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**Description of two extraordinary new species of freshwater stingrays of
the genus *Potamotrygon* endemic to the rio Tapajós basin, Brazil
(Chondrichthyes: Potamotrygonidae), with notes on other Tapajós stingrays**

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Abstract

Stingrays from the rio Tapajós basin are reviewed based on material collected from its lower (i.e. from the mouth-lake to Itaituba), middle (from about the São Luiz rapids to the confluence of rios Juruena and Teles Pires), and upper (above the Juruena-Teles Pires confluence) segments. Two new species endemic to the mid and upper Tapajós, discovered long ago and common in the ornamental fish trade, are described. *Potamotrygon albimaculata* **sp. nov.** is part of the black stingray species group, and is diagnosed by its blackish brown dorsal disc color with numerous and generally evenly-spaced small whitish spots and faint ocelli, multiple rows of thorns broadly spread on dorsal and lateral tail, pelvic fins with broadly rounded apices, and two angular cartilages with the posterior far more slender but about as wide as the anterior angular. *Potamotrygon jabuti* **sp. nov.** is diagnosed by its marbled color pattern that undergoes remarkable change with growth as adults have elaborate designs of beige, golden to yellowish-orange spots or ocelli surrounded by a slender beige to golden mesh-like pattern, but neonates have simple, well-separated ocelli; this species also has a single to double row of tail thorns varying in their development, monognathic heterodonty with teeth of intermediate lateral rows of upper jaws larger and hexagonal, and two robust, more or less equally developed angular cartilages. Both species co-occur in the relatively fast-flowing mid and upper Tapajós basin, but mostly occupy different areas of the river, with *P. albimaculata* **sp. nov.** more abundant in its central troughs but foraging at its margins, whereas *P. jabuti* **sp. nov.** is also present in smaller streams over rocky, sandy and leafy substrates. The Tapajós basin includes at least seven stingray species, but additional species probably also occur. *Potamotrygon motoro*, *P. orbignyi*, *P. humerosa*, *Potamotrygon* sp., and *Paratrygon aiereba* are present in the lower Tapajós mouth-lake, which may also include *Plesiotrygon* and *Heliotrygon* species. In addition to the new species described herein, *P. orbignyi* and *Paratrygon* cf. *aiereba* occur in the mid and upper Tapajós, along with another form (*Potamotrygon* cf. *scobina*) known only from the region of the São Luiz rapids. Therefore, three additional new species may be present in the Tapajós basin, which has one of the most diverse stingray assemblages known together with the rios Negro and Tocantins-Araguaia.

Key words: *Potamotrygon albimaculata* **sp. nov.**, *Potamotrygon jabuti* **sp. nov.**, Neotropical region, morphology, systematics, taxonomy, Brazilian Shield, endemism

Introduction

The most important early work that contributed species descriptions of Neotropical freshwater stingrays (Potamotrygonidae) was the epochal revision and classification of elasmobranchs by Müller & Henle (1841), which summarized knowledge of the group and described two new species, *Trygon aiereba* (= *Paratrygon aiereba*) and *Taeniura motoro* (= *Potamotrygon motoro*). The number of potamotrygonid species increased substantially shortly thereafter with the accounts on the fishes of rio Branco by Schomburgk (1843) and especially of rios Tocantins and Araguaia by Castelnau (1855), who described four species available in *Potamotrygon* (two presently valid). Duméril's (1865) review included one new form (*Taeniura magdalenae* credited to A. Valenciennes) and recognized 10 species of potamotrygonids (six presently valid), a significant increase from the three treated in Müller & Henle (1841); subsequent revisions, however, recognized fewer species than Duméril (Günther, 1870; Garman, 1877). Günther (1880) and Vaillant (1880) together described three additional forms, such that by the end of the 19th Century 10 to 13 potamotrygonid species were being recognized (out of 15 available); of these, only eight are presently considered valid.

In the 20th Century, potamotrygonid diversity increased most notably in two specific periods, one as a result of Samuel Garman's (1913) comprehensive review 36 years after having first worked on the group (Garman, 1877), and the other due to the laudable efforts of the Argentine jesuit and ichthyologist Mariano Castex and colleagues in the 1960s. Even though some of the new species described by these authors have been placed in synonymy (Rosa, 1985; Carvalho *et al.*, 2003; Silva & Carvalho, 2011a; Loboda & Carvalho, 2013), and that some of their conclusions contributed to subsequent taxonomic confusion (see Rosa, 1985; Carvalho *et al.*, 2003; Loboda & Carvalho, 2013), their works stand as milestones to any serious student of Neotropical freshwater stingrays.

The recent descriptions of *Potamotrygon wallacei* Carvalho, Rosa & Araújo, 2016 and *P. rex* Carvalho, 2016 from the rios Negro and Tocantins, respectively, has increased to 30 the number of species recognized as valid in the four genera of Neotropical freshwater stingrays (Rosa, 1985; Carvalho & Lovejoy, 2011; Carvalho, 2016; Carvalho *et al.*, 2016). The taxonomic diversity of the family has been in steady increase for the past decade (e.g. Rosa *et al.*, 2008; Carvalho & Lovejoy, 2011; Carvalho & Ragno, 2011; Carvalho *et al.*, 2011, 2016; Silva & Carvalho, 2011a, b; Loboda & Carvalho, 2013; Fontenelle *et al.*, 2014). However, our understanding of potamotrygonid diversity is far from complete, and will continue to rise substantially in the near future as many new species have been discovered as a result of more comprehensive revisions (e.g. Fontenelle & Carvalho, unpubl.; Loboda & Carvalho, unpubl.). It is only through more encompassing studies that the elevated morphological variation present in many potamotrygonid species can be more fully understood (e.g. Silva & Carvalho, 2011a, 2015).

In this context, the present paper describes two new species discovered long ago during the ongoing systematic revision of the Potamotrygonidae; one species was determined to be new in the very early 1990s, the other in the early 2000s. But lack of significant series of specimens of these forms from throughout their ranges impeded thorough descriptions and more reliable diagnoses, a situation finally remedied by more field work, both my own and that of colleagues. Moreover, both species have very striking color patterns and figure prominently in the aquarium trade, such that their description has become essential. The present paper is part of a larger effort revising the morphology, systematics and evolutionary history of the Neotropical freshwater stingray clade (e.g. Carvalho, *in press*).

The rio Tapajós basin drains the western portion of the Brazilian crystalline shield and originates entirely within Mato Grosso state; its watershed forms rio Juruena draining the Serra dos Parecis and rio Teles Pires formed in the Serra do Roncador/Planalto de Mato Grosso region. The fishes of the mid and upper Tapajós basin were, until recently, *terra incognita* (Vari, 1988). Although precise figures are lacking, a very conservative estimate indicated that some 250 species of fishes occur there, of which at least 25% are endemic (Albert *et al.*, 2011), but more accurate sources cite much higher numbers (slightly more than 500 total species, with just under 20% endemic; Lima, 2010; Buckup *et al.*, 2011; Lima, pers. comm.). Nonetheless, the tally of endemic species increases rapidly as more studies are completed (see summary in Vari & Calegari, 2014). This rich diversity is to some degree expected as both main branches that form the Tapajós are clearwater and fast-flowing rivers laden with rapids and waterfalls that may serve as isolating barriers (Goulding *et al.*, 2003; Britski & Garavello, 2005; Britski & Lima, 2008; Vari & Calegari, 2014). This is evident in regard to stingrays, as their distribution in the Tapajós reflects the pattern of other Amazonian affluents draining the Brazilian plateau, in which endemic forms, including a black stingray species, occur in their mid and upland areas, whereas more widely distributed species are abundant in their lowland segments. Hence, the most common stingray species in the middle and upper rio Tapajós are the two endemic forms described below; the present paper also summarizes the occurrence of the Potamotrygonidae in the Tapajós basin.

Material and methods

Measurements and counts were modified from Bigelow & Schroeder (1953), Compagno & Roberts (1982), Rosa (1985) and Carvalho & Lovejoy (2011), and are described in detail in Carvalho & Lovejoy (2011). Proportional measurements are expressed as percentages of disc width (DW) and were taken to the nearest mm with tape measure and/or steel ruler. Counts of fin radials and vertebrae were made from x-ray radiographs, cleared and stained (c&s), and/or dissected specimens. Digital x-ray radiographs were taken at the Hospital Veterinário da Faculdade de Medicina Veterinária e Zootecnia da Universidade de São Paulo (FMVZ-USP), and analyzed using

Osirix for Mac OSX; x-ray radiographs were also taken with Kodak mammography film (Min-R2000) in the radiology section of the Hospital Central, USP, Ribeirão Preto campus. Tooth-row counts were made using a stereomicroscope and directly on specimens after manual dissection of the jaws, or from radiographs, and include the total number of tooth rows. Cleared and stained specimens were prepared following Dingerkus & Uhler (1977). Ventral lateral-line canals were observed after superficial dissection of the skin. Anatomical terminology is as follows: Carvalho *et al.* (2004) for skeletal structures, Deynat & Séret (1996) for dermal denticles, Taniuchi & Ishihara (1990) for clasper structures, and Garman (1888), Ewart & Mitchell (1892), and Chu & Wen (1979) for ventral lateral-line canals. Specimens were captured in the field with the aid of hand nets, by hook and line, and/or long-lines placed during the night and checked a few times before sunrise, baited with bony fishes (usually characiforms). Specimens were photographed fresh or still alive, injected with strong formalin in the field, and maintained, as far as possible, in a straight position during fixation. The designations middle and upper rio Tapajós refer to the segment above São Luiz rapids (just upriver from Itaituba and downriver from Pimental) and above the confluence of rios Jurueña and Teles Pires, respectively. Anatomical abbreviations are provided in the figure legends. Institutional abbreviations follow Sabaj Pérez (2014). All material is deposited in MZUSP. Abbreviations used throughout the text are DL for disc length, DW for disc width, and TL for total length. Comparative material examined of *P. rex*, *P. henlei* and *P. leopoldi* are listed in Carvalho (2016); material of other species is listed in Loboda & Carvalho (2013), Silva & Carvalho (2015) and before the Acknowledgements.

Genus *Potamotrygon* Garman, 1877

Trygon [in part]: Müller & Henle, 1841: 167, 197, 198 (*T. hystrix*); Schomburgk, 1843: 182 (*T. garrapa*); Castelnau, 1855: 103 (*T. hystrix*); Duméril, 1865: 608, 609 (as a genus and subgenus for *T. hystrix*); Günther, 1870: 482 (*T. hystrix*); Günther, 1880: 7, 8 (*T. hystrix*, *T. brachyurus*, and *T. reticulatus*); Engelhardt, 1912: 647 (*T. hystrix* var. *ocellata*).

Taeniura [in part]. Müller & Henle, 1841: 197, 198 (*T. motoro*); Duméril, 1865: 618, 621–625 (*T. motoro*, *T. mülleri* [sic], *T. orbignyi*, *T. magdalenae*, *T. dumerilli*, and *T. henlei*); Günther, 1870: 483, 484 (*T. motoro*, *T. mülleri* [sic], *T. orbignyi*, *T. magdalenae* and *T. humboldtii*); Vaillant, 1880: 251, 252 (*T. constellata*).

Taenura [sic]: Castelnau, 1855: 101, 102, pl. 48 (as a subgenus of *Trygon* in text for *T. dumerilli*, *T. mulleri*, *T. henlei*, and *T. d'orbignyi* [sic], but as genus in plate 48).

Toemura [sic]: Castelnau, 1855: pl. 49 (*T. d'orbignyi* [sic]).

Potamotrygon Garman, 1877: 208, 210–214 (*P. humboldtii*, *P. motoro*, and *P. dumerilli*).

Ellipesurus [in part]: Miranda Ribeiro, 1907: 140, 183–187 (*E. reticulatus*, *E. hystrix*, *E. motoro*, and *E. orbignyi*) (account repeated in Miranda Ribeiro, 1923).

Paratrygon: Fowler, 1948: 5–10 (*P. brachyurus*, *P. circularis*, *P. humerosus*, *P. hystrix*, *P. laticeps*, *P. motoro*, *P. reticulatus*, *P. scobina*, *P. signatus*, and *P. ajereba* [sic], the latter deemed congeneric with the preceding species [*Disceus thayeri* Garman, 1877 also recognized]).

Diagnosis. A potamotrygonid genus distinguished from *Paratrygon* Duméril, 1865, *Plesiotrygon* Rosa, Castello & Thorson, 1987, and *Heliotrygon* Carvalho & Lovejoy, 2011 by the following combination of characters: disc broadly oval to circular, usually tapering posteriorly towards insertions, with small median protuberance on anterior snout, and not anteriorly concave; head generally broad and clearly raised above disc; eyes relatively large, two to three times smaller than interorbital distance, and bulging, somewhat pedunculate; spiracles well developed, rhomboidal and lacking posterior protuberance; teeth variably developed, with triangular to rhomboidal cusps frequently more pointed in adult males, varying from 20–50 rows in upper and lower jaws in adults; some species with monognathic heterodonty with larger hexagonal, flattened lateral cusps; pelvic fins broad and only partially concealed underneath disc; tail stout and muscular, its width generally about two-thirds interorbital distance; tail not whip-like, relatively short, usually less than disc width in adults, proportionally greater in neonates and small juveniles, and terminating shortly posterior to caudal stings; tail with dorsal and ventral finfolds (usually low in adults), with fleshy lateral ridges; tail laterally compressed posterior to caudal stings; enlarged thorns on dorsal tail surface, usually extending from tail base to caudal stings but absent posterior to caudal stings; tail thorns variable, from four to five evenly distributed series to a single irregular series; tail thorns with broad bases and acute high to relatively low crowns; thornlets on lateral tail frequently present, extending posteriorly beyond caudal stings; dermal denticles covering dorsal disc, more intense on mid-disc, sometimes with small and large denticles (some species very prickly); larger dermal denticles usually stellate with multiple radiating coronal ridges; caudal stings

well developed and robust, with very acute extremity and anteriorly pointed lateral serrations, these greater toward sting center and extremity; dorsal disc, pelvic fins and tail generally very colorful, with numerous different patterns, including spotted, ocellated, reticulated, marbled and/or a combination of these; ventral surface generally creamy white but some species darker on disc margins, pelvic fins, and ventral tail; one or two broad angular cartilages present, when two present these positioned in parallel in hyomandibular-Meckelian ligament; a few species with a small additional angular element abutting hyomandibulae, posterior to anterior angular; anterior angular slightly to strongly concave; anterior ceratobranchials medially fused to some degree, although variable; coracoid bar not anteroposteriorly expanded; anterior ventral lateral-line canals not forming complex reticulate or honeycombed pattern; pectoral radial elements varying from about 90–110; total vertebrae also variable but usually between 100–125 centra.

Type species. Generally considered to be *Trygon histrix* Müller & Henle, 1836 (dated here according to Sherborn & Griffin, 1934) by designation of Jordan (1919), but Kottelat (2013) considers *Pastinaca humboldtii* Roulin (made available in Lesson, 1829) to be the type species as designated by Eigenmann (1910).

Included species. Twenty-seven species presently recognized: *Potamotrygon albimaculata*, **sp. nov.** (described below), *P. amandae* Loboda & Carvalho, 2013, *P. boesemani* Rosa, Carvalho & Wanderley, 2008, *P. brachyura* (Günther, 1880), *P. constellata* (Vaillant, 1880), *P. falkneri* Castex & Maciel, 1963, *P. henlei* (Castelnau, 1855), *P. histrix* (Müller & Henle, 1836), *P. humerosa* Garman, 1913, *P. jabuti*, **sp. nov.** (described below), *P. leopoldi* Castex & Castello, 1970, *P. limai* Fontenelle, Capretz & Carvalho, 2014, *P. magdalenae* (Valenciennes, 1865), *P. marinae* Deynat, 2006, *P. motoro* (Müller & Henle, 1841), *P. ocellata* (Engelhardt, 1912), *P. orbigny* (Castelnau, 1855), *P. pantanensis* Loboda & Carvalho, 2013, *P. rex* Carvalho, 2016, *P. scobina* Garman, 1913, *P. schroederi* Fernandez-Yépez, 1958, *P. schuhmacheri* Castex, 1964, *P. signata* Garman, 1913, *P. tatianae* Silva & Carvalho, 2011, *P. tigrina* Carvalho, Sabaj-Perez & Lovejoy, 2011, *P. wallacei* Carvalho, Rosa & Araújo, 2016, and *P. yepezi* Castex & Castello, 1970. *Potamotrygon constellata* and *P. ocellata* are poorly defined and tentatively considered valid pending further studies.

***Potamotrygon albimaculata*, sp. nov.**

(Figs. 1–20, Tables 1–2)

Holotype. MZUSP 105016, adult female, 790 mm TL, 531 mm DL, 500 mm DW, left bank of rio Teles Pires near Pousada Santa Rosa, rio Tapajós basin, Mato Grosso state, Brazil, 08°46'45"S, 057°27'55"W, col. M.R. de Carvalho, F. Marques, M. Carvalho & A. Datovo (field no. MT05.21) (Figs. 1, 2).

Paratypes. (5 specimens). MZUSP 103922, juvenile male, 470 mm TL, near mouth of igarapé Ponto Frio, Comunidade Pimental, right margin of rio Tapajós, Pará state, Brazil, 4°33'05"S, 056°16'43"W, 10.x.2005, col. M.R. de Carvalho, M. Cardoso, M.L.G. de Araújo & S.M.V. Melo (field no. TJ05.39); MZUSP 104999, adult female, 641 mm TL, same data as holotype (field no. MT05.16) (Fig. 6); MZUSP 105001, adult male, 605 mm TL, same data as holotype (field no. MT05.04) (Fig. 3); MZUSP 105006, adult male, 665 mm TL, same data as holotype (patch of skin removed for SEM of denticles) (field no. MT05.09) (Fig. 4); MZUSP 105010, juvenile female, 515 mm TL, same data as holotype (field no. MT05.13) (Fig. 8).

Diagnosis. A species of *Potamotrygon* endemic to the mid and upper rio Tapajós, diagnosed by its unique color pattern, composed of an intense, uniform dark brown to blackish-brown dorsal color with whitish, circular spots on dorsal disc and tail base, usually smaller than eye-diameter, sometimes forming faint ocelli, and not closely packed together; spots sometimes irregular in shape or vermiform, but not fused together to form more elaborate markings; ventral color dark brown, more intense closer to disc margins and fading toward central disc, with creamy white ventral snout, anterior disc area, and branchial slit region, with few small, faint whitish to grayish blotches on dark brown ventral disc, pelvic fins and ventral tail base. In addition, *P. albimaculata*, **sp. nov.**, can be diagnosed from congeners by the combination of having numerous regularly distributed dorsal tail thorns in irregular parallel rows, with thorns evenly spread out and covering all of dorsal and most of lateral tail region, with a relatively large space between individual thorns (i.e. thorns not closely packed together) (only *P. leopoldi* has a vaguely similar pattern of dorsal tail thorns, but with fewer thorns in a less broad but well defined band on central dorsal tail area); pelvic fins with broadly circular apices (also present in *P. rex*, *P. henlei* and *P. leopoldi*, but these black stingray species have distinct and specific color patterns); absence of discrete labial grooves (strong grooves

present at least in *P. orbignyi*, *P. humerosa*, *P. marinae*, and *P. constellata*); and two angular cartilages, with anterior angular cartilage more stout than slender posterior angular (single angular present in *P. tigrina*, *P. schroederi*, *P. constellata*, *P. magdalenae*, *P. histrix*, *P. schuhmacheri*, *P. orbignyi*, *P. humerosa*, *P. marinae*, and *P. wallacei*; anterior angular broad and posterior angular absent or very small, abutting hyomandibula, in *P. signata*, *P. pantanensis* and *P. amandae*; anterior and posterior angulars present in addition to a small lateral element in *P. limai* and *P. scobina*).

Description. Moderately large-sized stingray (holotype largest examined specimen, 790 mm TL, 531 mm DL, 500 mm DW). Disc rounded, only slightly oval, disc length just greater than disc width (DL 104.9–114.2% DW); greatest disc width slightly anterior to its mid-length. Disc tapers only slightly closer to pectoral insertion. Anterior snout with very small knob-like protuberance, more developed in neonates and juveniles and smaller in adults. Anterior disc margin broadly convex, especially in larger adult specimens. Head relatively flat, not greatly protruding above disc (Fig. 9a), and not particularly broad. Eyes moderately large, somewhat bulging in live specimens, flattened in preserved material (Figs. 9b, 12). Eye diameter 3.6–5.9% DW, between 2–3 times in interorbital distance. Preorbital distance 22.5–26.0% DW, about twice interorbital distance in larger specimens. Spiracles relatively large and broadly rhomboidal in live specimens, more slender in preserved specimens (Fig. 9a). Spiracle elongate and wide, much greater than eyes. Interspiracular distance 15.0–20.0% DW, greater than interorbital distance. Spiracles extending anterolaterally to at least mid-diameter of eyes.

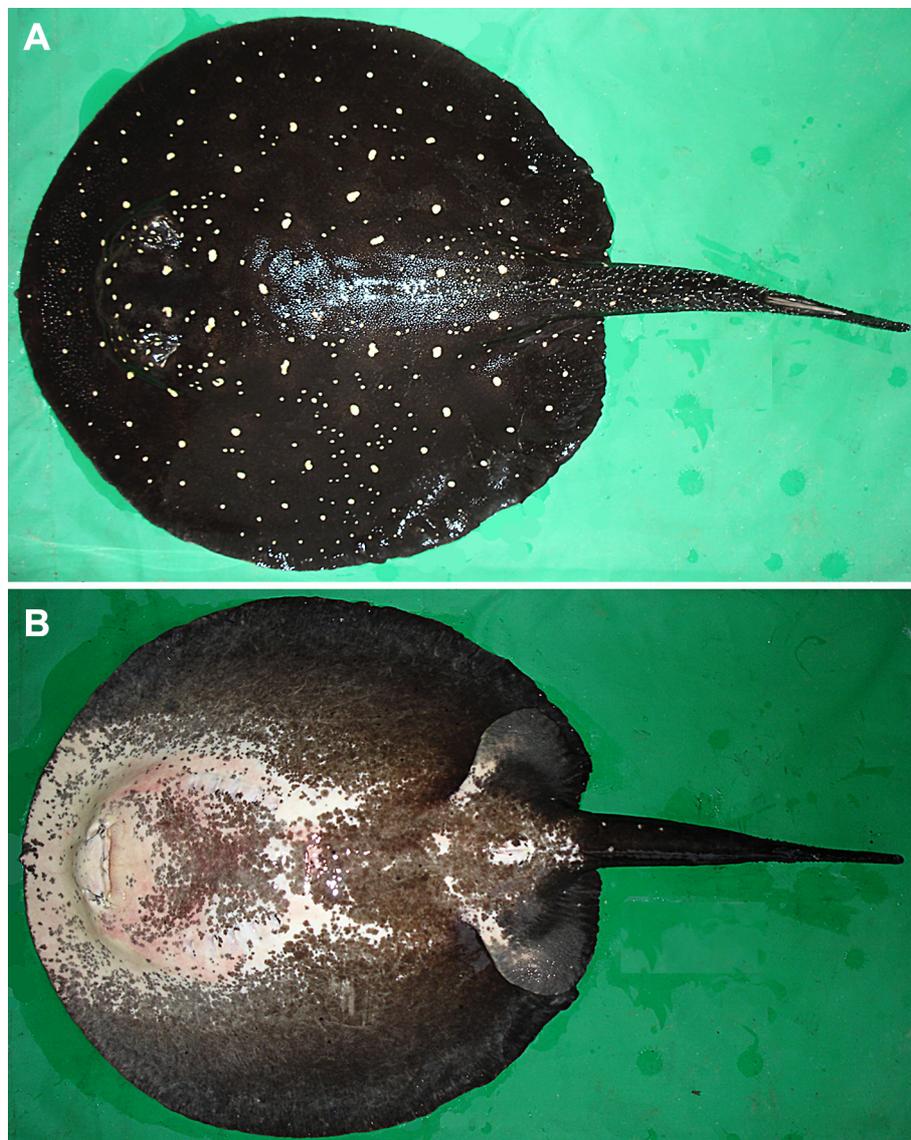


FIGURE 1. Dorsal (A) and ventral (B) views of freshly collected holotype of *Potamotrygon albimaculata*, sp. nov.

TABLE 1. Measurements of specimens of *Potamotrygon albimaculata*, **sp. nov.** Ranges, means, and standard deviations were calculated from measurements of all specimens (N).

	MZUSP 105016 holotype			N	Range			Mean			SD		
	mm	% DW			mm	% DW		mm	% DW		mm	% DW	
Total length	790.0	158.0		23	383–790	139.7–178.0	554.1	166.0	107.8	7.8			
Disc length	531.0	106.2		23	245–582	104.9–114.2	368.7	109.9	81.4	2.9			
Disc width	500.0	100.0		23	231–544	100.0–100.0	336.4	100.0	78.8	0.0			
Interorbital space	66.0	13.2		23	28–66	8.0–15.0	40.4	12.0	11.0	1.3			
Interspiracular space	85.0	17.4		23	45–85	15.0–20.0	59.3	17.8	10.6	1.2			
Eye diameter	21.0	4.2		23	12–27	3.6–5.9	15.6	4.6	4.2	0.6			
Spiracle length	25.0	5.0		23	20–38	5.0–10.5	24.8	7.6	4.2	1.5			
Preorbital length	115.0	23.0		23	58–125	22.5–26.0	80.6	24.1	17.1	0.9			
Prenasal length	75.0	15.0		23	34–75	12.4–16.4	48.7	14.5	11.5	0.9			
Preoral length	103.0	20.6		23	49–111	19.2–22.6	70.0	20.8	16.2	1.0			
Internasal space	41.0	8.2		23	19–48	7.2–10.2	28.4	8.4	8.0	0.8			
Mouth width	48.0	9.6		23	26–52	8.9–16.5	36.1	10.9	7.3	1.7			
Distance between 1st gill slits	135.0	27.0		22	61–135	24.5–27.8	86.4	25.8	21.4	0.8			
Distance between 5th gill slits	106.0	21.2		22	43–106	16.6–21.2	62.4	18.5	17.5	1.1			
Branchial basket length	74.0	14.8		23	40–90	14.8–19.0	56.5	16.9	11.7	1.2			
Pelvic fin anterior margin length	112.0	22.4		23	53–112	20.2–27.9	79.1	23.7	15.7	1.9			
Pelvic-fin width	257.0	51.4		23	126–257	42.3–59.3	176.6	53.0	35.7	4.7			
Clasper internal margin	–	–		11	10–40	4.3–12.5	29.9	9.1	10.8	2.8			
Cloaca to clasper tip	–	–		11	36–103	15.6–27.1	75.4	22.5	24.1	4.3			
Cloaca to tail tip	341.0	68.2		23	164–341	46.9–82.0	242.7	73.3	41.7	7.1			
Tail width	77.0	15.4		23	19–80	8.2–17.7	47.1	13.7	16.6	2.3			
Snout to cloaca distance	432.0	86.4		23	205–467	82.0–93.8	293.8	87.5	66.2	2.6			
Disc insertion to post. pelvic margin	75.0	15.0		23	36–75	12.6–19.3	51.5	15.5	10.4	1.7			
Cloaca to sting origin	190.0	38.0		23	101–236	38.0–49.1	147.6	44.0	33.8	2.7			
Sting length	79.0	15.8		23	2–79	0.7–22.9	57.0	17.2	16.8	4.8			
Sting width	6.0	1.2		23	2–9	0.7–3.0	5.5	1.7	1.7	0.6			



FIGURE 2. Dorsal (A) and ventral (B) views of holotype of *Potamotrygon albimaculata*, **sp. nov.** (MZUSP 105016, adult female, 790 mm TL, 531 mm DL, 500 mm DW).

