	0.304992	-4.42959	-1.02383
Body width—pelvic insertion	2.565247	2.087403	1.527481
Disc width—anterior orbit	7.8332	-2.923	-3.97434
Body width—first dorsal-fin origin	5.548754	4.350322	-3.57919
Body width—second dorsal-fin origin	-5.17717	-0.25728	1.599927
Body depth—maximum	-13.6146	5.568089	0.186366
Body depth—pelvic-fin insertion	0.517397	-7.36896	-6.74694
Body depth—first dorsal-fin origin	-2.22797 7.03654	-0.52894	5.57503
Body depth—second dorsal-fin origin	7.92654	2.092115	4.50604

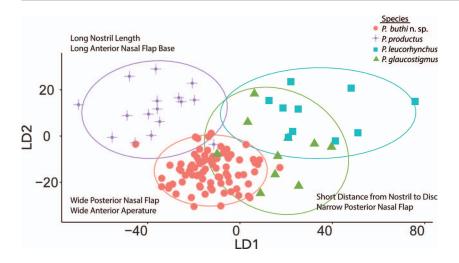


Fig. 9. LDA with 95% confidence ellipses of three known species of guitarfishes found in the Gulf of California (*P. glaucostigmus, P. leucorhynchus, P. productus*) and *P. buthi*, new species, based on 12 morphometric characters relating to nasal morphology. Plotted here is LD1 vs. LD2. LD1 primarily loaded with anterior nasal flap base length and distance from nostril to disc margin. LD2 primarily loaded with nostril length, anterior aperture width, and anterior nasal flap base length.

orbit. While there is overlap in other morphometric nasal characters, P. buthi can also be distinguished by its smaller nostril length, shorter anterior nasal flap base, smaller posterior and posterolateral nasal flap width, and a shorter distance between anterior nasal flaps. There also appears to be wide variation in some of the characters of P. buthi (Table 1). For example, snout length (14-19% TL) exhibited a greater variation in length than *P. productus* (15–17% TL). Both P. buthi and P. productus had large ranges in disc length to total length ratios, varying almost 10% (39-47% vs. 41-47% TL). This is likely due to the large range in specimen sizes (TL). While measurements were scaled as a percentage of TL, growth does not appear to be isometric, with tail length elongating with growth. Juvenile specimens of *P. buthi* and *P.* productus are also easier to distinguish than adults, with more pronounced differences in disc width, tip of snout width, interorbital scales, and thorns along the rostrum (Figs. 4, 5). Adult specimens of *P. productus* have less pronounced thorns than juveniles, and while disc width is still wider than P. buthi, it is more difficult to visually recognize. Additionally, disc length appears to be quite different in only juvenile specimens of P. buthi and P. productus, with P. buthi having a longer disc length than juvenile specimens of P. productus at the same total length. This difference is not observed at larger sizes, suggesting these species may grow and develop differently; however, this needs to be explored further.

As previously mentioned, there is much taxonomic controversy within the family, and the genus *Pseudobatos* is likely to change again with recent, unpublished analysis of

DNA sequence data (Peter Last, pers. comm.). While morphometric and statistical analyses highlight *P. buthi* as distinct from its congeners, future genetic analysis would aid in determining the phylogenetic placement and characterization within this group. In order to do this, further sampling is needed to obtain fresh specimens of *P. buthi* from the Gulf of California. It is unknown if *P. buthi* is still present in the Gulf of California as *P. buthi* was last caught in the Gulf of California in April 1961 (SIO 61-183). However, it seems likely that *P. buthi* has been caught and misidentified as *P. productus*.

Finally, there is more than just taxonomic research needed on this group. While the number of species descriptions of guitarfishes is continuing to increase, we lack a basic biological understanding of many of these species. The general biology and life history traits of 14 of the 31 species in the family Rhinobatidae are unknown, including comparative species from this description: *P. glaucostigmus*, *P. planiceps*, and *P. prahli* from the eastern North Pacific (Moore, 2017).

MATERIAL EXAMINED

Pseudobatos glaucostigmus: LACM 6530-4, female, 325 mm TL, Mexico, Gulf of California, Sinaloa; UCLA W51-22, male, 334.7 mm TL, Mexico, Gulf of California, Sinaloa Camaron Beach; UCLA W56-117, 2 females, 238.5–319.4 mm TL, male, 240.2, Mexico, Gulf of California, Sinaloa Bahia Topolobampo; UCLA W58-46, 2 females, 446.0–468.0 mm TL, 3 males,

Table 4. Linear discriminant analysis loadings based on characters relating to nasal morphology for the type specimens of P. buthi, new species (n = 82), and associated congeners (n = 10).

Nasal character	LD1	LD2	LD3
Nostril length	43.77076	304.7173	405.2623
Anterior aperture—width	82.76912	-283.555	-445.972
Anterior nasal flap—base length	212.2042	344.9395	71.62146
Anterior nasal flap—width	115.25	-14.6944	-154.307
Posterolateral nasal flap—total length	-8.69895	-85.0812	117.1585
Posterolateral nasal flap—width	-123.253	-412.462	668.55
Posterior nasal flap—base length	6.679548	35.69191	-91.5116
Posterior nasal flap—width	-121.699	-79.0051	74.94099
Distance across anterior nasal apertures	87.46056	-108.099	-233.291
Internarial distance—minimum	27.72144	172.5853	36.04765
Distance between anterior nasal flaps	-65.3202	38.09061	14.32056
Distance from nostril to disc margin	-231.288	178.6837	-44.8242

443.3–459.0 mm TL, Mexico, Gulf of California, Sinaloa Bahia Topolobampo.