Nasal curtain slightly more broad posteriorly, trapezoidal, with small median indentation more visible in live specimens (Fig. 9c). Nasal curtain covers almost all of mouth opening (more visible in live or fresh specimens). Posterior margin of nasal curtain with small fringes. Nostrils very slender, moderately elongate. Mouth slightly arched and relatively small, its width just greater than internasal distance. Posterior margin of mouth with small median notch. Labial folds absent. Integument posterior to mouth slightly rugose. Floor of mouth with five buccal papillae. Preoral distance 19.2–22.6% DW, just smaller than preorbital distance. Teeth very small and numerous, set in quincunx, in 28–44/25–58 total longitudinal rows in large juveniles and adults; 40/46 in adult male (MZUSP 105001), 32/38 in large juvenile male, almost adult (MZUSP 103922); 28/32 in female almost adult (MZUSP 120446); holotype with 44/58. In some preserved specimens, few exposed median tooth rows present on both upper and lower dental plate (not in live specimens nor fresh material). Tooth crown rhomboidal in apical view,

with slightly concave anterior margin; mature males with very small cusps. Branchial basket relatively wide, distance between first pair of gill slits up to one-fourth DW, distance between fifth gill slits up to about one-fifth DW. Fifth gill slits about half of width of first gill slit; gill slits weakly sinuous.

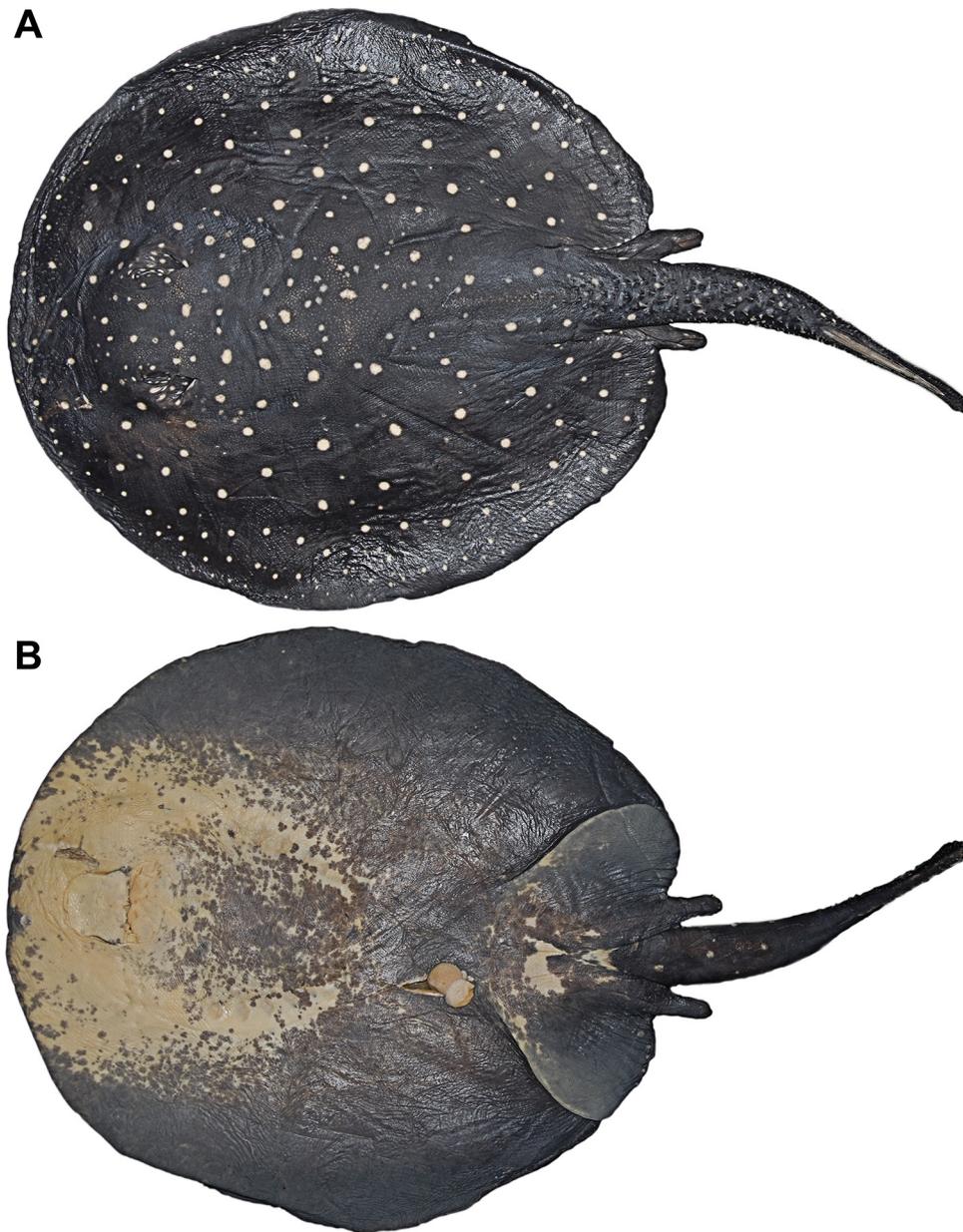


FIGURE 3. Dorsal (A) and ventral (B) views of *Potamotrygon albimaculata*, **sp. nov.** (MZUSP 105001, paratype, adult male, 605 mm TL, 405 mm DL, 372 mm DW).

Pelvic fins moderately broad and broadly rounded at apices, with strongly convex anterior margin (Fig. 9d). Pelvic fins almost entirely covered by disc, visible in dorsal view only at area of pectoral fin insertions, barely protruding posteriorly beyond disc. Claspers in adult males relatively short and stout, extending posteriorly to up to one-fourth tail length. Tail only moderately long, its length much smaller than disc width. Tail length slightly greater in neonates and smaller juveniles. Tail tapering only slightly to level of caudal stings, without abrupt lateral constriction at level of caudal stings. Tail extremity a short distance posterior to caudal stings. Tail width at base about two-thirds interorbital distance. Lateral tail ridges well developed, fleshy, present from tail base to close to caudal sting origin. Tail in cross-section slightly flattened dorsoventrally. Tail with low, poorly developed dorsal and ventral finfolds; dorsal and ventral caudal folds greater in neonates and small juveniles, usually reduced to low ridges in adults. Caudal stings only moderately long, relatively slender; one to two stings present. Lateral barbs greater at sting anterior third to about its midlength; barbs closer to sting base very small and more numerous.

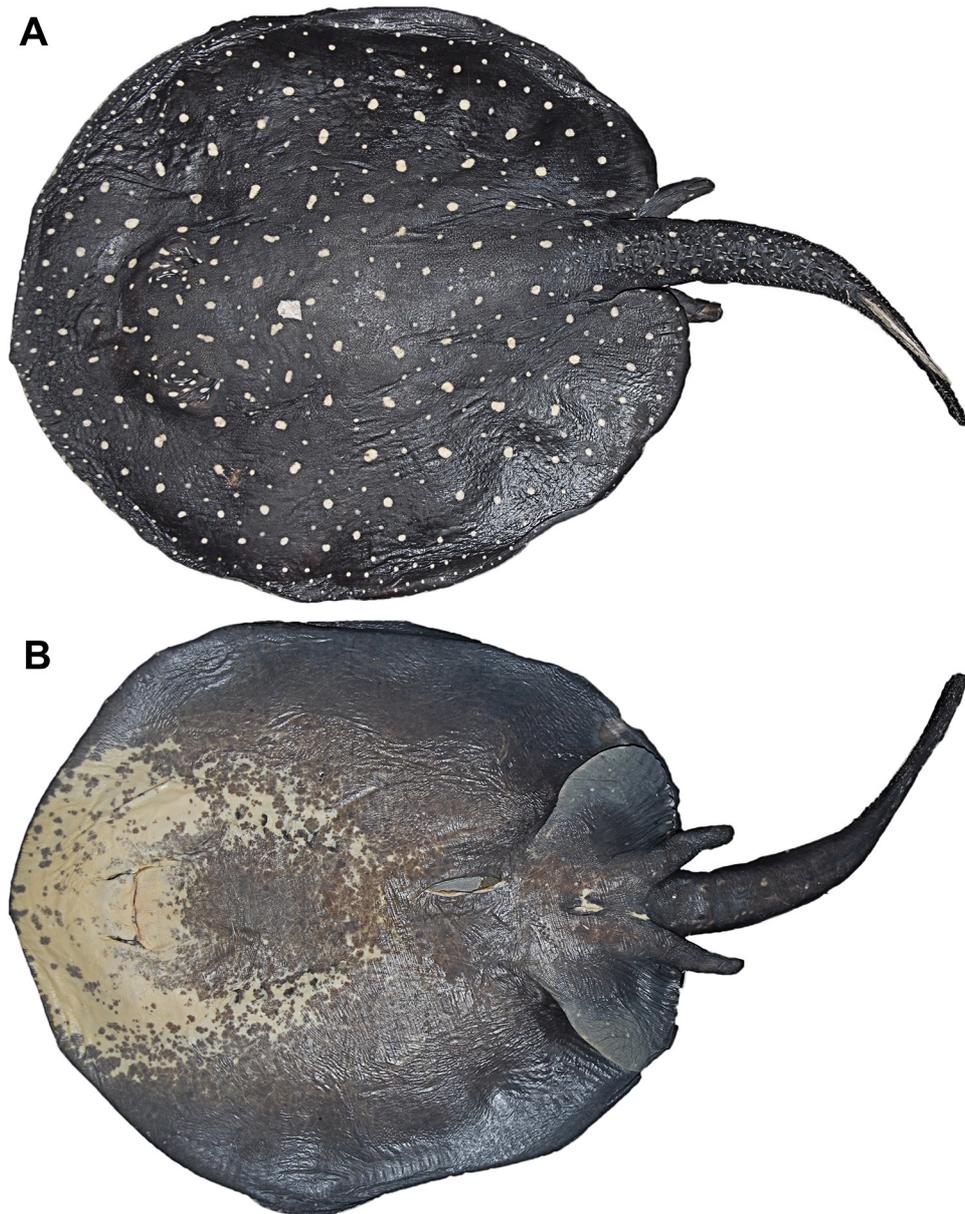


FIGURE 4. Dorsal (A) and ventral (B) views of *Potamotrygon albimaculata*, **sp. nov.** (MZUSP 105006, paratype, adult male, 665 mm TL, 432 mm DL, 385 mm DW).

Coloration. *Adults.* Dorsal surface of disc intense uniform dark brown to blackish-brown, with white to creamy-white, circular spots on dorsal disc and tail base (Figs. 1–10, 12). In some specimens dark brown to blackish color more intense closer to spots, and more faded in regions in between spots (more noticeable is some specimens when thick mucous covering removed). Spots smaller than eye-diameter, larger generally on intermediate disc areas between outer disc and central disc, or on postero-central disc. Spots sometimes form faint ocelli, with slightly darker brown outer margins and light-colored centers. Spots and dorsal markings not closely packed together, appearing less numerous with growth as larger adults have fewer spots. Spots sometimes irregular in shape or vermiform on central disc, but not fused together to form more elaborate markings; spots sometimes more grouped and small on central disc posterior to eyes. Spots more or less organized in concentric rows on disc, with smallest spots on outer disc rows near disc margin. Small spots sometimes grouped more closely on eyes and inside spiracles (holotype; Figs. 1, 2), and between larger spots on central disc. Pelvic fins and tail with same pattern of disc, with few spots on tail.

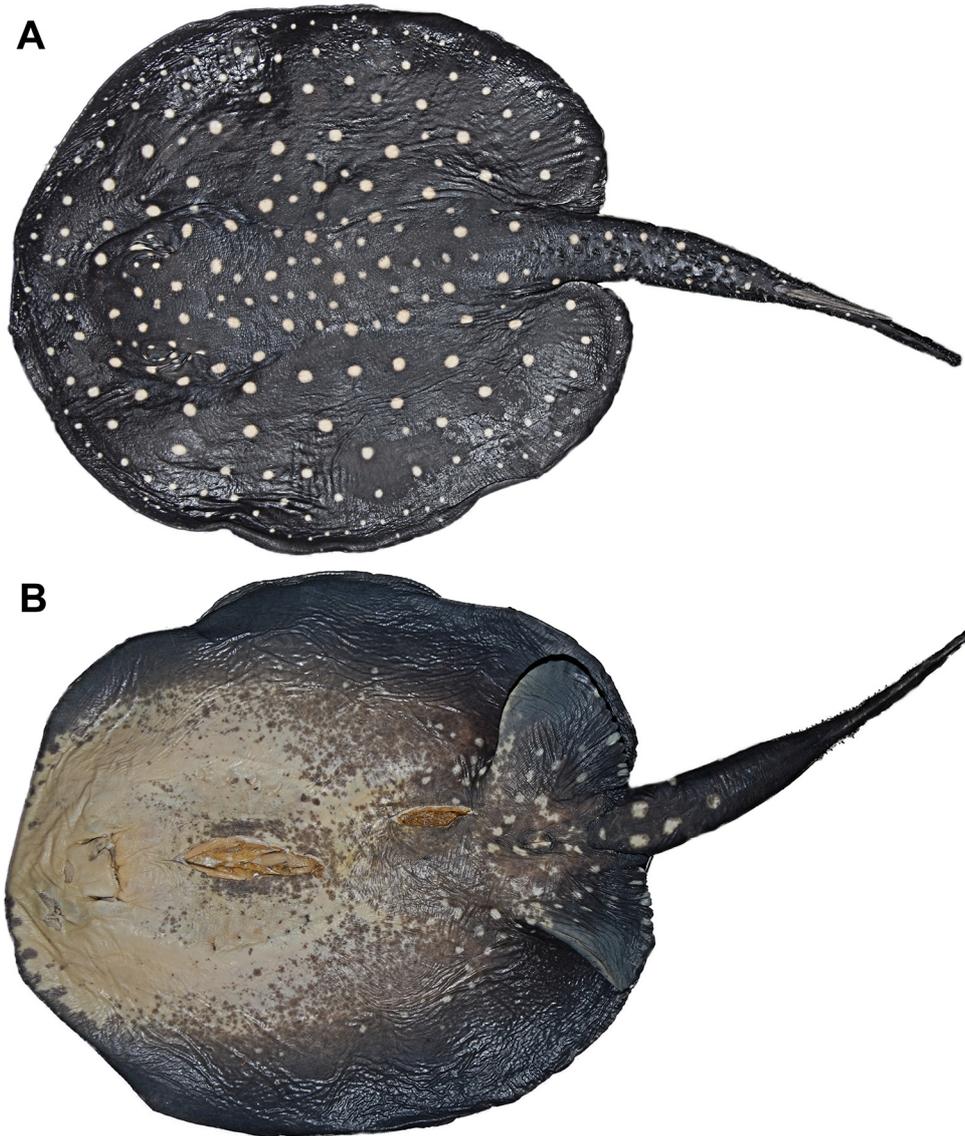


FIGURE 5. Dorsal (A) and ventral (B) views of *Potamotrygon albimaculata*, **sp. nov.** (MZUSP 105007, juvenile male, 473 mm TL, 301 mm DL, 275 mm DW).

Lateral and posterior ventral disc dark brown, more intense closer to disc margins and fading slightly toward disc center, with creamy white ventral snout, anterior disc, and branchial slit areas; interbranchial region mottled with dark brown color (Figs. 1–8, 11, 12f). Anterolateral disc mottled dark brown. Isolated brown to grayish specks present on creamy white areas. Ventral pelvic fins and ventral tail dark brown, but anterior pelvic fins and area in between pelvics commonly creamy white in larger specimens. Few small (smaller or about equal to eye diameter), faint, subcircular to circular whitish to grayish spots or blotches present on dark brown areas of ventral disc, pelvic fins, and ventral tail base.

Neonates and small juveniles. Neonates with striking dark brown to blackish reticulate pattern on disc delimiting light brown spaces with very small whitish spots at center (Fig. 13); dark reticulate pattern very strong on tail; tail appearing banded laterally with alternate light and dark brown bands. Dark reticulate pattern becomes uniform dark blackish-brown pattern after about one month (R. Hardwick and G. England, pers. comm.). Field collected small juveniles (MZUSP 120447, 207 mm TL, 134 mm DL, 111 mm DW) with more uniform dark brown color with numerous closely packed spots (compared to larger juveniles and adults); spots on central disc larger than outermost disc spots in juveniles, slightly smaller than eye diameter; small spots on disc periphery more numerous in double, irregular, more or less concentric rows. Ventrally neonates and small juveniles with much

smaller dark brown areas, confined to posterior and outer disc and posterior pelvic fins; dark brown color increases with size. Numerous small whitish spots or ocelli present on darker ventral areas, smaller towards posterior disc margins.

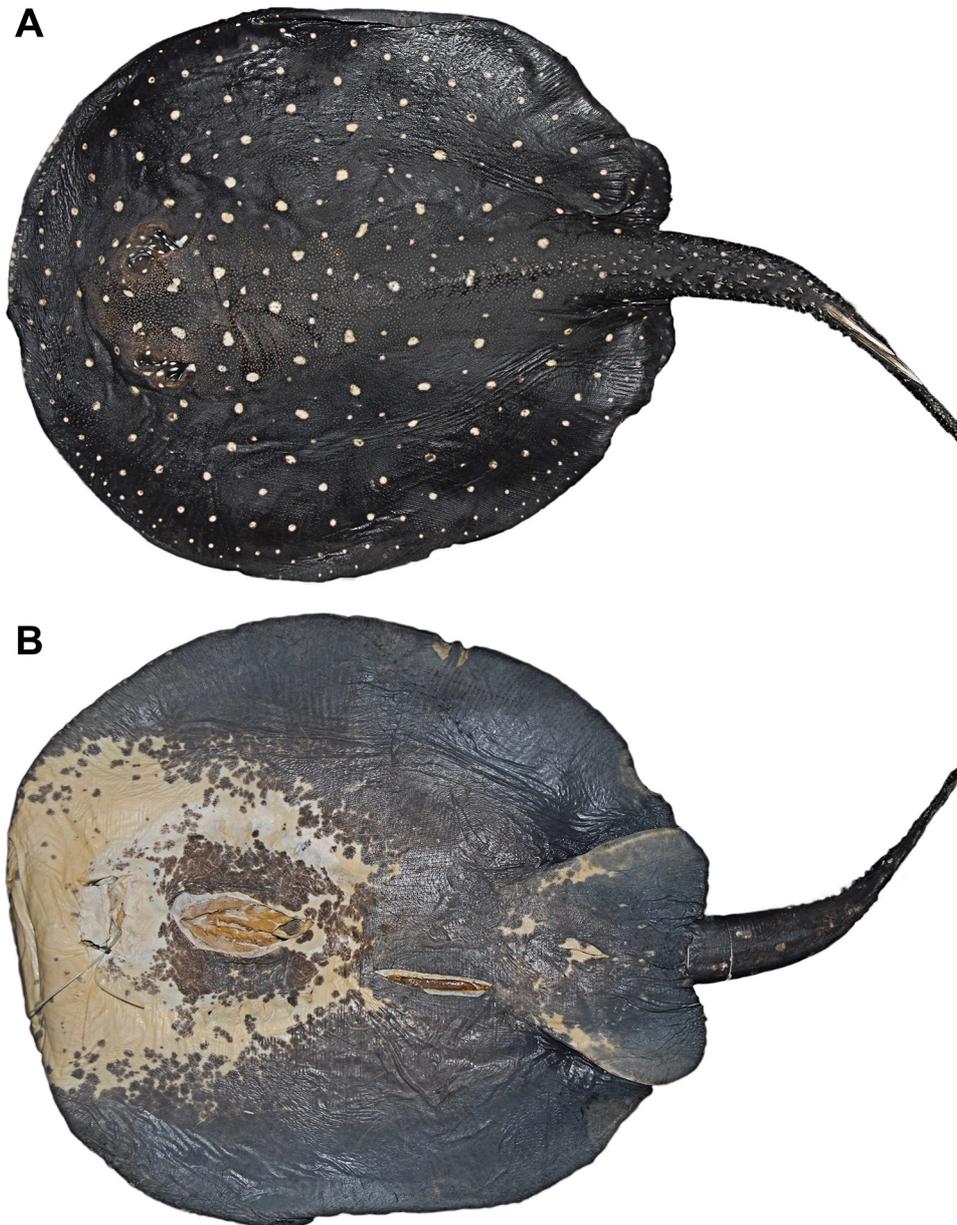


FIGURE 6. Dorsal (A) and ventral (B) views of *Potamotrygon albimaculata*, **sp. nov.** (MZUSP 104999, paratype, adult female, 641 mm TL, 425 mm DL, 390 mm DW).

Dermal denticles and thorns. Dorsal surface of disc, pelvic fins and tail with more or less uniform covering of small denticles (up to 1 mm across in larger specimens), but denticles more closely packed on dorsal mid-disc, on head, and base of tail regions; denticles more spaced apart and slightly smaller closer to disc margins; disc in general not very prickly. In some larger specimens (e.g. holotype), denticles grouped on anterior snout region. Denticles relatively small, but with wide, subcircular basal plates and stellate crowns with radiating ridges (Fig. 14). Small denticles more numerous on tail base and at tail sides, with more developed crowns on tail sides. Crowns usually with five major coronal ridges, subdivided into numerous coronal dichotomies.

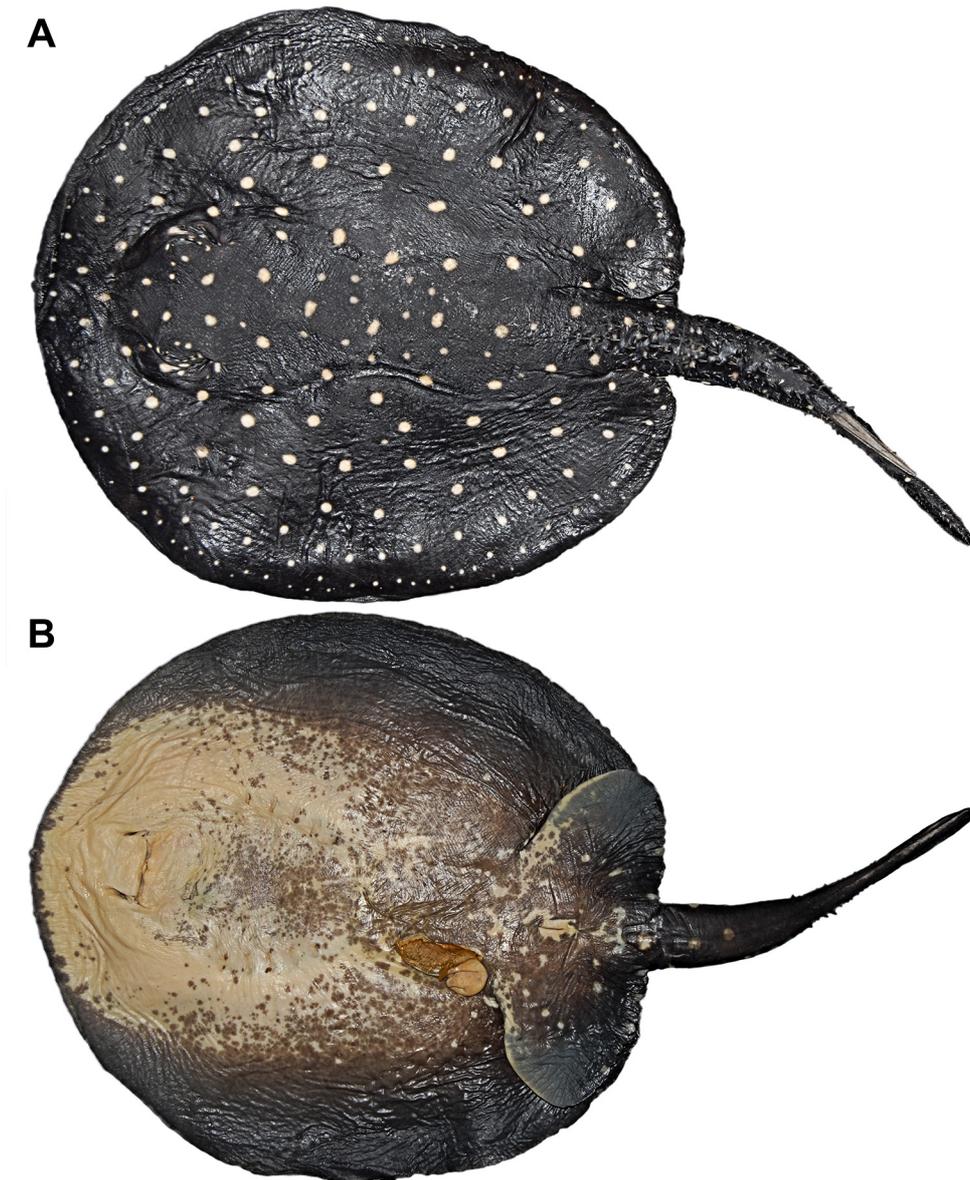


FIGURE 7. Dorsal (A) and ventral (B) views of *Potamotrygon albimaculata*, **sp. nov.** (MZUSP 105008, juvenile female, 441 mm TL, 286 mm DL, 267 mm DW).

Enlarged thorns on tail extending from posterior to level of pelvic girdle, anterior to tail origin at close to level of disc insertion, posteriorly to caudal stings. Tail with usually four or five more or less parallel rows of sharp, tall and evenly spaced thorns (Figs.15–17). Anteriormost thorns usually in a single (sometimes double) irregular row; anterior thorns organized into a triangular patch on anterior tail base (Fig. 17). Thorns arranged in single to multiple irregular, somewhat parallel rows from anteriormost thorns on tail base. Thorns in semi-parallel rows occupy almost all of tail dorsal and lateral surface, not just central aspect of tail; lateralmost rows of thorns reach close to tail ridges on tail sides. Distance between thorns crowns in an individual row rather great. Thorns tall, more or less raked to erect, slender, and very sharp. Tallest thorns in central rows on dorsal tail. In live specimens thorns covered with slender integument and mucous, but in preserved specimens thorn crowns exposed. Anterior thorns generally smaller; greatest thorns on mid tail and closer to caudal stings. Thornlets on lateral tail at level of caudal stings and distal tail extremity small but numerous and sharp, with erect cusps. Thorn bases rounded to rhomboidal (Fig. 16), with ridges ascending to thorn crowns. Small, sharp thorns on tail sides extend to posterior tail extremity. No bucklers or tubercles with hypertrophied and tall bases on disc or tail.

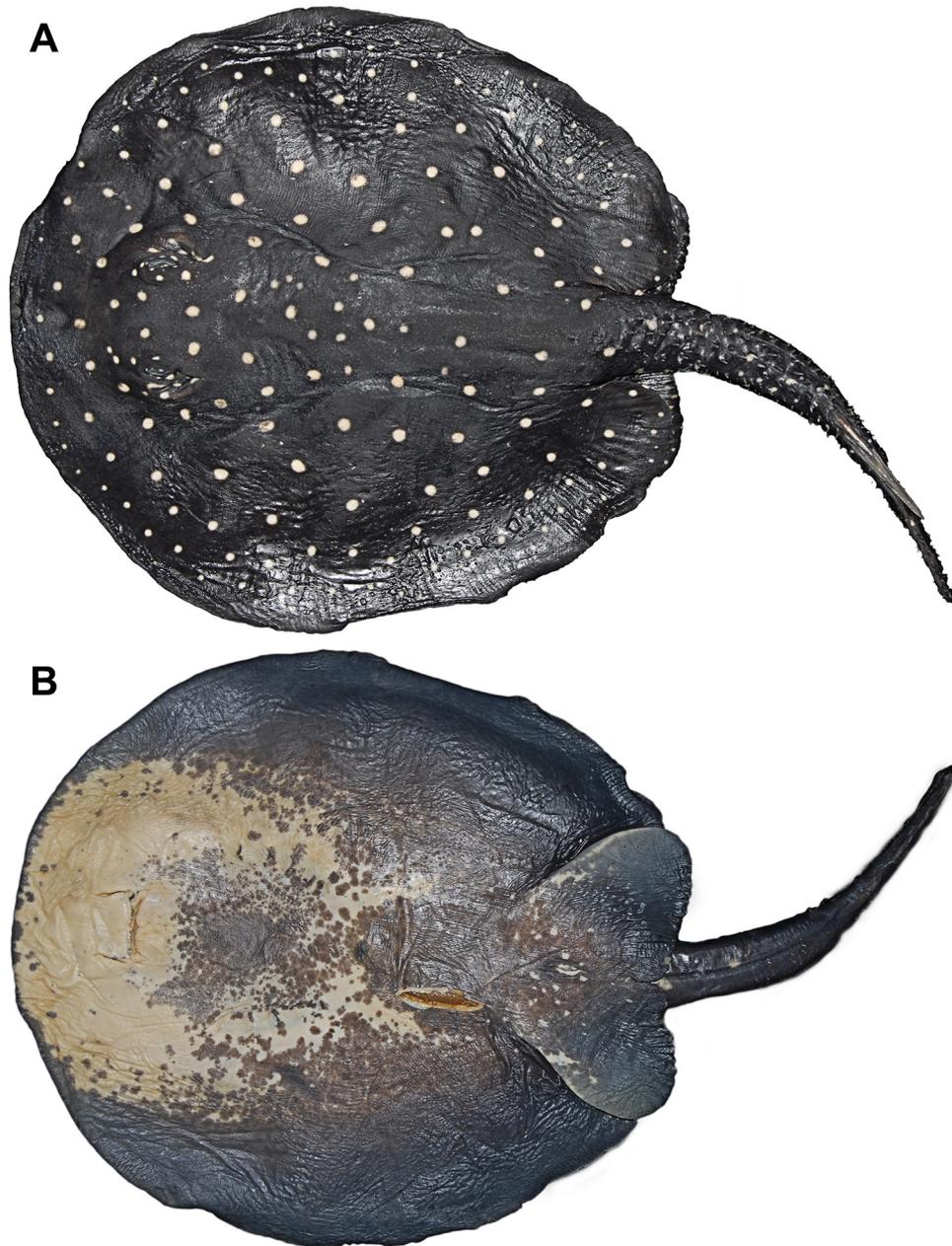


FIGURE 8. Dorsal (A) and ventral (B) views of *Potamotrygon albimaculata*, **sp. nov.** (MZUSP 105010, juvenile female, 515 mm TL, 340 mm DL, 301 mm DW).

Ventral lateral-line canals. Suborbital loop (**sol**), formed by branches of infraorbital canal (**ioc**), anteriorly curved toward midline (Fig. 18), extending in parallel to hyomandibular canal (**hyoc**) near anterior disc margin. Medial component of infraorbital canal irregularly undulated; external portion of infraorbital canal extends posteriorly to close to first gill slit, forming small, slightly tapering infraorbital loop (**iol**). Orbitonasal component of supraorbital canal parallel to medial branch of infraorbital canal, external and oblique to nostrils, and undulated, forming narrow prenasal loop (**pnl**). Mandibular canal (**man**) short, oblique, and just posterior to mouth. Anterior jugular loop subtriangular, slender; posterior jugular loop (**pjl**) broad, rectangular, formed medially by straight jugular canal (**jug**). Subpleural component of hyomandibular canal (**hyoc**) extends towards outer disc at branchial slits. Anterior subpleural tubules (**ast**) present anteriorly, branching from anterior segment of hyomandibular canal. Posterior subpleural tubule (**pst**) single, extending obliquely toward outer disc margin. Subpleural loop (**spl**) broadly triangular.

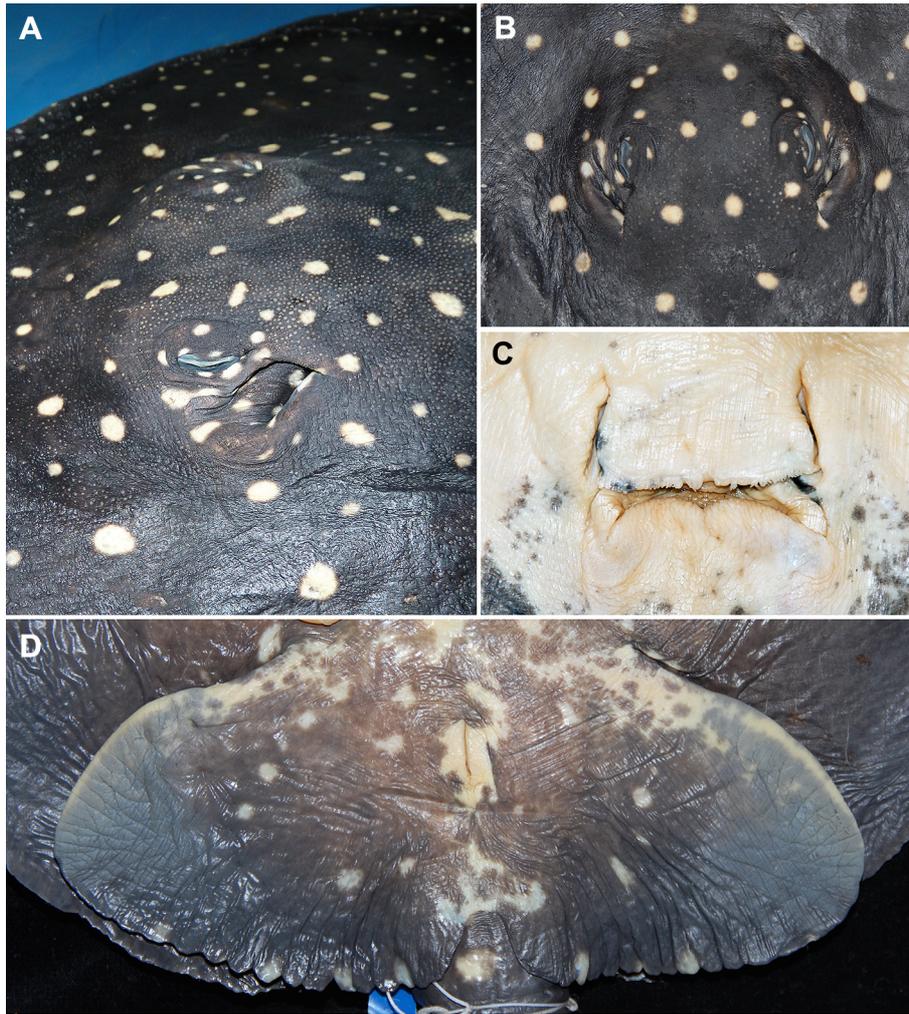


FIGURE 9. Morphological details of *Potamotrygon albimaculata*, **sp. nov.** A) Dorsolateral view of head region (paratype, MZUSP 105006, 665 mm TL); B) Dorsal view of eyes and spiracles (MZUSP 105010; 515 mm TL); C) Close-up of nasal region (MZUSP 105010); D) Ventral view of pelvic fins (MZUSP 105008; 441 mm TL).

Skeletal features. Neurocranium greatest width at level of pre- and postorbital processes and about one-half its greatest length (Figs. 19, 20a, b). Nasal capsules broadly rounded anteriorly, with broadly triangular anterior median indentation; internasal septum very slender. Nasal apertures (**no**) broad, markedly oval and short, much wider than long. Preorbital process (**prp**) posterolaterally directed, triangular. Postorbital process (**pop**) projecting anterolaterally, very straight and not broad, rectangular, and not particularly robust. Supraorbital process (**sp**) well defined, anterior to postorbital process, and sharply triangular. Neurocranium most slender at posterior third of orbit. Otic capsule short, about as wide as orbital region; hyomandibulae tightly and obliquely articulated to neurocranium. Precerebral (**pcf**) and frontoparietal (**fpf**) fontanelles about three-fourths length of neurocranium. Precerebral fontanelle circular, slightly broader than long, about half length of frontoparietal fontanelle; frontoparietal fontanelle much longer than wide, medially constricted and tapering. Epiphysial bar laterally triangular, slender at center and almost complete even in adults. Parietal fossa shallow. Antorbital cartilage laterally compressed, very slender in dorsoventral view, and widest at articulation with posterolateral nasal capsule; antorbitals extend posteriorly to just beyond level of preorbital processes. Prespiracular cartilages (**psc**) laterally concave and slender, weakly calcified.

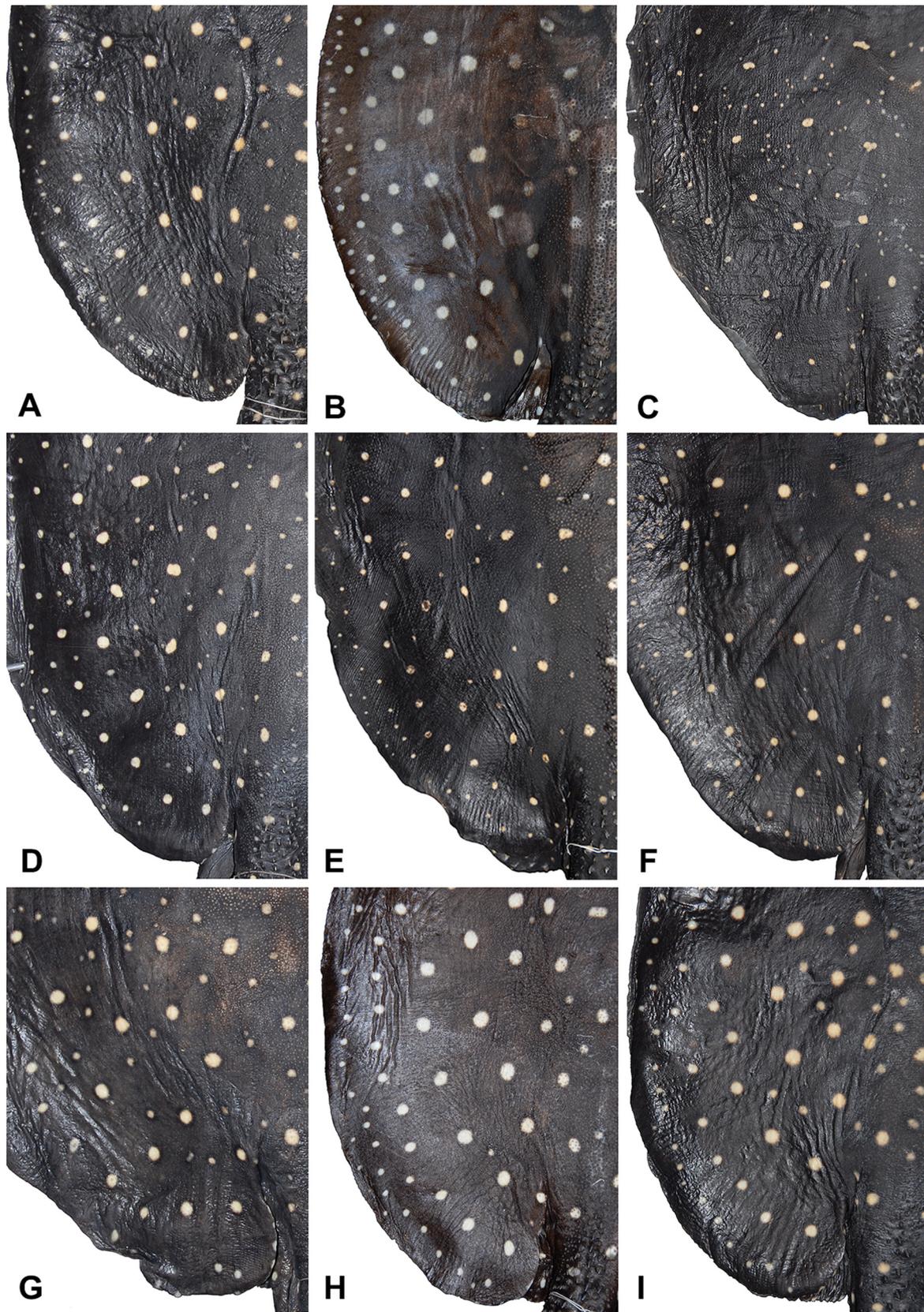


FIGURE 10. Dorsal view of posterolateral disc region in *Potamotrygon albimaculata*, *sp. nov.*, showing variation in dorsal color pattern. A) MZUSP 105008 (441 mm TL); B) MZUSP 103933 (440 mm TL); C) MZUSP 105016 (holotype, 790 mm TL); D) MZUSP 105006 (665 mm TL); E) MZUSP 104999 (641 mm TL); F) MZUSP 105001 (605 mm TL); G) MZUSP 105003 (598 mm TL); H) MZUSP 103930 (578 mm TL); I) MZUSP 105007 (473 mm TL). Specimens not to scale.

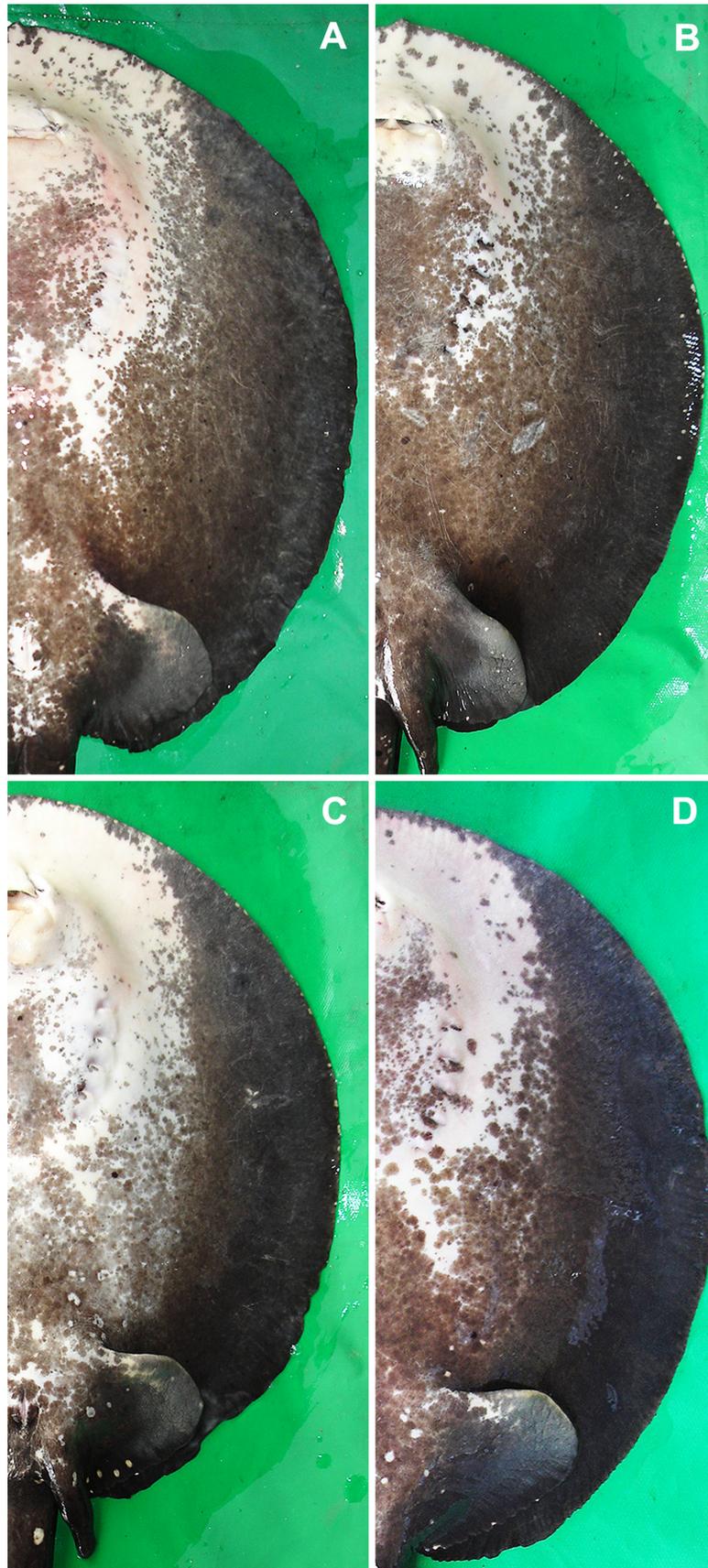


FIGURE 11. Ventral disc in *Potamotrygon albimaculata*, **sp. nov.**, showing variation in ventral color pattern; all specimens freshly collected. A) MZUSP 105016 (holotype, 790 mm TL); B) MZUSP 105006 (665 mm TL); C) MZUSP 105005 (631 mm TL); D) MZUSP 105010 (515 mm TL). Not to scale.

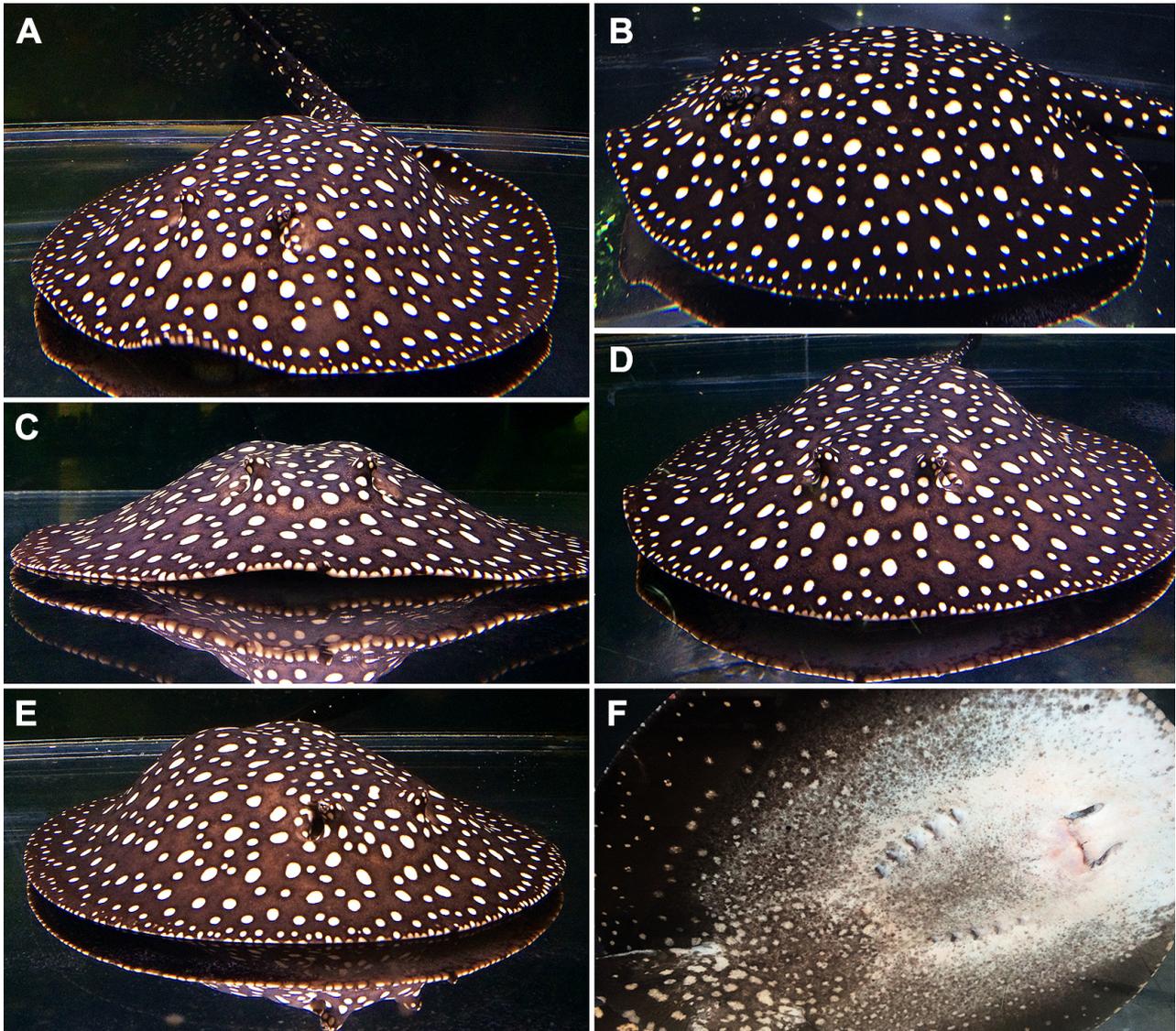


FIGURE 12. Live adult female specimen of *Potamotrygon albimaculata*, **sp. nov.**, in aquarium, shortly before giving birth to two pups (courtesy of G. England and R. Hardwick).

Meckel's cartilages (**Mc**) much stouter than palatoquadrates, with robust dorsally projecting lateral processes, and moderately developed posterolateral corners (not greatly protruding) (Figs. 19, 20a, b). Palatoquadrates slender, stouter at midwidth. Hyomandibulae (**hyo**) relatively slender, stouter at midlength. Hyomandibulae extend laterally to just beyond level of propterygium. Two angular cartilages present. Anterior angular cartilage (**aac**) robust and anteriorly concave, its length close to one-third length of hyomandibula. Posterior angular (**pac**) slender, less calcified and with much smaller width and length than anterior angular. Both angulars anteroposteriorly compressed, taller than long, and positioned perpendicular to neurocranium.

Cervicothoracic synarcual almost as long as neurocranium; synarcual greatest width at lateral stays, about equal to neurocranial width at orbits. Medial crest very elongate and slender, almost as long as synarcual length. Two to three vertebrae, anteriormost only a partial centrum, incorporated into synarcual. Thoracolumbar synarcual very slender, not strongly calcified, and relatively short. Transition from mono- to diplospondyly occurs at about fifth to sixth centrum posterior to rear margin of pelvic girdle. Individual vertebral centra occurring caudally to about one-half length of caudal sting. Weakly calcified notochordal extension (cartilaginous rod) present distally posterior to individual centra.

Propterygium (**pro**) and metapterygium (**met**) laterally compressed, tall and slender. Propterygium widest posteriorly (Figs. 20a–c), greatly tapering anteriorly, stouter at base than meso- and metapterygium, and with a slender anterior propterygial segment (**apr**) articulating with 4–5 radial elements lateral to nasal capsule; anterior

radial articulating with anterior propterygial segment bifurcated. Mesopterygium (**mes**) flattened, anteriorly elongated, with weakly convex external margin frequently with small median indentation, and concave anterointernal margin abutting propterygium. Metapterygium more broadly arched than propterygium, with three additional posterior segments decreasing in size caudally. Pectoral radials sometimes fused at base, especially at junctions of pro- and mesopterygium and mes- and metapterygium. Pectoral radials slender and elongate close to pectoral basals, widening slightly and shortening toward mid-disc, and slender again distally, bifurcating at about the 10th segment from basals (depending on location in disc); some 26 radial segments (from basals to outer disc margins) present at mid-disc.