Pseudobatos leucorhynchus: LACM W58-278, 2 females, 353.2–442.0 mm TL, 2 males 386.2–515.2 mm TL, Panama, Panama Bay Vilzy; UCLA W53-273, 3 males, 518.1–546.4 mm TL, female, 300.9 mm TL, Panama, Panama Bay Rio Pacora; UCLA W53-317, female, 262.7, male, 206.6, Panama, Gulf of Panama Chimán.

Pseudobatos productus: UCLA W48-3, female, 216.9 mm TL, California, San Pedro; UCLA W49-375, 2 males, 229.7–379.6 mm TL, female, 242.7 mm TL, California, Newport Bay; UCLA W50-128, 2 females, 262.8–364.5 mm TL, 2 males, 298.5–346.1 mm TL, California, Los Angeles Co., Long Beach; UCLA W50-128, 2 males, 251.2–279.8 mm TL, California, Los Angeles Co., Long Beach; UCLA W52-248, 2 males, 239.0–250.3 mm TL, Mexico, Gulf of California, Bahia Santa Maria; UCLA W76-2, 3 males, 276.4–408.4 mm TL, female, 439.3 mm TL, California, Los Angeles Co., Belmont Shore.

Pseudobatos prahli and Pseudobatos planiceps: Images examined from FishBase (Froese and Pauly, 2019), Last et al. (2016b), and Robertson and Allen (2015).

KEY TO GUITARFISHES OF THE GULF OF CALIFORNIA

- 1b. No blue spots on dorsal surface
- 2a. White, almost transparent rostrum; rostral cartilages parallel, widely spaced, nasal tassel absent _______ *P. leucorhynchus*
- 2b. Light brown rostrum; rostral cartilage converging at tip, narrowly spaced, nasal tassel present or absent

ACKNOWLEDGMENTS

This study was completed as a requirement for the Masters degree in Ecology and Evolutionary Biology at the University of California Los Angeles. I would like to thank my Masters committee, D. Buth, M. Gordon, and N. Pinter-Wollman, for their constructive criticism on this manuscript and support. I would also like to thank R. Feeney for his hospitality at the LACM and for performing the radiographs; P. Last, for his confirmation of the morphometrics, meristics, and assistance

with the methodology; F. Torres for her assistance in translating the English abstract to Spanish; P. Hastings and B. Frable (SIO) for their assistance with loans and specimens; and D. Kirkbride for his unwavering support.

LITERATURE CITED

- Compagno, L. J. V. 1984. FAO Species Catalogue. Vol. 4. Sharks of the World. An Annotated and Illustrated Catalogue of Shark Species Known to Date. Part 1. Hexanchiformes to Lamniformes. FAO Fisheries Synopsis No. 125, Vol. 4, Part 1. FAO, Rome.
- Froese, R., and D. Pauly (Eds.). 2019. FishBase. World Wide Web electronic publication. www.fishbase.org, version (02/2019).
- Kassambara, A., and F. Mundt. 2017. factoextra: extract and visualize the results of multivariate data analyses. R package version 1.0.5. https://CRAN.R-project.org/package=factoextra
- Last, P. R. 2004. *Rhinobatos sainsburyi* n.sp. and *Aptychotrema timorensis* n.sp.—two new shovelnose rays (Batoidea: Rhinobatidae) from the eastern Indian Ocean. Records of the Australian Museum 56:201–208.
- Last, P. R., L. J. V. Compagno, and K. Nakaya. 2004. *Rhinobatos nudidorsalis*, a new species of shovelnose ray (Batoidea: Rhinobatidae) from the Mascarene Ridge, central Indian Ocean. Ichthyological Research 51:153–158.
- Last, P. R., S. Corrigan, and G. P. Naylor. 2014. *Rhinobatos whitei*, a new shovelnose ray (Batoidea: Rhinobatidae) from the Philippine Archipelago. Zootaxa 3872:31–47.
- Last, P. R., B. Séret, and G. P. Naylor. 2016a. A new species of guitarfish, *Rhinobatos borneensis* sp. nov. with a redefinition of the family-level classification in the order Rhinopristiformes (Chondrichthyes: Batoidea). Zootaxa 4117:451–475.
- Last, P. R., W. White, M. R. de Carvalho, B. Séret, M. Stehmann, and G. P. Naylor. (Eds.). 2016b. Rays of the World. CSIRO Publishing, Melbourne, Australia.
- Moore, A. 2017. Guitarfishes: the next sawfishes? Extinction vulnerabilities and an urgent call for conservation action. Endangered Species Research 34:75–88.
- R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/
- Robertson, D. R., and G. R. Allen. 2015. Shorefishes of the Tropical Eastern Pacific: online information system. Version 2.0. Smithsonian Tropical Research Institute, Balboa, Panamá.
- Sabaj, M. H. 2019. Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an Online Reference. Version 6.5 (22 May 2018). Electronically accessible at http://www.asih.org/, American Society of Ichthyologists and Herpetologists, Washington, D.C.
- Venables, W. N., and B. D. Ripley. 2002. Modern Applied Statistics with S. Fourth edition. Springer, New York.
- Wickham, H. 2009. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.
- Wickham, H., J. Hester, and W. Chang. 2018. devtools: tools to make developing R packages easier. R package version 1.13.5. https://CRAN.R-project.org/package=devtools