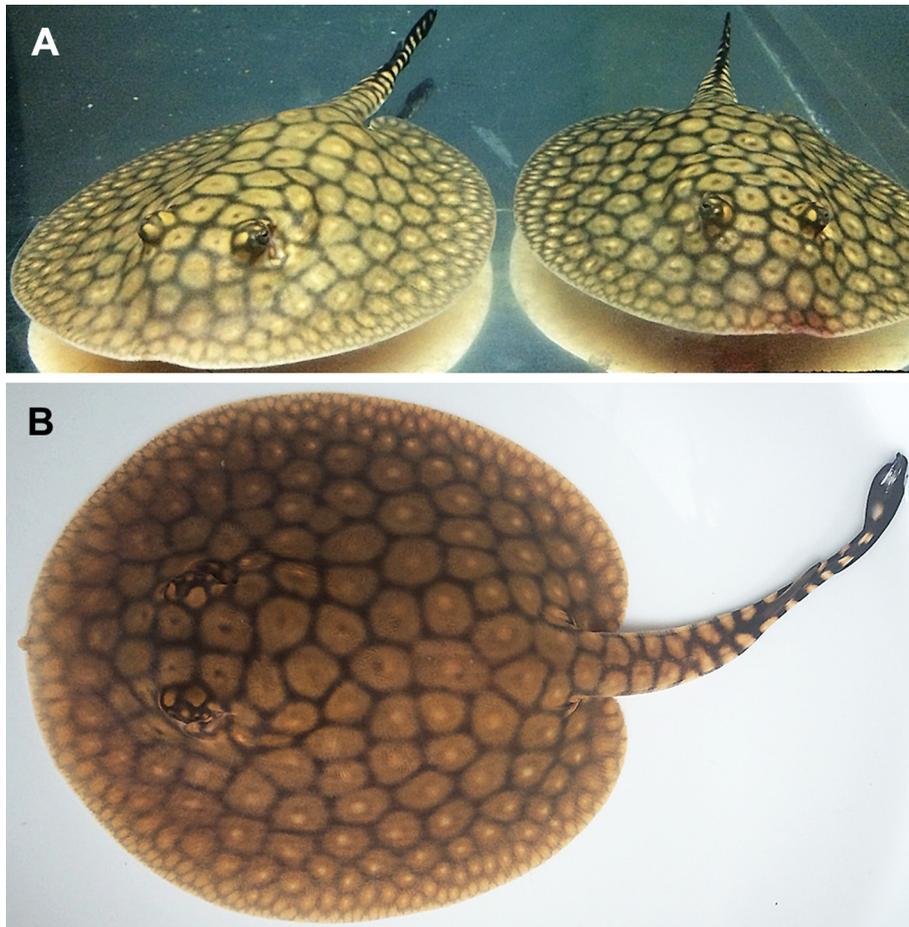


FIGURE 13. Live neonates (A) of *Potamotrygon albimaculata*, **sp. nov.**, shortly after birth (mother is depicted in Fig. 12); (B) Same specimen on left side in A in dorsal view (courtesy of G. England and R. Hardwick). Note color changes from neonate to adult (cf. Figs. 12 and 13).

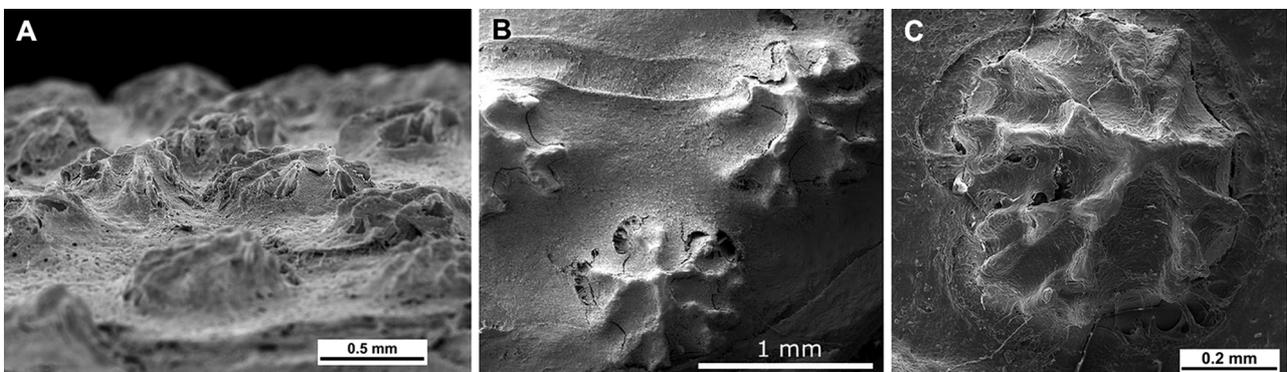


FIGURE 14. SEM photos of dorsal denticles from anterior mid-disc in *Potamotrygon albimaculata*, **sp. nov.**, in lateral (A) and dorsal (B, C) views (all MZUSP 105006).

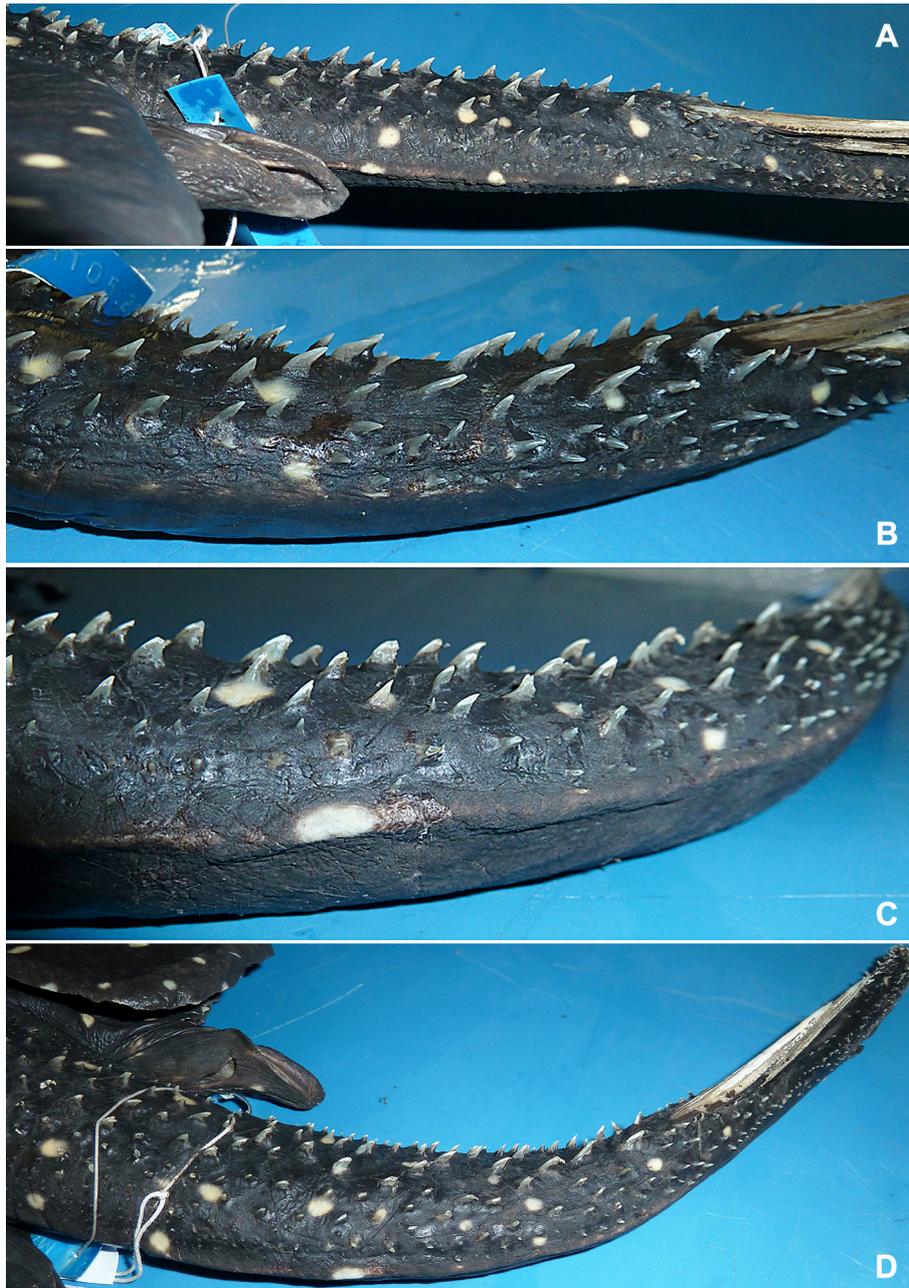


FIGURE 15. Lateral and dorsolateral views of tail of *Potamotrygon albimaculata*, **sp. nov.**, showing development and arrangement of tail thorns. A) MZUSP 105001 (605 mm TL); B) MZUSP 105021 (holotype, 790 mm TL); C, D) MZUSP 105006 (665 mm TL).

Median prepelvic process of pelvic girdle very slender and long, extending anteriorly to close to thoracolumbar synarcual, longer than maximum width of pelvic girdle. Pelvic girdle with concave anterior margins lateral to median prepelvic process. Lateral prepelvic processes, at anterior corners of girdle, triangular and well developed. Iliac processes extending dorsoposteriorly; ischial processes broadly triangular. Three obturator foramina present, arranged in an oblique row. Posterior margin of puboischiadic bar very concave. Basipterygium stout and somewhat short, with sinuous external margin articulating with pelvic radials. First enlarged radial articulates directly to lateral aspect of pelvic girdle; posteriormost radial larger, articulating directly with intermediate segment of clasper. Proximal pelvic radial element (articulating with basipterygium) much longer than other radial elements; some six radial elements present from basipterygium to outermost pelvic fin margin at greatest pelvic fin width, bifurcating at fourth (anterior radials) to second (posterior radials) segment from basipterygium. Anteriorly, second pelvic radial element short and stout, but second radials posteriorly more elongate and slender. Clasper with

two basal (intermediate) segments (Fig. 20d), second basal (**b2**) slightly more elongate than first (**b1**). Axial cartilage (**ax**) elongate, about twice length of terminal elements. Dorsal marginal cartilage (**dm**) greater than ventral marginal (**vm**); accessory terminal cartilage (**at**) slightly longer than ventral terminal (**vt**); dorsal terminal 2 cartilage (**dt2**) smallest element of terminal group.

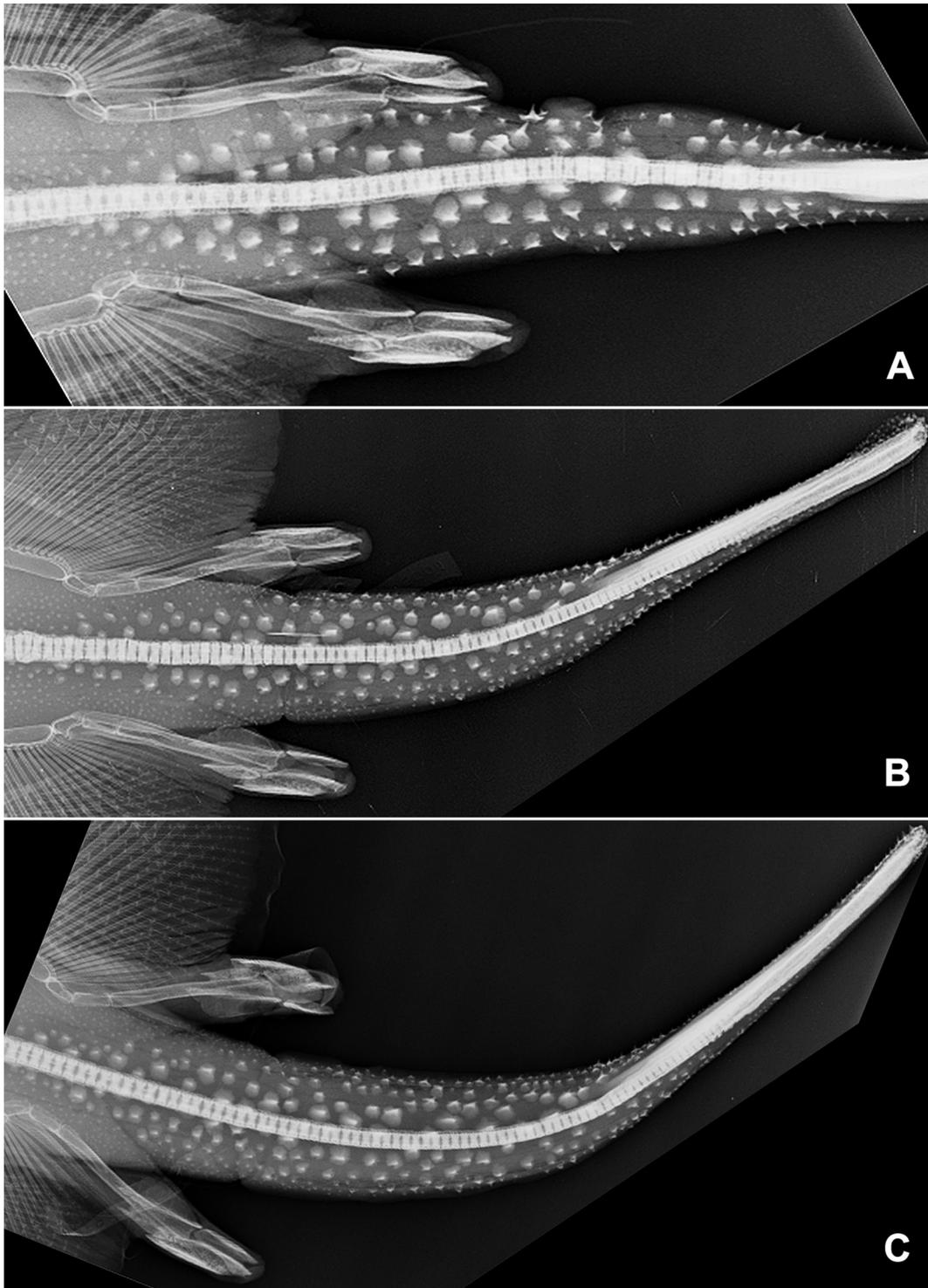


FIGURE 16. Dorsal view of tail in radiographs of *Potamotrygon albimaculata*, **sp. nov.**, showing organization of tail thorns; all specimens are adult males. A) MZUSP 120446 (541 mm TL); B) MZUSP 105001 (605 mm TL); C) MZUSP 105006 (665 mm TL).

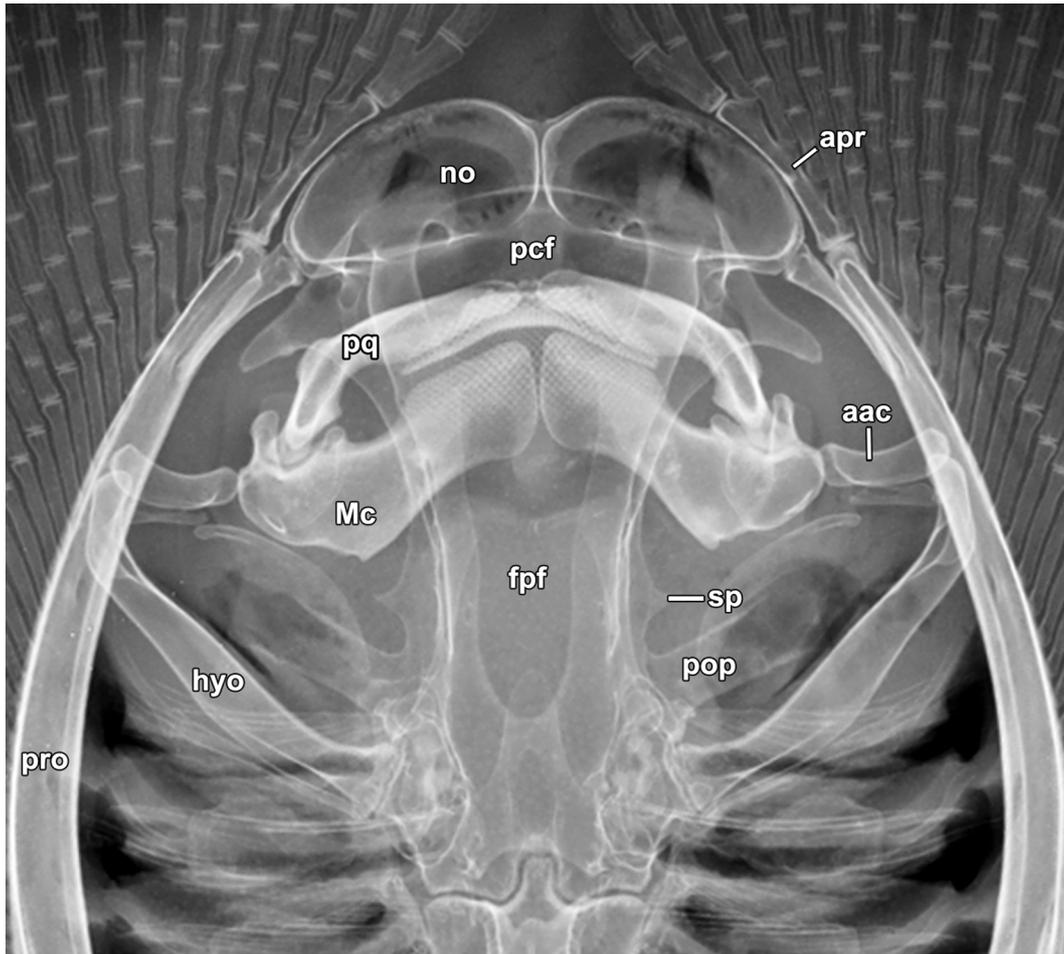


FIGURE 19. Radiograph of head skeleton of *Potamotrygon albimaculata*, **sp. nov.** (MZUSP 105006, 665 mm TL). Abbreviations: **aac**, anterior angular cartilage; **apc**, anterior segment of propterygium; **fpf**, frontoparietal fontanelle; **hyo**, hyomandibula; **Mc**, Meckel's cartilage; **no**, nasal opening (nasal aperture); **pcf**, precerebral fontanelle; **pop**, postorbital process; **pq**, palatoquadrate; **pro**, propterygium; **prp**, preorbital process; **sp**, supraorbital process.

TABLE 2. Counts taken on specimens of *Potamotrygon albimaculata*, **sp. nov.** A) MZUSP 103922 (470 mm TL); B) MZUSP 103930 (578 mm TL); C) MZUSP 104999 (641 mm TL); D) MZUSP 105016 (790 mm TL); E) MZUSP 105001 (605 mm TL); F) MZUSP 105008 (441 mm TL); G) MZUSP 105006 (665 mm TL); H) MZUSP 103926 (760 mm TL); I) MZUSP 120446 (541 mm TL).

CHARACTER	A	B	C	D	E	F	G	H	I	Range	Mode
Prepelvic vertebrae	29	28	28	27	27	28	27	26	25	25–29	28
Monospondylous vertebrae	34	34	35	33	32	34	33	32	30	32–35	33
Diplospondylous vertebrae	84	84	78	77	75	77	77	67*	74	74–84	77
Total vertebrae	118	118	113	110	107	111	110	99*	104	104–118	110
Propterygial radials	48	49	44	47	44	44	45	46	44	43–49	44
Mesopterygial radials	12	12	14	14	13	13	14	14	15	12–15	14
Metapterygial radials	36	39	38	39	38	36	38	35	38	35–39	38
Total pectoral radials	96	100	96	100	95	93	97	95	97	93–100	95
Pelvic-fin radials	23	24	24	27	23	24	21	27	21	20–27	24

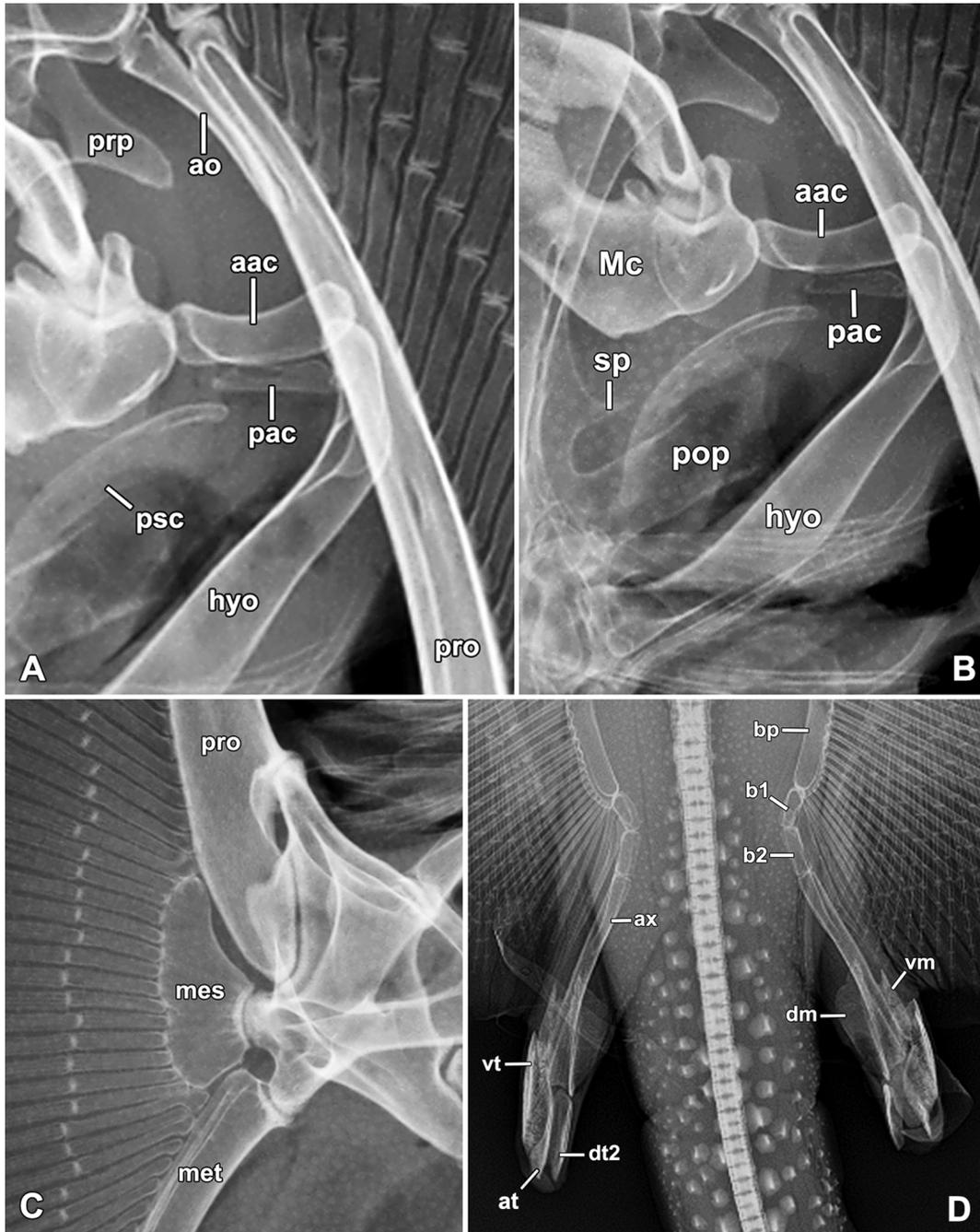


FIGURE 20. Skeletal features of *Potamotrygon albimaculata*, *sp. nov.*, from radiographs, in dorsoventral view. A) Head region of MZUSP 105006 (665 mm TL); B) Head region of MZUSP 105001 (605 mm TL); C) Basal cartilages and their articulation with scapulocoracoid (MZUSP 105006); D) Base of tail region, showing distribution and development of dermal denticles and thorns, and clasper skeleton (MZUSP 105006). Abbreviations: **aac**, anterior angular cartilage; **ao**, antorbital cartilage; **at**, accessory terminal cartilage; **b1**, basal (intermediate) segment 1; **b2**, basal (intermediate) segment 2; **bp**, basipterygium; **dm**, dorsal marginal cartilage; **dt2**, dorsal terminal 2 cartilage; **hyo**, hyomandibula; **Mc**, Meckel's cartilage; **mes**, mesopterygium; **met**, metapterygium; **pac**, posterior angular cartilage; **pop**, postorbital process; **pro**, propterygium; **prp**, preorbital process; **psc**, prespiracular cartilage; **sp**, supraorbital process; **vm**, ventral marginal cartilage; **vt**, ventral terminal cartilage.

Geographic distribution. *Potamotrygon albimaculata* is endemic to the mid and upper rio Tapajós in Amazonas, Pará and Mato Grosso states, Brazil (Fig. 21). It is not believed to be present downriver from the São Luiz rapids, closer to Itaituba, but stray individuals may descend the rapids when the water-level is high (M.L.G. de Araújo, pers. comm.); it is absent in the lower rio Tapajós. It is not known if this species occurs in rio Juruena below the Salto Augusto cataracts as it has not been collected in this river; but it is expected to occur in its lower

segment at least downriver from the major rapids between Salto Augusto and Barra de São Manuel (near the confluence with rio Teles Pires); it does not occur above Salto Augusto. This species was not collected in rio Jamanxim.

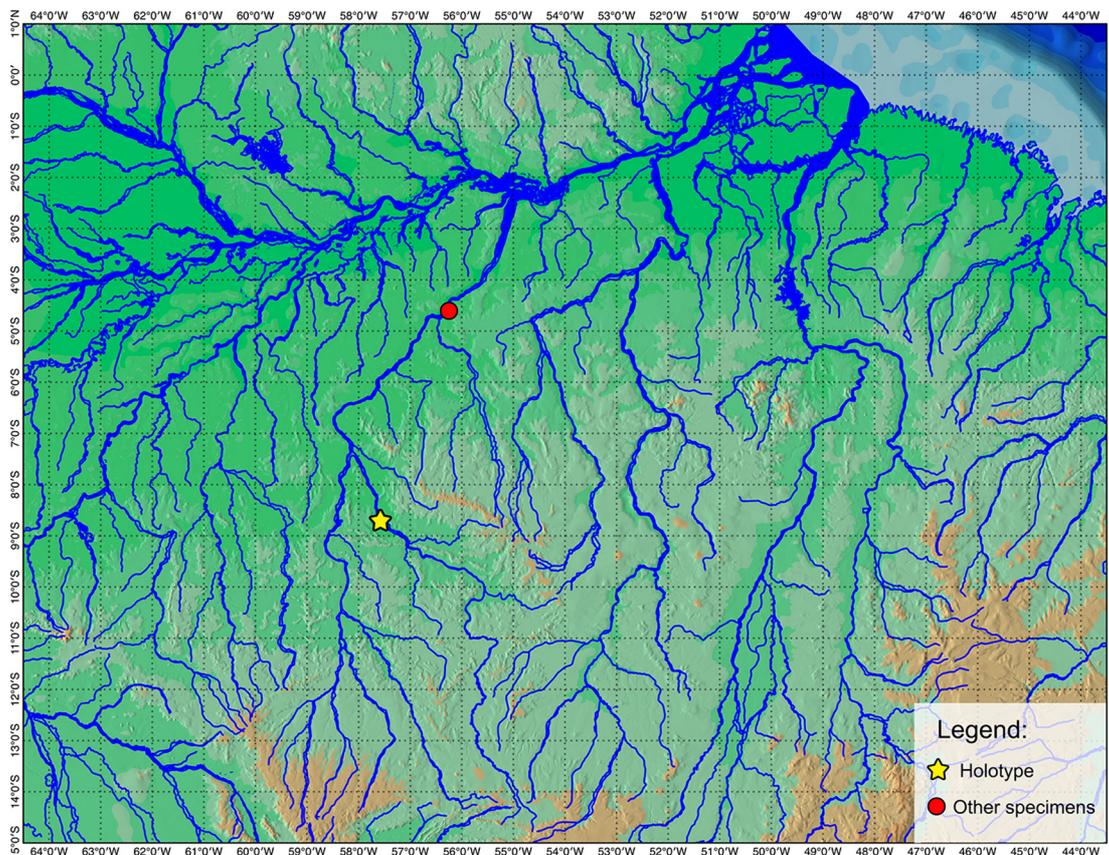


FIGURE 21. Map showing distribution of *Potamotrygon albimaculata*, **sp. nov.**, in the middle and upper rio Tapajós. Symbols indicate multiple specimens.

Common name. In Portuguese, this species frequently goes by the name "pretinha do Tapajós"; in English, the adopted common name is Tapajós freshwater stingray. In the aquarium trade this species is most frequently called "P14" or Itaituba ray.

Etymology. From the Latin *albus*, meaning white, and *macula* for spot, in reference to its conspicuous dorsal color pattern. Gender feminine.

Biological notes. *Potamotrygon albimaculata* occurs predominantly in the deeper river trough during the day and closer to shore when foraging at night; it was captured mostly at night. It is not believed to occur in smaller affluents and streams (it was not observed there). This species exhibits matrotrophic viviparity (embryos are nourished by both yolk sac and trophonemata), and gestation occurs simultaneously with vitellogenesis (M.L.G. de Araújo, pers. comm.). Gestation is four months long and parturition occurs when waters are rising (usually during the months of September/October, but this is variable). Fecundity ranges from 1–4 embryos, but usually two embryos are born per gestation (M.L.G. de Araújo, pers. comm.). Males become sexually mature at between 541–598 mm TL, as a juvenile male 541 mm TL, 359 mm DL, and 326 mm DW (MZUSP 120446) is almost adult, and definite adult males are known at 598 mm TL, 404 mm DL, 376 mm DW (MZUSP 105003) and 605 mm TL, 405 mm DL, 372 mm DW (MZUSP 105001); females are adult at slightly larger sizes. Embryos are born at 100–110 mm DW.

Specimens of *P. albimaculata* have a very thick mucous coating that easily sheds when captured, such that preserving them was more difficult compared to other potamotrygonids collected. The thick mucous easily comes off when they are handled, and this stingray species is not very hardy when captured in the field, perishing rather quickly.

Comparisons with congeners. *Potamotrygon albimaculata* is readily distinguished from all congeners due to

its unique color pattern, even though there are similarities with other black stingrays (*P. henlei*, *P. leopoldi*, and *P. rex*) in relation to both dorsal and ventral color. The black stingrays, occurring in Amazonian affluents draining the Brazilian Shield (*P. rex* in mid and upper rio Tocantins, *P. henlei* in rios Araguaia and lower Tocantins, and *P. leopoldi* in rio Xingu), form a species-group based on features discussed in Carvalho (2016), such as broadly rounded pelvic-fin apices and aspects of dorsal and ventral color, as well as having similar general proportions. An evolutionary affinity of *P. albimaculata* with other black stingrays reinforces a closer biogeographical relationship between the upper Tapajós basin and other north-flowing rivers draining the crystalline Brazilian Shield (see also Hubert & Renno, 2006; Lima & Ribeiro, 2011; Buckup *et al.*, 2011), and not a closer relationship to rio Paraguai as demonstrated by other fishes (even though an affinity to rivers of the Brazilian Shield is maintained; Lima *et al.*, 2007; Carvalho & Albert, 2011; Ribeiro *et al.*, 2013).

Potamotrygon albimaculata is distinct from *P. henlei*, *P. leopoldi*, and *P. rex* in having a strong blackish-brown color with yellowish to creamy white, rounded spots or faint ocelli smaller than eye diameter on disc, pelvic fins and tail. The spots in *P. albimaculata* are widely spaced apart (fewer on dorsal mid-disc region, more on disc margins) and do not coalesce to form more complex shapes, rosettes or vermiculations (some very minute, irregular spots are present on dorsal disc in some specimens). In contrast, the dorsal color pattern in *P. henlei* is blackish- to grayish-brown, with relatively few yellowish to light orange, usually round but also irregular, elongate or hour-glass shaped ocelli on disc. The ocelli in *P. henlei* have thin black contours and lighter centers, are sometimes sickle-shaped, and are much larger than the eyes. *Potamotrygon leopoldi* also has an intense black dorsal color as in *P. albimaculata*, but with large, relatively few and incomplete yellow ocelli or incomplete rings or sickle-shaped figures with black centers on mid-disc. The color pattern in *P. rex* is far more complex than the three species above, usually blackish-brown with intense yellow to orange spots, mostly smaller than eye-diameter, that form distinct concentric clusters on dorsal disc and tail (these larger on central disc, smaller towards disc margins and on dorsal tail), separated by a reticulate pattern formed by the dark background color. In *P. rex* larger ocellate spots also occur at the center of clusters on posterior and outer disc, and spots sometimes coalesce to form vermiculate shapes. Of the above species, *P. albimaculata* has the most regular dorsal color pattern, with specimens varying mostly in number of spots and/or faint ocelli on disc and in the presence of small irregular markings, usually in larger specimens (such as in the holotype).

Ventral color patterns are also similar in the black stingray species, but consistent differences are present, even though the patterns themselves vary to some degree within each species (as seen in the intraspecific variation in dorsal color). In *P. albimaculata* ventral color is dark brown anterolaterally, laterally and posteriorly on disc and fading toward central disc, with creamy white ventral snout, anterior disc area, and branchial slit region (also in between pelvic fins in many specimens), with generally few small, faint whitish to grayish spots and blotches on dark brown ventral disc, pelvic fins and ventral tail base. In contrast, *P. henlei* usually has a greater portion of the ventral disc creamy white, and darker portions of its ventral disc are lighter, usually light brown to grayish near disc margins and on pelvic fins (sometimes only on posterior pelvic fins). *Potamotrygon henlei* also has a ventral mottled pattern, with whitish to yellowish spots on darker ventral disc areas. *Potamotrygon leopoldi* is similar to *P. henlei* in ventral color, either with a wider whitish area on central disc or with a mostly grayish to faded brown disc, with whiter areas on ventral snout, gill slits and anterior pelvic fins; *P. leopoldi* usually also has a mottled lighter pattern on darker ventral regions. In *P. rex*, ventral color is more complex (as in dorsal color), dominated by a dark brown to dark gray disc, pelvic fins and tail, with creamy white spots (smaller than eye diameter) on central disc, pelvic fins and more numerous and smaller on ventral snout region, and usually with smaller creamy white areas restricted to an oblique streak over gill slits and anterior pelvic fins in most specimens, and sometimes with a creamy white snout and/or nasoral region.

The black stingray species cluster into two groups on the basis of their dorsal thorn patterns. *Potamotrygon albimaculata* is closer to *P. leopoldi* in this regard, with four or more rows of thorns (more regularly arranged in comparison to *P. henlei* and *P. rex*), with thorn rows more spaced apart, whereas *P. henlei* and *P. rex* are similar in usually having a slender, double irregular row of thorns, with rows positioned closely together (Carvalho, 2016). *Potamotrygon albimaculata* differs from *P. leopoldi* in having more rows that occupy the entire dorsal and lateral surfaces of the tail, whereas in *P. leopoldi* the thorn rows are regularly positioned on a band on dorsal tail; *P. albimaculata* also has more total thorns than *P. leopoldi*. The thorns are, in general, slightly less elongate, less slanted and more erect in *P. albimaculata*, which also has a more intense covering of acute thornlets on lateral and posterior tail regions, especially near caudal stings.

Tooth morphology and number of tooth rows is another means to separate black stingray species. In *P.*

albimaculata the teeth are very small and numerous, without hexagonal, plate-like teeth as in *P. henlei* and, to a lesser degree *P. rex* and *P. leopoldi* (Carvalho, 2016). The number of tooth rows in *P. albimaculata*, up to 40/46 in larger adults, is similar to *P. rex* (up to 44/47), significantly more than in *P. henlei* (26/30 in larger specimens), and slightly more than in *P. leopoldi* (35/36 in adult male holotype, up to 38 rows in larger *P. leopoldi* specimens examined). Dermal denticles are more similar in *P. rex* and *P. albimaculata* in being more strictly stelliform with tall crowns and more or less evenly elongated, numerous crown dichotomies (more than in *P. henlei*). The star-shaped, larger denticles in *P. leopoldi* (smaller denticles are also present in this species) have even fewer crown dichotomies than in *P. albimaculata*, *P. rex* and *P. henlei* (Carvalho, 2016; Carvalho & Lemos, unpubl.).

Potamotrygon albimaculata cannot be confused with *P. marinae* from French Guiana and Suriname, a species with a blackish-brown dorsal color and numerous small, yellow spots assembled in groups separated by a dark reticulate pattern; ventrally, this species is predominantly gray to grayish-brown with creamy white areas on anterior and central disc and ventral snout area (Silva & Carvalho, 2015). Furthermore, *P. marinae* has a single angular cartilage (double in *P. albimaculata*), a single, slender and mostly regular row of dorsal tail thorns (vs. multiple rows covering entire dorsal tail surface in *P. albimaculata*), well-defined labial ridges or grooves on lower jaw corners (absent in *P. albimaculata*), a longer tail (means of 81.2% DW in *P. marinae* vs. 73.3% DW in *P. albimaculata*), and many other features (for *P. marinae*, see Silva & Carvalho, 2015).

Other material examined. (19 specimens). MZUSP 103898, adult female, Comunidade Pimental, right margin of rio Tapajós, Pará state, Brazil, 4°33'05"S, 056°16'43"W, 11.x.2005, col. M.R. de Carvalho, M. Cardoso, M.L.G. de Araújo & S.M.V. Melo (field no. TJ05.42); MZUSP 103918, juvenile male, 383 mm TL, data as in MZUSP 103898, 9.x.2005 (field no. TJ05.33); MZUSP 103926, adult female, 760 mm TL, same data as MZUSP 103898, 12.x.2005 (field no. TJ05.45); MZUSP 103930, adult female, 578 mm TL, aquarium trade, rio Tapajós (probably above Itaituba at Pimental, above Cachoeira São Luiz), Pará state, Brazil; MZUSP 103931, juvenile female, 481 mm TL, data as in MZUSP 103930; MZUSP 103932, adult female, 668 mm TL, data as in MZUSP 103930; MZUSP 103933, juvenile male, 440 mm TL, data as in MZUSP 103930; MZUSP 105003, adult male, 598 mm TL, same data as holotype (dissected for lateral line) (field no. MT05.06); MZUSP 105005, adult male, 631 mm TL, same data as holotype (field no. MT05.08); MZUSP 105007, juvenile male, 473 mm TL, same data as holotype (field no. MT05.10); MZUSP 105008, juvenile female, 441 mm TL, same data as holotype (field no. MT05.11); MZUSP 120446 (6 specs.), 445–595 mm TL, 1 adult female, 3 juvenile females, 2 juvenile males, all from aquarium trade, rio Tapajós (probably above Itaituba at Pimental, Cachoeira São Luiz), Pará state, Brazil; MZUSP 120447, juvenile male, 207 mm TL, 134 mm DL, 111 mm DW, aquarium trade, rio Tapajós, Pará state, Brazil (c&s) (field no. TJ05.48); MZUSP 120448, neonate female, 230 mm TL, aquarium trade, rio Tapajós, Pará state, Brazil.

***Potamotrygon jabuti*, sp. nov.**

(Figs. 22–45, Tables 3–4)

Potamotrygon motoro [in part]: Rosa, 1985: p. 492 (MZUSP 25578 listed as *P. motoro* in material examined).

Potamotrygon sp.: Fontenelle & Carvalho, 2016: pp. 253, 257 (morphology of brain).

Holotype. MZUSP 105023, adult female, 789 mm TL, 487 mm DL, 453 mm DW, rio Jamanxim, rio Tapajós basin, near Novo Progresso, Pará state, Brazil, 07°09'30"S, 055°25'55"W, col. M.R. de Carvalho, F. Marques, M. Carvalho & A. Datovo (field no. MT05.28) (Figs. 22, 23).

Paratypes. (8 specimens). MZUSP 25578, adult female, igarapé Uruá or Boa Vista, left bank affluent, rio Tapajós, next to bridge at km 62 of highway BR 230, 04°30'S, 056°15'W, Pará state, Brazil, 31.i.1979, col. J.C. Oliveira (Figs. 30, 31); MZUSP 103920, Comunidade Pimental, mouth of igarapé Ponto Frio, right margin of rio Tapajós, Pará state, Brazil, 4°33'05"S, 056°16'43"W, 10.x.2005, col. M.R. de Carvalho, M. Cardoso, M.L.G. de Araújo & S.M.V. Melo (field no. TJ05.37) (Fig. 24); MZUSP 103921, data as in MZUSP 103920, 10.x.2005 (field no. TJ05.38); MZUSP 105002, near Pousada Santa Rosa, left bank of rio Teles Pires, rio Tapajós basin, Mato Grosso state, Brazil, 08°46'45"S, 057°27'55"W, col. M.R. de Carvalho, F. Marques, M. Carvalho & A. Datovo (skin patch removed for SEM study) (field no. MT05.05) (Fig. 26); MZUSP 105011, data as in MZUSP 105002 (field no. MT05.15) (Fig. 25); MZUSP 105013, data as in MZUSP 105002 (field no. MT05.18); MZUSP 105038, juvenile male (almost adult), data as in holotype (field no. MT05.43) (Fig. 29); MZUSP 105040, adult female, data as in holotype (field no. MT05.45) (Fig. 27).

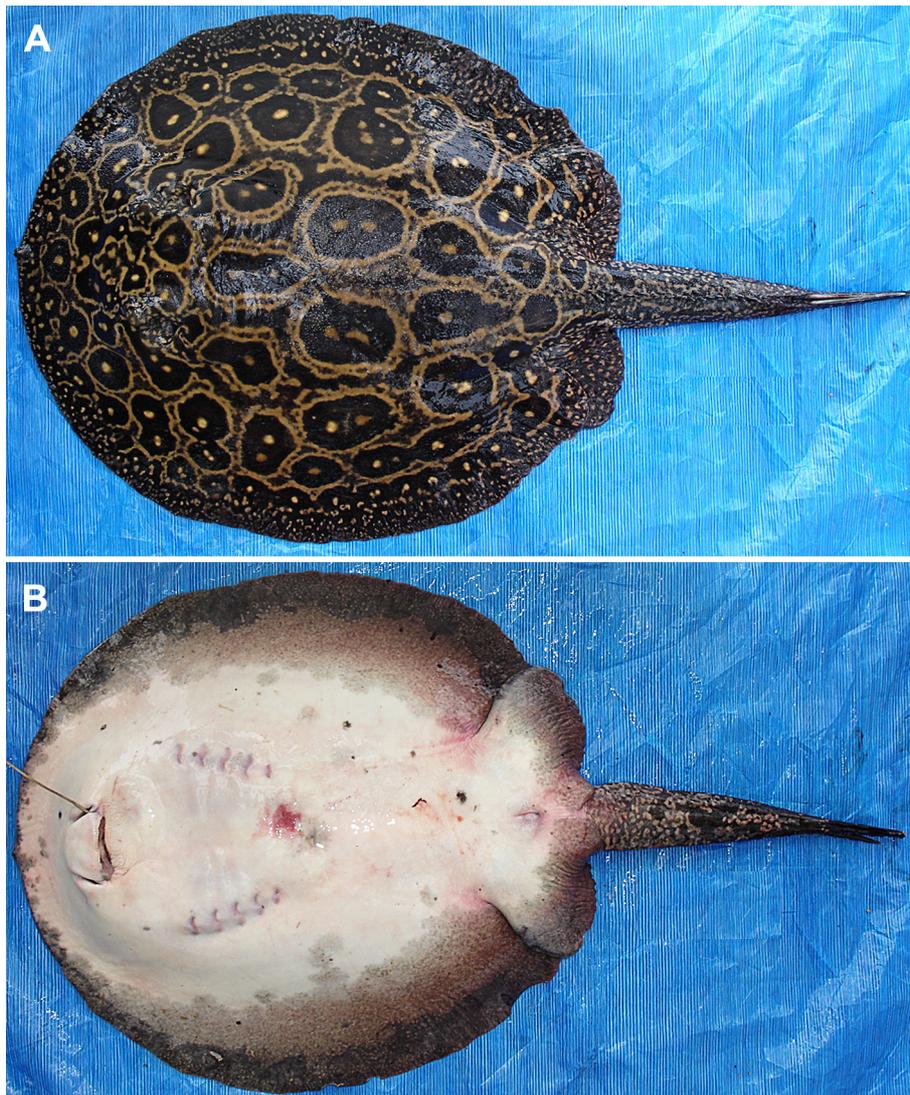


FIGURE 22. Dorsal (A) and ventral (B) views of freshly collected holotype of *Potamotrygon jabuti*, **sp. nov.**

Diagnosis. A species of *Potamotrygon* endemic to the mid and upper rio Tapajós, diagnosed by its unique dorsal color pattern that undergoes a remarkable ontogenetic transformation; color pattern in adults composed of a dark brown to greenish-brown color with elaborate, bright, marbled designs with irregularly shaped, bright yellow, golden to yellowish-orange spots or dark-centered ocelli, usually smaller than eye-diameter and surrounded by smaller spots, and encircled by yellowish to golden lines (these sometimes double) forming a mesh-like pattern that delimits large rosette-like, cerebriform or ocellar figures, larger on central disc, with figures frequently coalescing forming elongated shapes, and with numerous small vermiculate, sickle-shaped and/or reniform spots in between lines and scattered on disc and base of tail; tail with numerous reniform or vermiculate bright yellow to yellowish-orange spots, sometimes forming a slender reticulate pattern, and usually in isolated clusters on posterolateral tail. Additional features that in combination further diagnose *P. jabuti*, **sp. nov.**, include: monognathic heterodonty, with teeth of intermediate lateral rows of upper jaw larger and hexagonal, forming a crushing surface (present also in *P. motoro*, a species distinct in color pattern with isolated and well-defined tricolored ocelli on dorsal disc); dorsal tail thorns arranged in single to double irregular rows, with thorns generally closely packed together; lack of defined labial grooves (distinct labial grooves present at least in *P. orbignyi*, *P. humerosa*, *P. marinae*, and *P. constellata*); and presence of two well developed angular cartilages, with anterior angular cartilage just slightly greater than posterior angular (single angular present in *P. tigrina*, *P. schroederi*, *P. constellata*, *P. magdalenae*, *P. histrix*, *P. schuhmacheri*, *P. orbignyi*, *P. humerosa*, *P. marinae*, and *P. wallacei*; anterior angular broad and posterior angular absent or very small, abutting hyomandibula, in *P. signata*, *P. pantanensis* and *P. amandae*; anterior and posterior angulars present in addition to a small lateral element in *P. limai* and *P. scobina*).

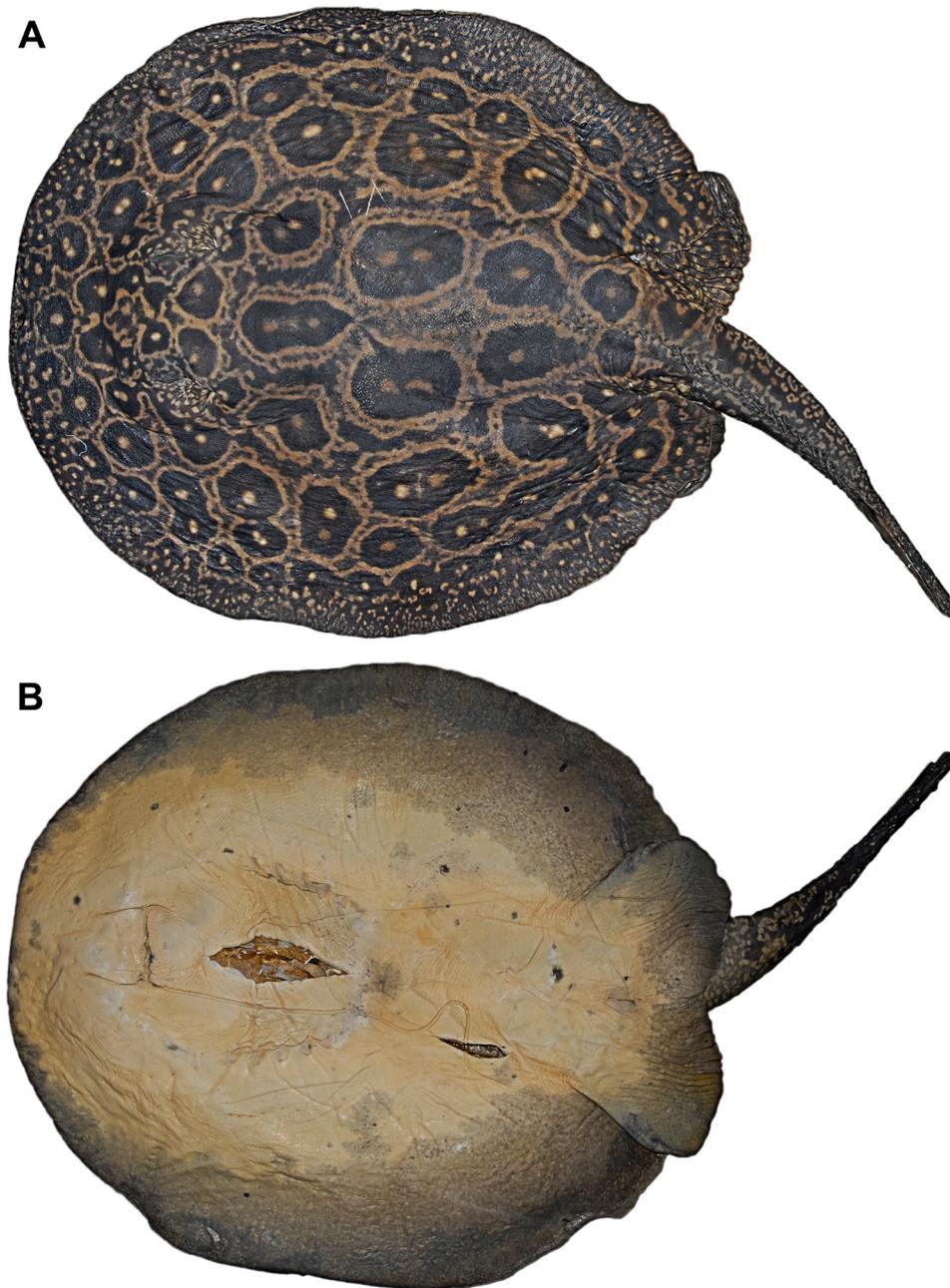


FIGURE 23. Dorsal (A) and ventral (B) views of holotype of *Potamotrygon jabuti*, **sp. nov.** (MZUSP 105023, adult female, 739 mm TL, 487 mm DL, 453 mm DW).

Description. A moderately large-sized species, largest examined specimen 810 mm TL, 512 mm DL, 465 mm DW (largest in TL, not in DL or DW). Disc slightly oval, its length greater than disc width (DL 103.6–116.9% DW); disc widest slightly anterior to its mid-length. Disc tapers posterior to its mid-length. Knob-like protuberance on anterior snout small, more developed in neonates and juveniles. Anterior disc broadly convex, more so in larger specimens. Head moderately robust, slightly raised above disc (Fig. 32a), and somewhat broad. Eyes moderately large (Figs. 32a–c), their diameter 3.3–7.2% DW, bulging in live specimens but less so in preserved specimens. Eyes fit between 2–3 times in interorbital distance. Preorbital snout 22.0–28.6% DW. Spiracles moderately large, larger than eyes, rhomboidal in live specimens and more slender in preserved material (Fig. 32a). Interorbital distance 13.0–20.0% DW, slightly smaller than interspiracular distance. Anterior margin of spiracles at level of mid-diameter of eye.

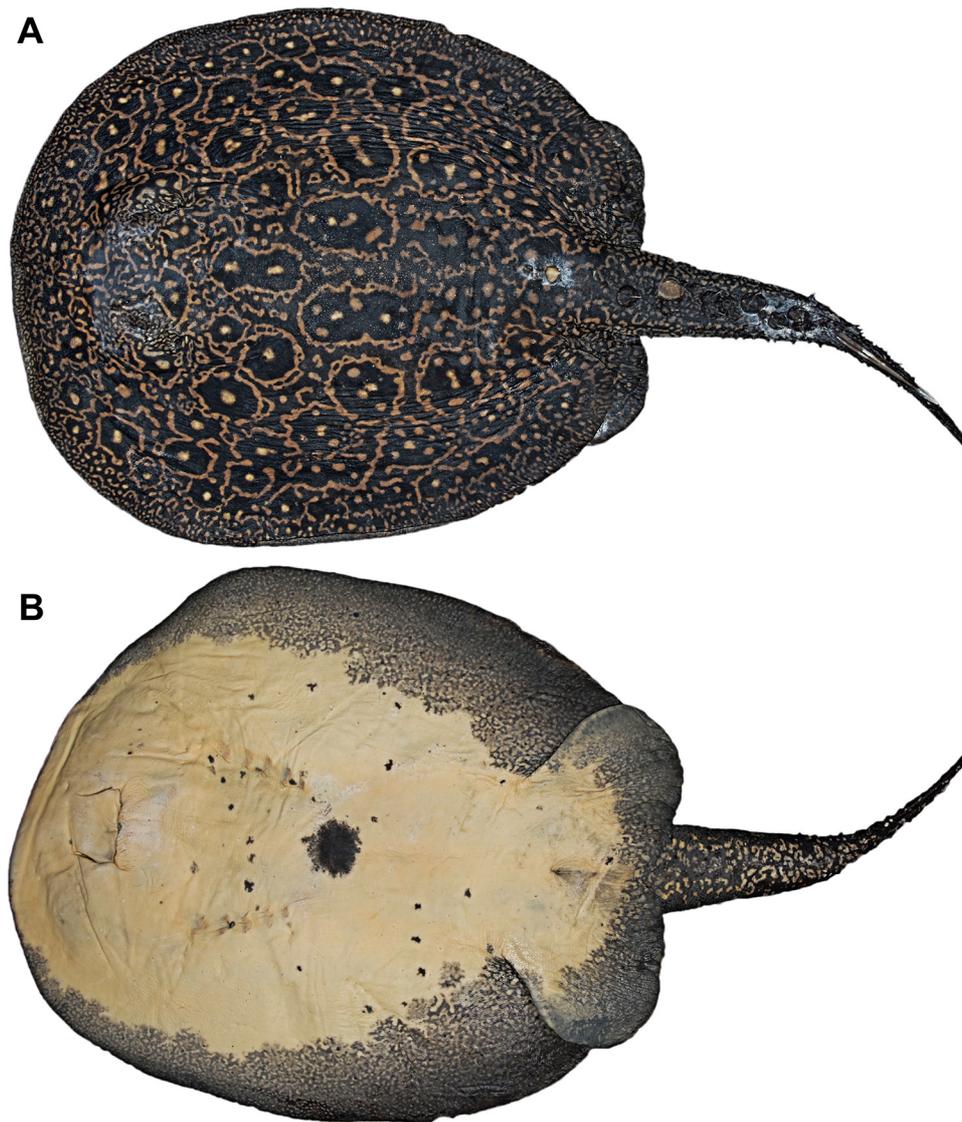


FIGURE 24. Dorsal (A) and ventral (B) views of *Potamotrygon jabuti*, **sp. nov.** (MZUSP 103920, paratype, adult female, 810 mm TL, 512 mm DL, 465 mm DW).

Nasal curtain trapezoidal, somewhat broader posteriorly (Fig. 32d). Posterior margin of nasal curtain relatively straight, without median indentation, and with very small fringes, more visible in live specimens (sometimes missing in preserved material). Nasal curtain extends over mouth opening in fresh material. Nostrils moderately long and slender. Mouth relatively small, its width 8.9–15.1% DW, greater than internasal distance. Posterior margin of mouth with small median indentation. Labial folds absent from lower jaw corners. Integument posterior to mouth only slightly rugose. Five buccal papillae present on mouth floor. Preoral distance 19.0–25.4% DW, smaller than preorbital distance. Teeth large, with usually rhomboidal crowns; larger specimens of both sexes with larger, somewhat hexagonal teeth on intermediate lateral rows in upper jaws (fifth row counting from lateralmost row in some larger specimens); hexagonal teeth more pronounced in larger females; teeth of adult males with more pronounced, pointed cusps on central rows of both tooth bands. Few exposed median tooth rows present on lower dental plate in some preserved specimens. Teeth set in quincunx, in 17–29/23–33 total longitudinal rows in larger juveniles and adults; 22/24 in large adult female (holotype), 23/28 in adult female (MZUSP 25578), 27/32 in adult male (MZUSP 105004), 24/27 in large juvenile male, almost adult (MZUSP 105038). Branchial basket wide; distance between first pair of gill slits up to one-third DW, distance between fifth gill slits close to one-fourth disc width. Fifth gill slits about half of width of first gill slit; gill openings weakly sinuous.

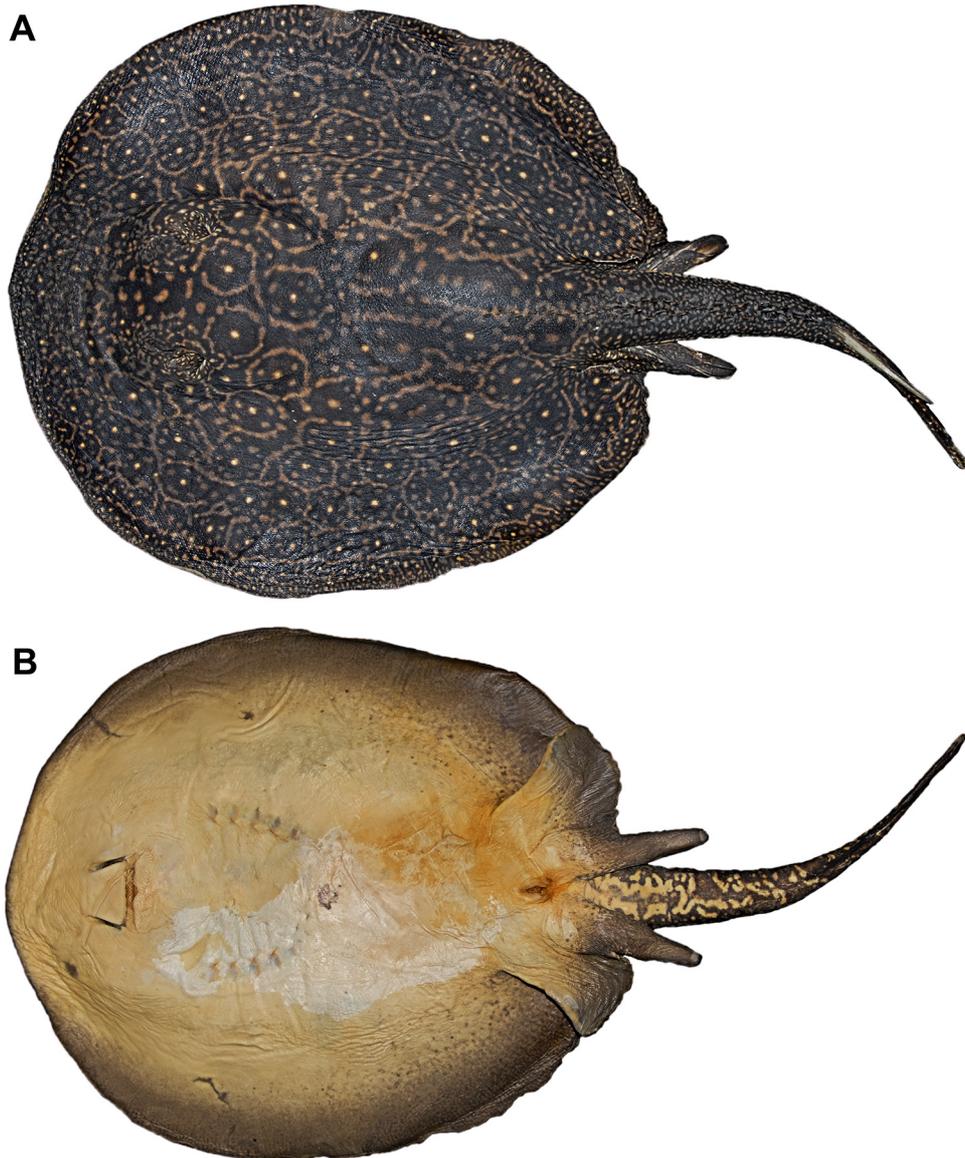


FIGURE 25. Dorsal (A) and ventral (B) views of *Potamotrygon jabuti*, **sp. nov.** (MZUSP 105011, paratype, adult male, 702 mm TL, 445 mm DL, 390 mm DW).

Pelvic fins only moderately wide, about one-half disc width when measured together, and not broadly rounded at apices, with more or less straight anterior margin. Pelvic fins protrude slightly beyond posterior disc margins. Claspers in adult males relatively stout (Fig. 40), extending posteriorly to between one-third to one-fourth tail length. Tail only moderately long, its length about three-fourths of disc width. Tail slightly longer in neonates and smaller juveniles. Tail tapering only slightly to level of caudal stings, with slight lateral constriction at level of caudal stings. Tail not greatly elongated beyond caudal stings. Tail width at base usually about two-thirds to almost equal to interorbital distance. Lateral tail ridges well developed, fleshy, present from tail base to close to caudal sting origin. Tail in cross-section slightly flattened dorsoventrally. Tail with slender dorsal and ventral finfolds, greater in neonates and small juveniles; tail folds usually lower, ridge-like in larger adults. Caudal stings long and slender; usually one to two stings present. Lateral barbs greater at sting anterior third to about its midlength; barbs smaller and more numerous closer to sting base, and absent from sting base.

Coloration. *Adults.* Coloration very elaborate and extremely variable among specimens examined, but a general marbled pattern is present and unique for this species. Color pattern is age/size related to a large extent, changing remarkably with growth (Fig. 35). Larger specimens have the dorsal surface of disc, pelvic fins and dorsal and lateral tail dark brown to greenish-brown, with a complex marbled pattern of bright designs composed

of irregularly shaped, bright yellow, golden to light yellowish-orange spots or light- or dark-centered ocelli, usually smaller than eye-diameter and surrounded by smaller spots, and encircled by yellowish to golden lines (these sometimes double; e.g. in holotype, Fig. 23) forming a mesh-like pattern that delimits large rosette-like, cerebriform or ocellus-like figures (Figs. 22–35, 37). These figures larger on central disc, frequently coalescing forming elongated shapes, smaller closer to outer disc where they contact each other and frequently fuse, and arranged into concentric rows. Numerous small (smaller than eye diameter) vermiculate, sickle-shaped and/or reniform spots usually present in between lines and scattered on disc and base of tail. Dorsal snout and head region sometimes only with complex reticulate pattern formed by yellow to golden slender lines and/or spots. Pelvic fins with small, yellow to golden vermiculate to reniform spots. Mid-sized specimens approaching sexual maturity, or only recently sexually mature, with numerous larger ocellated figures on dorsal disc with broad outlines and beige to light brown centers, larger on central disc, and also smaller toward disc periphery; these specimens usually lack small vermiculate and reniform spots in between ocelli (which develop slightly later during growth) (e.g. Figs. 28, 29, 35c). Tail with numerous reniform or vermiculate bright yellow to yellowish-orange spots, sometimes forming a slender reticulate pattern, and usually in isolated clusters on posterolateral tail.

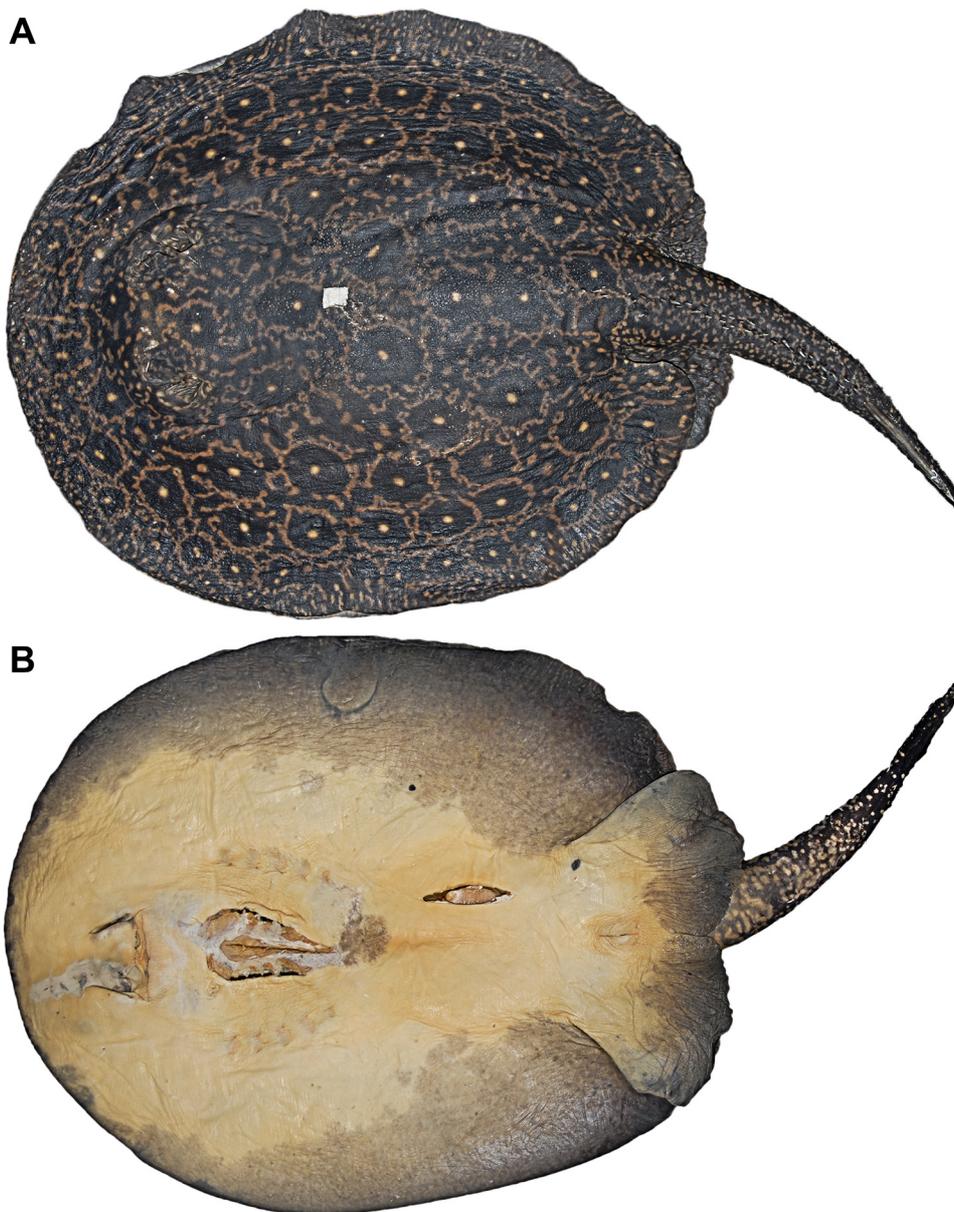


FIGURE 26. Dorsal (A) and ventral (B) views of *Potamotrygon jabuti*, **sp. nov.** (MZUSP 105002, paratype, adult female, 660 mm TL, 475 mm DL, 416 mm DW).

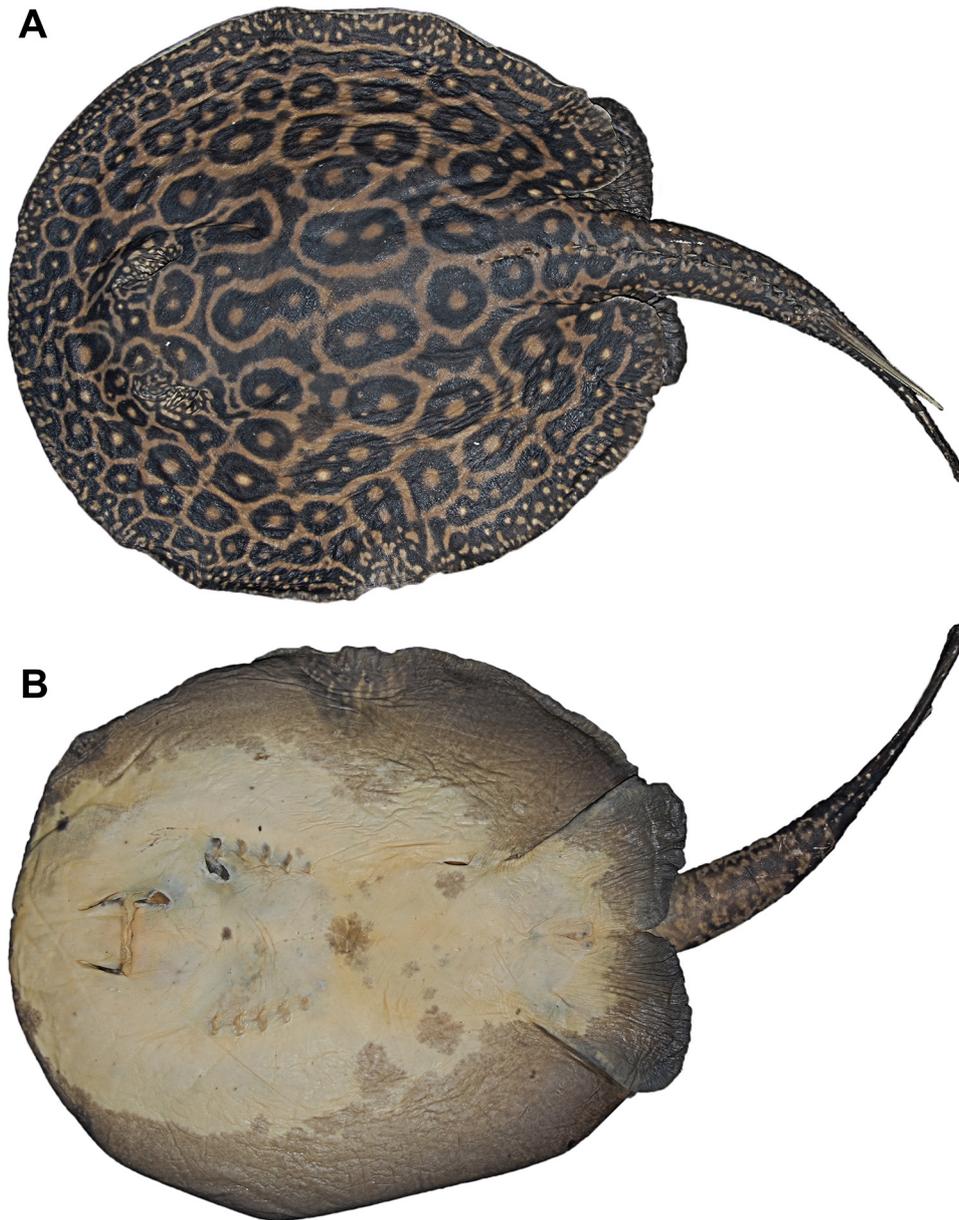


FIGURE 27. Dorsal (A) and ventral (B) views of *Potamotrygon jabuti*, **sp. nov.** (MZUSP 105040, paratype, adult female, 600 mm TL, 385 mm DL, 351 mm DW).

Ventral color mostly creamy white to light beige (Fig. 36). Outer disc region brown, light brown to gray, mottled with small, yellow, orange or brown reniform spots sometimes forming small vermiculate pattern; outer disc pattern also present on anterolateral disc, posterior pelvic fins (posterior to cloaca) and claspers, lacks a well defined inner margin, and usually wider toward posterior disc; anteriormost ventral snout with small, isolated blotches and speckles; outer disc color pattern sometimes extending toward ventral disc center posterior to gill basket; outer disc pattern much brighter in live specimens. Darker blotches, smaller than eye diameter also scattered on ventral disc in some specimens. Diffuse, grayish to brownish, more or less circular but usually irregularly shaped, central blotch present on coracoid region, lacking in some specimens, and varying in size (frequently about as wide as nasal curtain). Ventral tail base with large yellowish to creamy spots and elongated marks, interspersed with dark brown to greenish-brown background tail color; ventral tail in some specimens with small yellow to orangish spots forming vermiculate pattern.

Neonates and small juveniles. Specimens of *P. jabuti* undergo an extraordinary makeover in coloration shortly after birth (Figs. 35, 38). Neonates with light brown to pinkish- or orangish-brown color, with numerous ocellated

spots, larger on central disc and more numerous and organized into concentric rows (sometimes coalescing) on outer disc (similar to *P. motoro*); ocelli orange or with background color in center a few hours after birth (Fig. 38a), and darker brown, slender ocelli outlines; ocelli at birth with yellowish centers; some ocelli usually elongated on central disc. Tail with reticulate dark brown pattern, with alternating darker and lighter bands posteriorly. In few months of growth, ocellated marks become more numerous and their outer layers become more broad and eventually merge into each other as they expand, eventually forming marbled, elaborate pattern (Fig. 38b); ocelli sometimes hidden by mucous covering in neonates. Light beige to yellowish patterns appear external to ocelli in juveniles, and dorsal background pattern becomes darker in larger juveniles. Ventrally, neonates light beige to pinkish-brown, without outer disc pattern of adults; distal ventral tail with alternate dark brown and beige bands.

Dermal denticles and thorns. Dorsal surface of disc somewhat prickly, with smaller dermal denticles surrounding larger, star-shaped denticles (Fig. 39) on disc and base of tail. Smaller denticles somewhat V-shaped in apical view on central disc, with elevated central crown and small accessory cusps pointing posteriorly. Dorsal mid-disc region with more intense covering of denticles, from head to tail base. Small denticles numerous on tail base, sometimes closely adjacent to stellate denticles. Larger stellate denticles surrounded by smaller denticles and relatively tall, reaching more than 1 mm in diameter. Stellate denticles with tall basal plates and usually seven coronal ridges, but up to 9 observed, and some observed stellate denticles incomplete, with fewer ridges. Coronal ridges usually not subdivided into coronal dichotomies.

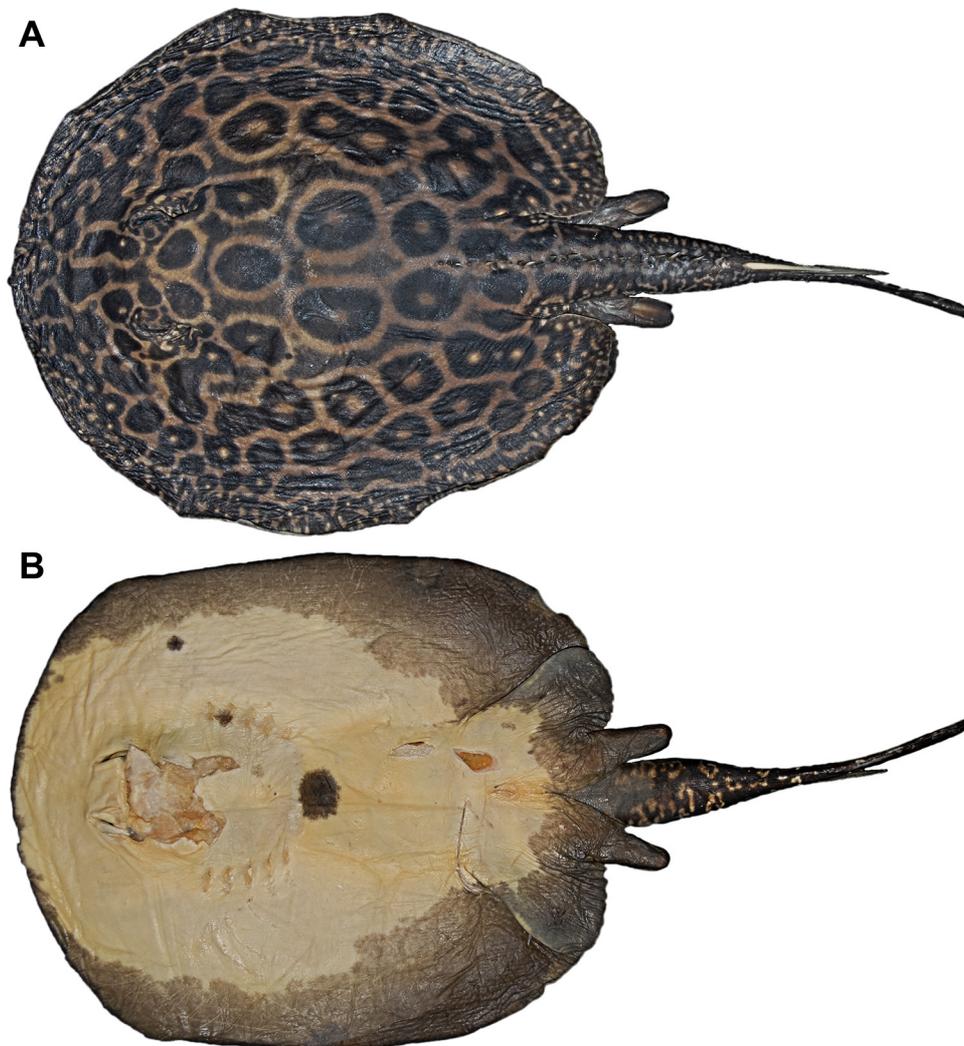


FIGURE 28. Dorsal (A) and ventral (B) views of *Potamotrygon jabuti*, **sp. nov.** (MZUSP 105039, adult male, 471 mm TL, 292 mm DL, 255 mm DW).

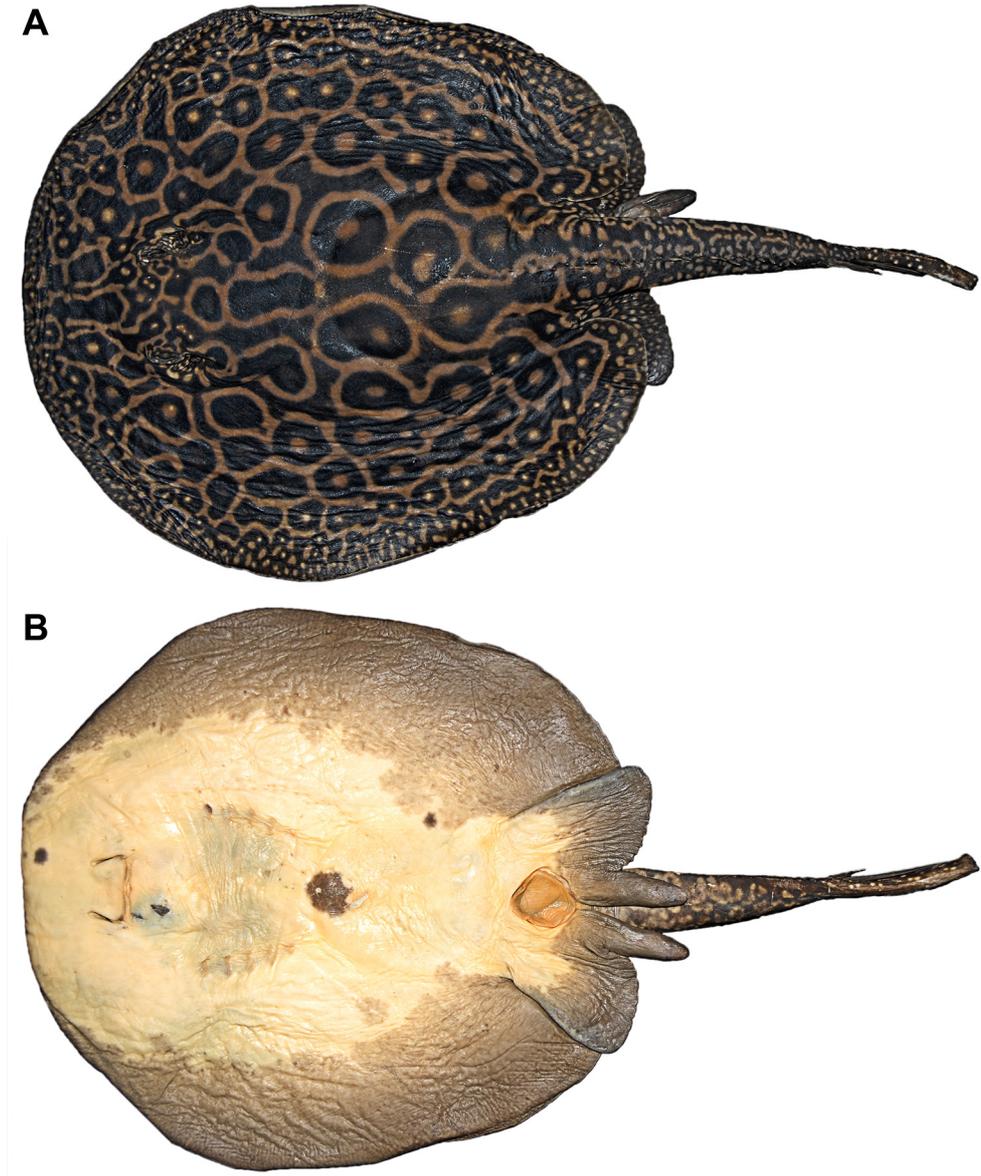


FIGURE 29. Dorsal (A) and ventral (B) views of *Potamotrygon jabuti*, **sp. nov.** (MZUSP 105038, paratype, juvenile (almost adult) male, 515 mm TL, 345 mm DL, 310 mm DW).

Tail thorns more developed and numerous in larger specimens. Thorns on anterior tail base slightly smaller and usually in a single irregular row, becoming a double irregular row posterior to level of pectoral-fin insertions (Figs. 32e, 40–42). Thorns in a very slender band anteriorly, but occupying a slightly wider portion of dorsal tail posteriorly, close to caudal stings. Distribution and height of enlarged thorns on tail somewhat variable. Specimens from rios Teles Pires and especially Jamanxim generally with lower thorns in either a more or less single row (with an occasional thorn forming a double row on midtail and/or closer to caudal stings), or in an irregular, slender double row posteriorly (e.g. Fig. 40a). Thorns in these specimens less acute and with smaller bases than those from mid rio Tapajós (just above São Luiz rapids). Specimens from mid Tapajós with a more developed double irregular row of thorns, occasionally with thorns in between rows, or even thorns in a single, irregular row (e.g. Fig. 42). Thorns in mid Tapajós specimens posteriorly curved, very tall and closely packed together, with broad bases and slender, laterally flattened crowns (e.g. Figs. 40b, 41e). Some specimens from mid Tapajós with very large bucklers with greatly expanded, striated bases and sharp crowns (Fig. 40c). Bucklers also present occasionally on posterolateral disc. Some specimens with tubercles, hypertrophied thorns with more flattened bases and elongated crowns, on posterior disc, rarely on anterolateral disc. In specimens from all localities, thorns generally greater closer to caudal stings. Lateral and posterior tail regions with many small, erect and sharp thornlets.

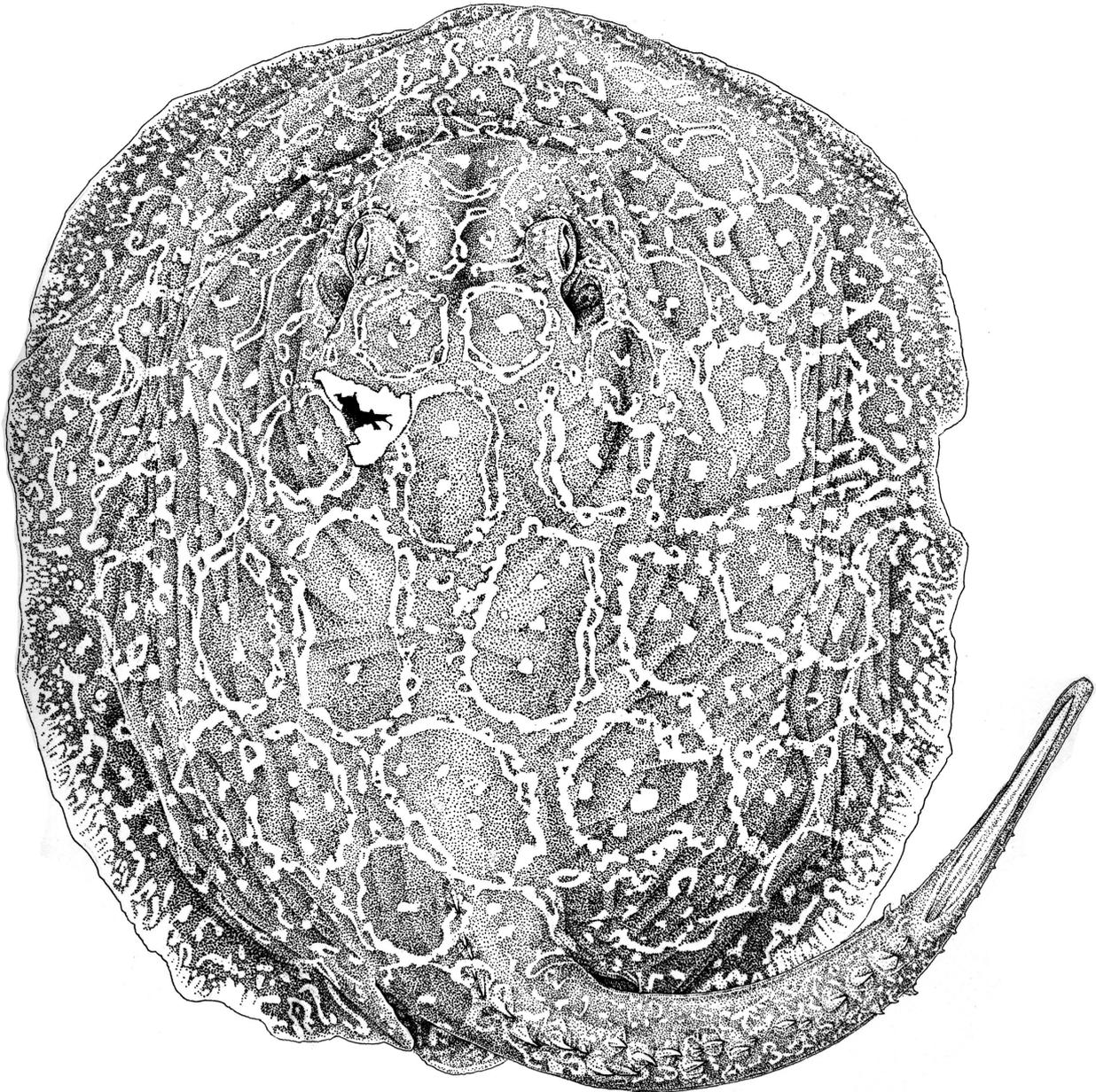


FIGURE 30. Illustration of dorsal side of adult female paratype MZUSP 25578 (700 mm TL), first adult specimen collected (in 1979), and which represents the lowermost record of *P. jabuti*, **sp. nov.**, in the Tapajós basin.

Ventral lateral-line canals. Suborbital loop (**sol**) formed by infraorbital canal (**ioc**), more or less slender, anteriorly curved toward midline (Fig. 43), and parallel to hyomandibular canal (**hyoc**) close to anterior disc margin. Lateral branch of infraorbital canal indented toward midline posterior to its center. Medial component of infraorbital canal undulated, with greater undulations at center; posterior portion of infraorbital canal extends to close to first gill slit, forming subtriangular infraorbital loop (**iol**). Orbitonasal component of supraorbital canal (**soc**) very undulated, extending in parallel to medial portion of infraorbital canal, closer to nostrils; orbitonasal component forms a broadly triangular prenasal loop (**pnl**). Mandibular canal (**man**) relatively elongate, sigmoid, and just posterior to mouth. Anterior jugular loop (**ajl**) more slender than subrectangular posterior jugular loop (**pjl**); jugular canal (**jug**) short and straight. Subpleural component of hyomandibular canal (**hyoc**) curved external to branchial slits, slightly undulated. Anterior subpleural tubules (**ast**) present anteriorly, reaching disc margin. External branch of hyomandibular canal very straight. Posterior subpleural tubule (**pst**) single, extending posteriorly past anterior pelvic fin margin. Subpleural loop (**spl**) somewhat slender, formed by posterior segments of hyomandibular canal, extending posteriorly to level of pelvic fin origin.

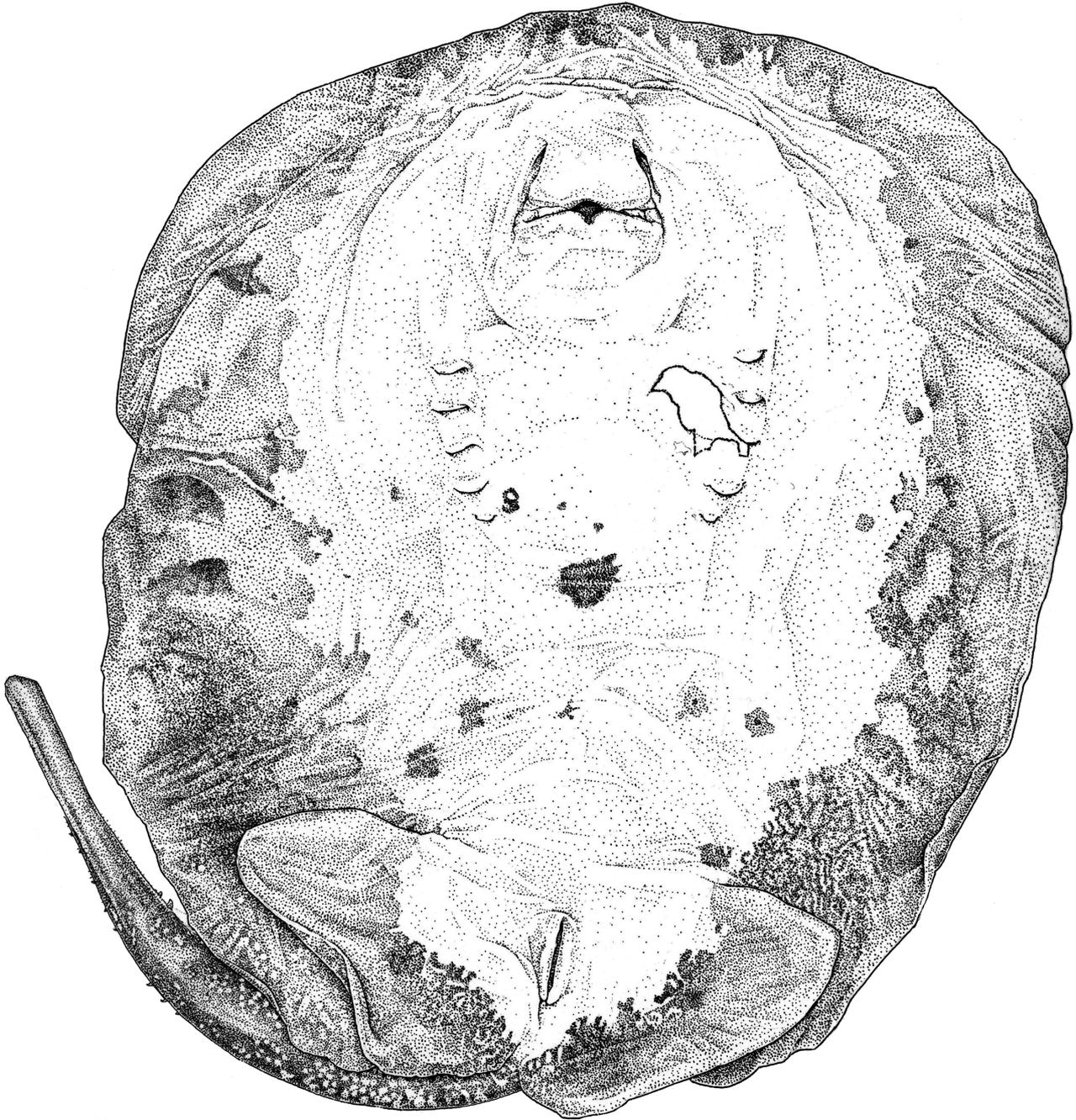


FIGURE 31. Illustration of ventral side of paratype MZUSP 25578.

Skeletal features. Neurocranial width about two-thirds its length, greatest width at level of pre- and postorbital processes, and most slender at posterior orbit (Figs. 44, 45a, b). Nasal capsules broadly rounded anteriorly, posteriorly more straight; median indentation concave to triangular, with slender internasal septum. Nasal apertures (**no**) much wider than long. Preorbital processes (**prp**) posterolaterally directed and broadly triangular. Postorbital processes (**pop**) projecting anterolaterally, rectangular, widening distally, and relatively broad with a slightly concave external margin. Supraorbital process (**sp**) just anterior to postorbital process and triangular, obscured by Meckel's cartilage in dorsoventral view. Otic capsule short, slightly wider than orbital region. Precerebral (**pcf**) and frontoparietal (**fpf**) fontanellae about three-fourths neurocranial length. Precerebral fontanelle broadly circular, about one-third to one-fourth length of neurocranium; frontoparietal fontanelle more slender and elongate, slightly constricted medially, and broadly triangular posteriorly, terminating at level of postorbital processes. Epiphysial bar incomplete. Parietal fossa shallow. Antorbital cartilage very slender in dorsoventral view, wider at articulation

with nasal capsule; antorbitals laterally compressed, extending posteriorly just beyond level of preorbital processes. Prespiracular cartilages (**psc**) slender, weakly calcified, obscured by lower jaws in dorsoventral view.

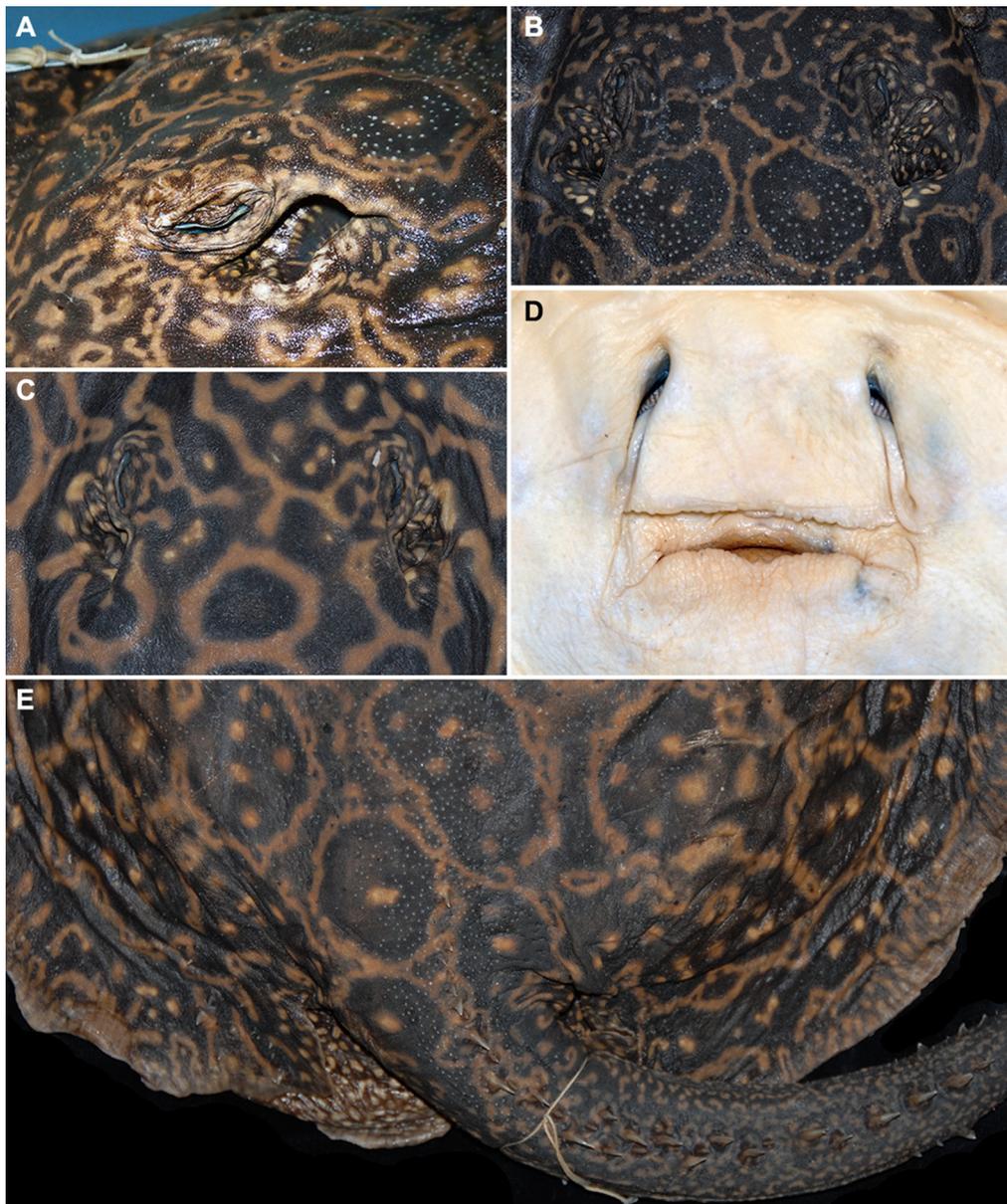


FIGURE 32. Morphological details of *Potamotrygon jabuti*, **sp. nov.** A) Dorsolateral view of head region (paratype, MZUSP 25578, 700 mm TL); B) Dorsal view of eyes and spiracles (MZUSP 103927, 710 mm TL); C) Dorsal view of eyes and spiracles (MZUSP 105038, 515 mm TL); D) Nasoral region (MZUSP 105013, 507 mm TL); E) Dorsal view of posterior disc, pelvic fins and tail base (MZUSP 25578).

Jaws heavily calcified. Meckel's cartilages (**Mc**) stouter than palatoquadrates, with robust, blunt, dorsally projecting lateral processes, and pointed posterolateral corners (Figs. 44, 45a, b). Palatoquadrate robust, wider medially, but more slender than Meckel's cartilage. Hyomandibula (**hyo**) relatively slender, laterally compressed, widest at midlength. Hyomandibulae extend anterolaterally to level of propterygium. A pair of robust angular cartilages present; anterior angular cartilage (**aac**) anteriorly concave and about one-fourth length of hyomandibula; posterior angular (**pac**) slightly smaller, less calcified, and frequently convex anteriorly. Angulars anteroposteriorly compressed, taller than long, and perpendicular to neurocranium, not obliquely positioned.

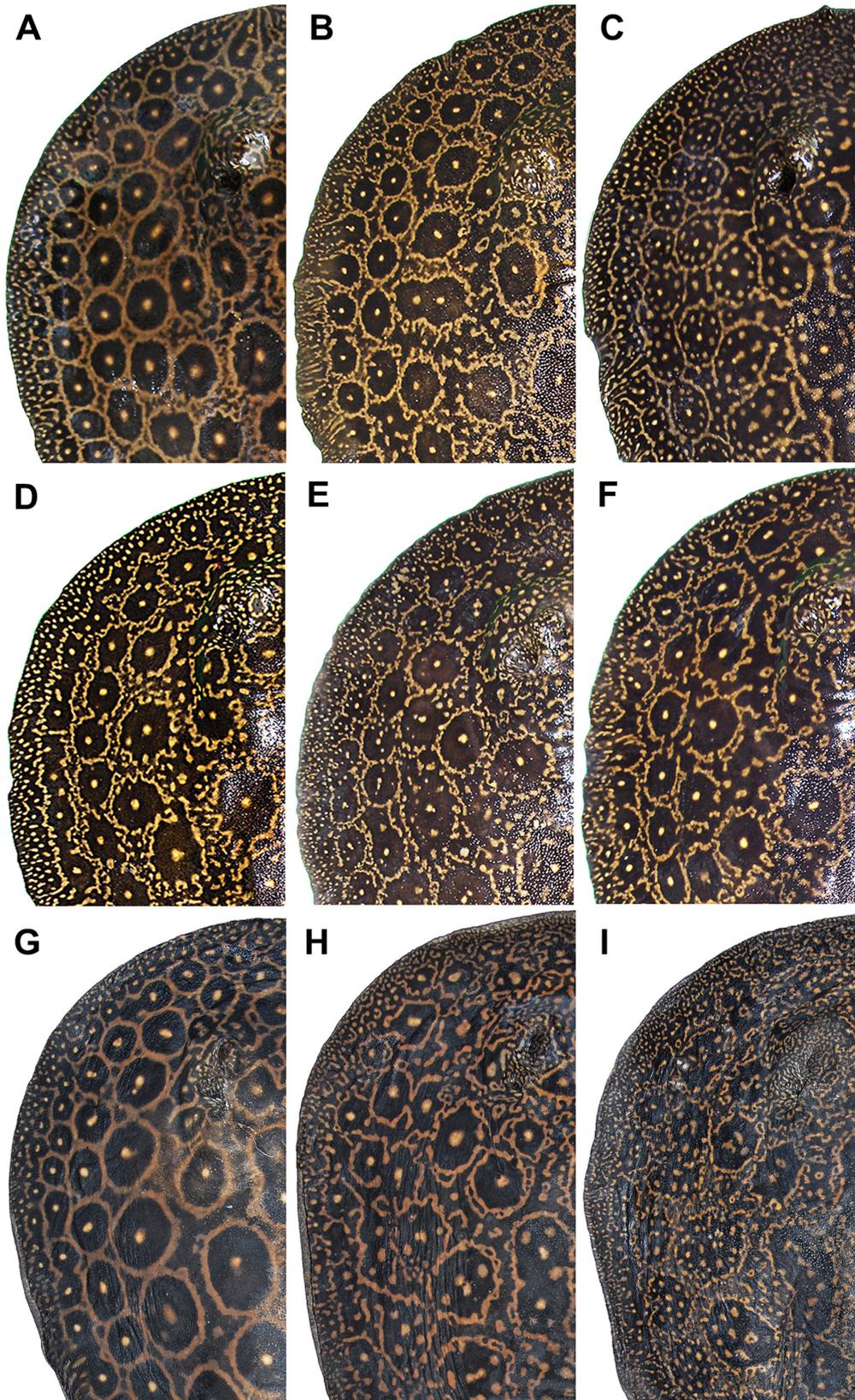


FIGURE 33. Dorsal view of anterolateral disc region in *Potamotrygon jabuti*, **sp. nov.**, showing variation in dorsal color pattern in specimens from the upper (rio Teles Pires, A–F) and middle (Comunidade Pimental, G–I) rio Tapajós (all images of freshly collected specimens). A) MZUSP 105015 (437 mm DL); B) MZUSP 105012 (712 mm DL); C) MZUSP 105011 (702 mm DL); D) MZUSP 105013 (507 mm TL); E) MZUSP 105009 (762 mm DL); F) MZUSP 105002 (660 mm DL); G) MZUSP 103921 (693 mm DL); H) MZUSP 103920 (810 mm TL); I) MZUSP 103919 (540 mm DL). Not to scale; some specimens horizontally inverted to facilitate viewing.

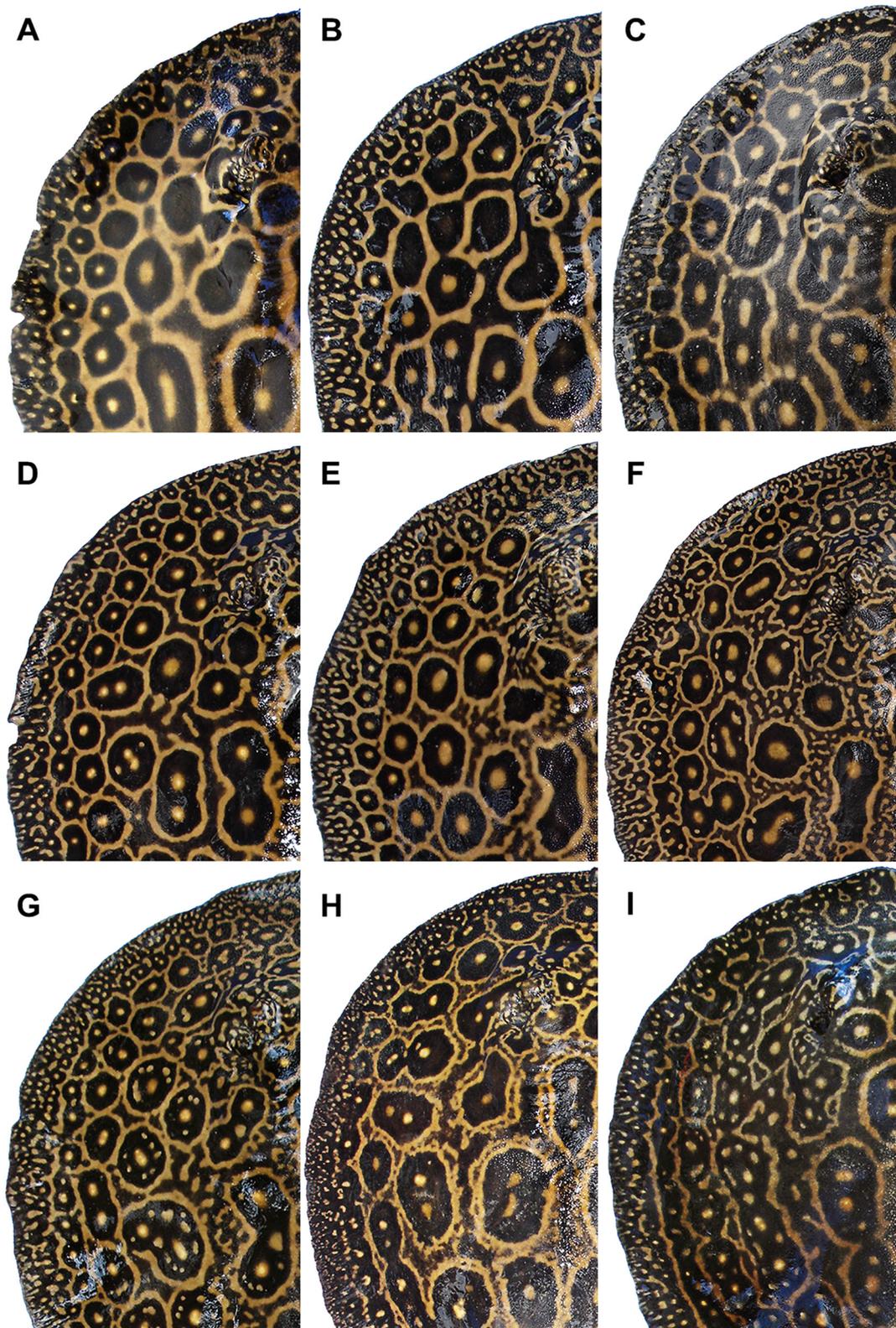


FIGURE 34. Dorsal view of anterolateral disc region in *Potamotrygon jabuti*, **sp. nov.**, showing variation in dorsal color pattern; all specimens shown just after being collected and are from proximal localities in rio Jamanxim. A) MZUSP 105025 (325 mm DL); B) MZUSP 105038 (515 mm TL); C) MZUSP 105018 (330 mm DL); D) MZUSP 105020 (485 mm TL); E) MZUSP 105017 (475 mm TL); F) MZUSP 105021 (390 mm DL); G) MZUSP 105037 (587 mm TL); H) MZUSP 105023 (739 mm TL); I) MZUSP 105027 (625 mm TL). Not to scale; some specimens horizontally inverted to facilitate viewing.

TABLE 3. Measurements of specimens of *Potamotrygon jabuti*, sp. nov. Ranges, means, and standard deviations were calculated from measurements of all specimens (N).

	MZUSP 105023 holotype		N	Range		Mean		SD	
	mm	% DW		mm	% DW	mm	% DW	mm	% DW
Total length	739.0	163.1	22	437–810	155.5–185.3	605.3	171.2	119.0	7.7
Disc length	487.0	107.5	23	275–542	103.6–116.9	398.6	110.6	88.6	3.7
Disc width	453.0	100.0	23	255–490	100.0–100.0	359.8	100.0	76.4	0.0
Interorbital space	70.0	15.4	23	40–73	13.0–20.0	54.2	15.2	9.7	1.5
Interspiracular space	90.0	19.8	23	49–98	17.0–22.0	71.3	19.8	15.9	1.1
Eye diameter	15.0	3.3	23	11–22	3.3–7.2	16.1	4.5	3.5	0.8
Spiracle length	19.0	4.2	23	16–40	4.2–9.2	26.5	7.3	7.6	1.1
Preorbital length	111.0	24.5	23	60–140	22.0–28.6	90.7	25.1	22.8	1.8
Prenasal length	71.0	15.6	23	38–80	13.7–17.5	55.8	15.5	12.1	0.9
Preoral length	105.0	23.1	22	55–112	19.0–25.4	81.0	22.7	17.8	1.4
Internasal space	40.0	8.3	23	18–48	6.7–10.3	30.5	8.4	8.3	0.9
Mouth width	50.0	11.0	22	24–70	8.9–15.1	41.0	11.2	15.2	1.9
Distance between 1st gill slits	118.0	26.0	22	59–151	21.9–32.5	92.6	25.7	25.2	2.2
Distance between 5th gill slits	85.0	18.7	22	49–105	17.8–22.6	69.3	19.4	16.2	1.0
Branchial basket length	65.0	14.3	22	39–85	14.3–20.4	59.2	16.7	12.1	1.3
Pelvic fin anterior margin length	104.0	22.9	23	59–130	19.4–27.9	87.0	24.3	18.9	2.1
Pelvic-fin width	225.0	49.6	23	130–258	46.0–60.6	186.7	51.9	41.9	3.7
Clasper internal margin	–	–	10	28–64	10.4–21.0	51.3	16.1	11.4	3.0
Cloaca to clasper tip	–	–	10	45–113	16.7–33.3	89.9	28.1	21.6	5.1
Cloaca to tail tip	311.0	68.6	22	194–365	59.0–88.6	269.2	76.7	46.6	7.0
Tail width	75.0	16.5	22	27–90	9.7–21.6	48.9	13.3	20.2	3.1
Snout to cloaca distance	412.0	90.9	23	187–455	73.3–95.3	325.0	89.7	79.9	4.8
Disc insertion to post. pelvic margin	69.0	15.2	23	40–72	12.7–20.0	55.3	15.6	10.2	2.2
Cloaca to sting origin	192.0	42.3	22	109–225	39.9–52.5	160.9	45.2	37.8	3.5
Sting length	100.0	22.0	22	58–100	12.2–27.1	77.8	22.3	14.5	3.0
Sting width	10.0	2.2	22	3–10	1.0–2.8	5.9	1.7	1.9	0.4

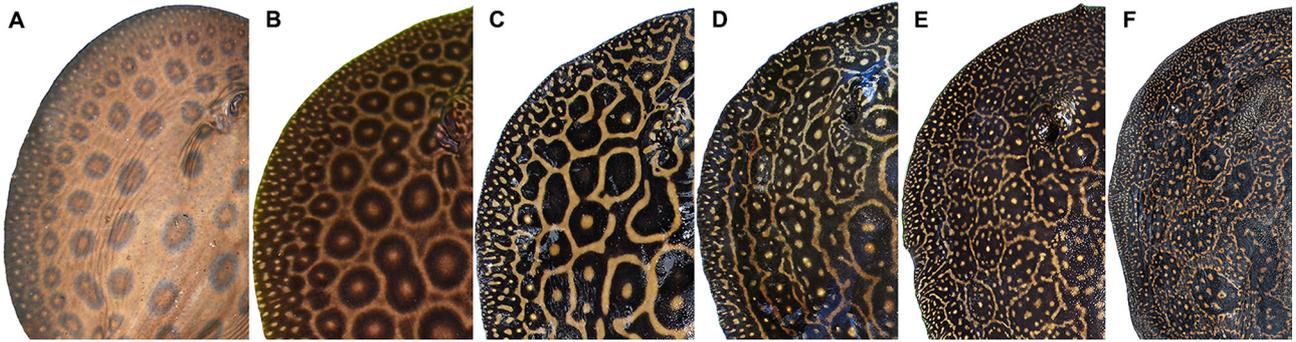


FIGURE 35. Transition in color pattern from neonate (A) to large adult (F) passing through intermediate stages (B–E). Note that images are *not* the same specimen over time, but represent different color morphs separated by size. A) Neonate hours old, in aquarium; B) Small juvenile some five months old, in aquarium; C) Specimen almost sexually mature (MZUSP 105038, 515 mm TL); D) Adult (MZUSP 105027, 625 mm TL); E) Adult (MZUSP 105011, 702 mm DL); F) Large adult female with elaborate late-stage color pattern (MZUSP 103919, 540 mm DL, 465 mm DW; tail amputated but specimen has largest disc of all specimens). A and B courtesy of R. Hardwick.

First (cervicothoracic) synarcual just shorter than neurocranium in total length, its greatest width about equal to width of precerebral fontanelle, at level of lateral stays. Medial crest very slender, extending anteriorly to almost posterior neurocranium. Two vertebrae appear to be incorporated into synarcual, anteriormost only a partial centrum. Thoracolumbar synarcual short and slender. Transition from mono- to diplospondyly usually occurs at fifth centrum posterior to rear margin of pelvic girdle. Individual vertebral centra occurring caudally to just beyond one-half of caudal sting length; cartilaginous rod present distally posterior to individual centra.

Propterygium (**pro**) laterally compressed, tapering anteriorly, and stouter at base where it articulates with scapulocoracoid (Fig. 45c); propterygium wider than meso- and metapterygium, and with a slender anterior propterygial segment (**apr**) articulating with 5–6 radial elements lateral to nasal capsule; anteriormost radial articulating with propterygium bifurcated. Mesopterygium (**mes**) flat and anteriorly slender, with faintly convex external margin, usually indented at midlength, and concave anterointernal margin where it contacts propterygium; radials articulating to mesopterygium frequently fused at base. Metapterygium (**met**) broadly arched, more so than propterygium; three smaller metapterygial posterior segments decreasing in size. Individual pectoral radials sometimes fused at base in between pectoral basals. Pectoral radials slender and elongate close to pectoral basals, slightly stouter and less wide toward mid-disc, and slender distally; pectoral radials bifurcate at 8th segment counting from basals at about mid-disc, and some 22 radial segments (from basals to outer disc margins) present at mid-disc.

Pelvic girdle anteriorly concave lateral to median prepelvic process; posterior margin concave. Median prepelvic process long and slender, extending anteriorly to close to thoracolumbar synarcual. Lateral prepelvic processes broadly triangular. Iliac processes extending dorsoposteriorly; ischial processes broadly triangular. Three obturator foramina present, positioned obliquely. Basipterygium slender, with weakly sinuous external margin for junction with pelvic radials; first enlarged radial articulates directly to lateral aspect of pelvic girdle; posteriormost radials slender, contacting first intermediate segment of clasper. Proximal pelvic radial, articulating with basipterygium, much longer than distal radials; some six radial segments present from basipterygium to outermost pelvic fin margin at greatest pelvic fin width, bifurcating at fourth (anterior radials) to second (posterior radials) segment from basipterygium. Anteriorly, second pelvic radial element short and stout, but second radials posteriorly more elongate and slender. Clasper with two basal (intermediate) segments (**b1**, **b2**) (Fig. 45d). Axial cartilage (**ax**) elongate, slightly less than twice length of terminal elements. Dorsal marginal cartilage (**dm**) slightly greater than ventral marginal (**vm**) and distally articulating to dorsal terminal 2 cartilage (**dt2**); accessory terminal (**at**) slightly longer than ventral terminal (**vt**).

Geographic distribution. *Potamotrygon jabuti* is endemic to the mid and upper rio Tapajós (Fig. 46). It has been captured in many localities, and is very common in rios Jamaxim and Teles Pires, and in the Tapajós main river near the village of Pimental. Its occurrence in the lower rio Jurueña is unknown (as in *P. albimaculata*). Clearly, most rapids are not barriers that impede its distribution, as *P. jabuti* has been sampled below *and* above many series of rapids. The São Luiz rapids, a series of more significant rapids upriver from Itaituba (and just

downriver from Pimental), is believed to be only a partial barrier during the high-water season, which may account for the information from local fishermen that *P. jabuti* is rare but has been seen close to Itaituba, downriver from the major rapids. The specimen with the verified lowermost record is MZUSP 25578, captured just above the São Luiz rapids.

Common name. In Portuguese this species is widely known as "jabuti" (see Etymology below); the English common name is Pearl freshwater stingray, the name most frequently used in the aquarium trade.

Etymology. The specific name *jabuti* is in reference to its similarity in dorsal color to the common land-dwelling tortoises (Testudinidae), especially when the disc is arched. A noun in apposition.

Biological notes. *Potamotrygon jabuti* was collected in the main rio Tapajós channel and in much smaller streams on rocky, sandy and leafy substrates; it was particularly abundant in rio Jamanxim, an area that provides many specimens for the ornamental fish trade. Its biological parameters that have been studied indicate a similar reproductive cycle as *P. albimaculata*, with simultaneous gestation and vitellogenesis, a four month gestational period, and parturition occurring when river levels are rising. Fecundity ranges from 1–4 embryos, but generally two are born per gestation in the wild (M.L.G. de Araújo, pers. comm.). According to field observations, there is sexual and ontogenetic segregation in *P. jabuti* (M.L.G. de Araújo, unpubl.). In aquaria, fecundity is generally greater, and at least four embryos are commonly born. Sexual maturity for males occurs from 460–470 mm TL, based on the material studied (MZUSP 105034 is juvenile at 460 mm TL, 296 mm DL, 270 mm DW, and MZUSP 105039 is clearly adult at 471 mm TL, 292 mm DL, 255 mm DW). However, MZUSP 105038 is exceptionally a large juvenile male (almost adult) at 515 mm TL, 345 mm DL, and 310 mm DW (all three specimens are from the same locality). Females are sexually mature at similar sizes. Embryos are born at about 110 mm DW. Collected specimens were more resilient than *P. albimaculata*, with a less pronounced and more durable mucous layer.

TABLE 4. Counts taken on specimens of *Potamotrygon jabuti*, **sp. nov.** A: MZUSP 105023 (holotype, 739 mm TL); B) MZUSP 105037 (587 mm TL); C) MZUSP 100030 (305 mm DL); D) MZUSP 25580 (596 mm TL); E) MZUSP 117801 (307 mm TL); F) MZUSP 103920 (810 mm TL); G) MZUSP 105011 (702 mm TL); H) MZUSP 105002 (660 mm TL); I) MZUSP 105015 (437 mm TL); J) MZUSP 25578 (700 mm TL); K) MZUSP 105038 (515 mm TL).

CHARACTER	A	B	C	D	E	F	G	H
Prepelvic vertebrae	31	30	29	24	30	30	30	29
Monospondylous vertebrae	34	35	34	31	35	35	25	35
Diplospondylous vertebrae	88	91	86	86	86	85	90	85
Total vertebrae	122	126	120	117	121	120	125	120
Propterygial radials	43	46	46	51	–	48	47	48
Mesopterygial radials	14	13	15	13	–	14	14	15
Metapterygial radials	43	41	42	38	–	43	41	40
Toral pectoral radials	100	100	103	102	–	105	102	103
Pelvic-fin radials	27	25	21	21	–	25	22	22

continued.

CHARACTER	I	J	K	Range	Mode
Prepelvic vertebrae	31	30	33	24–33	30
Monospondylous vertebrae	38	35	37	31–38	35
Diplospondylous vertebrae	86	93	89	85–93	86
Total vertebrae	124	128	126	117–128	120
Propterygial radials	46	48	46	43–48	46
Mesopterygial radials	15	15	15	13–15	15
Metapterygial radials	41	43	40	38–43	41
Toral pectoral radials	102	106	101	100–106	103
Pelvic-fin radials	25	25	21	21–27	25

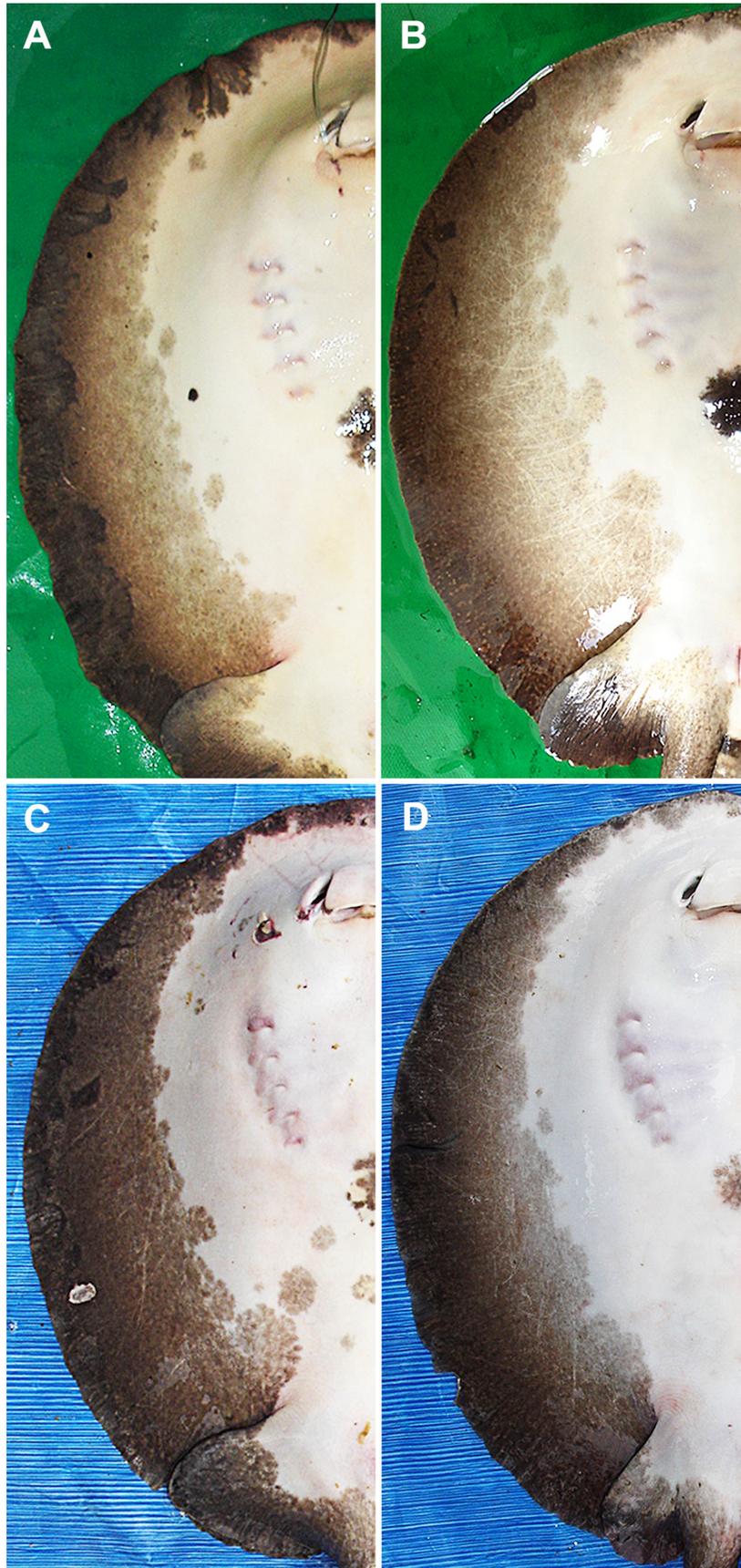


FIGURE 36. Ventral disc in *Potamotrygon jabuti*, **sp. nov.**, showing variation in ventral color pattern; all specimens freshly collected. A) MZUSP 105012 (712 mm TL); B) MZUSP 105013 (507 mm TL); C) MZUSP 105024 (420 mm TL); D) MZUSP 105018 (330 mm TL). Not to scale.

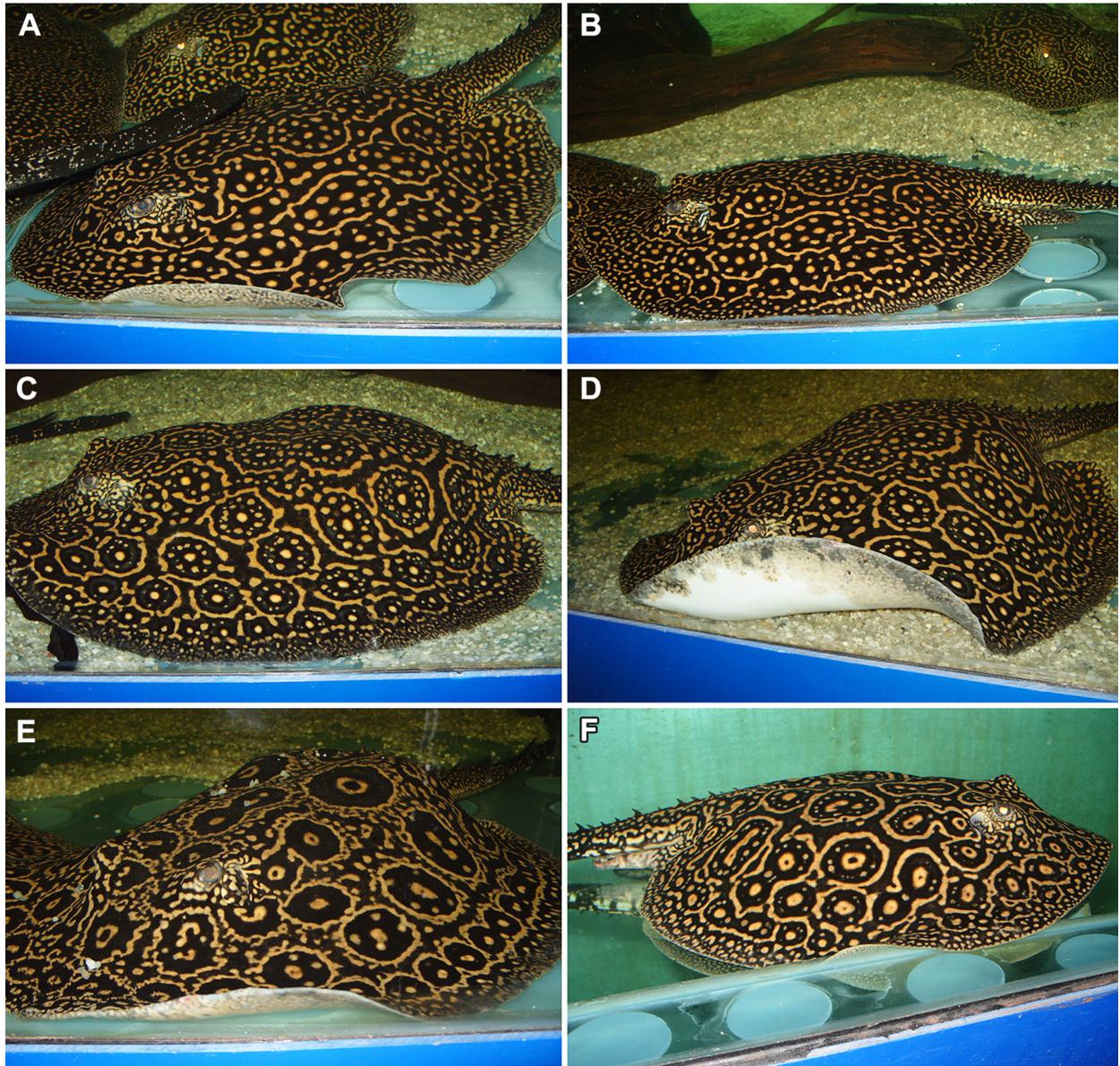


FIGURE 37. Live adult specimens of *Potamotrygon jabuti*, sp. nov., in aquarium (courtesy of R. Hardwick).

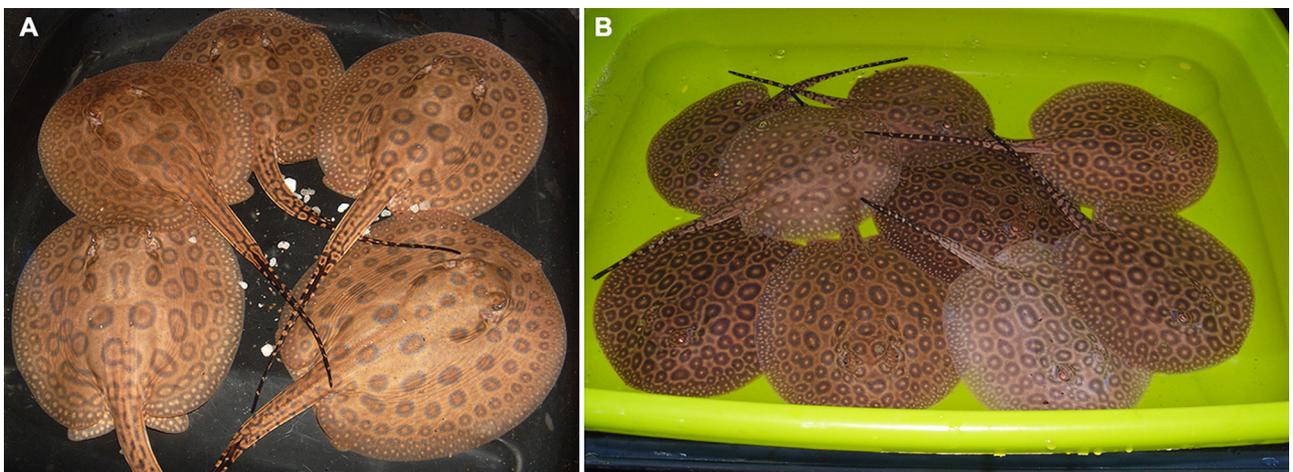


FIGURE 38. Live neonates (A) of *Potamotrygon jabuti*, sp. nov., shortly after birth; B) Small juveniles about five months old (courtesy of R. Hardwick). Note color change in just five months from neonate to small juvenile (for adults, see Figs. 22–35).

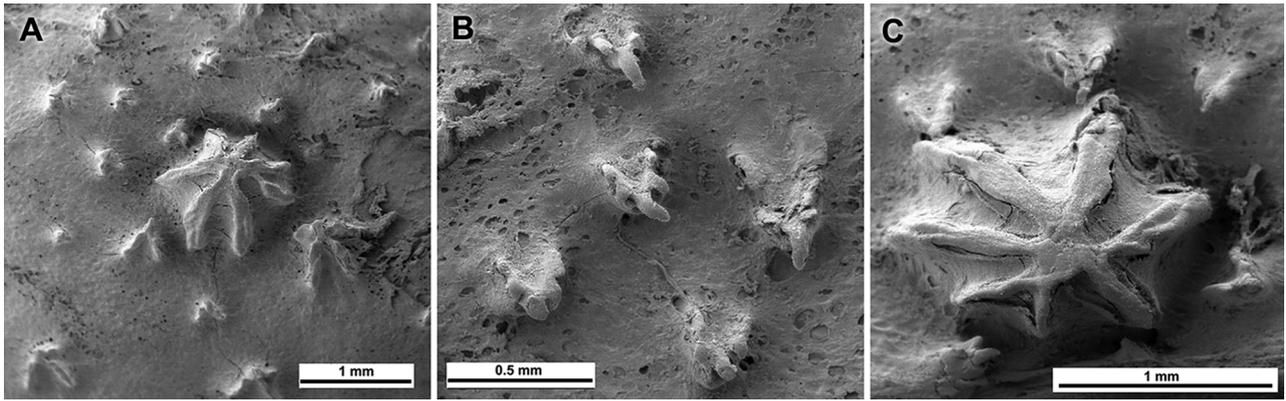


FIGURE 39. SEM photos of dorsal denticles from anterior mid-disc in *Potamotrygon jabuti*, **sp. nov.**, in dorsal view, showing larger and smaller denticles (A, C), and smaller denticles (B) (all MZUSP 105002).

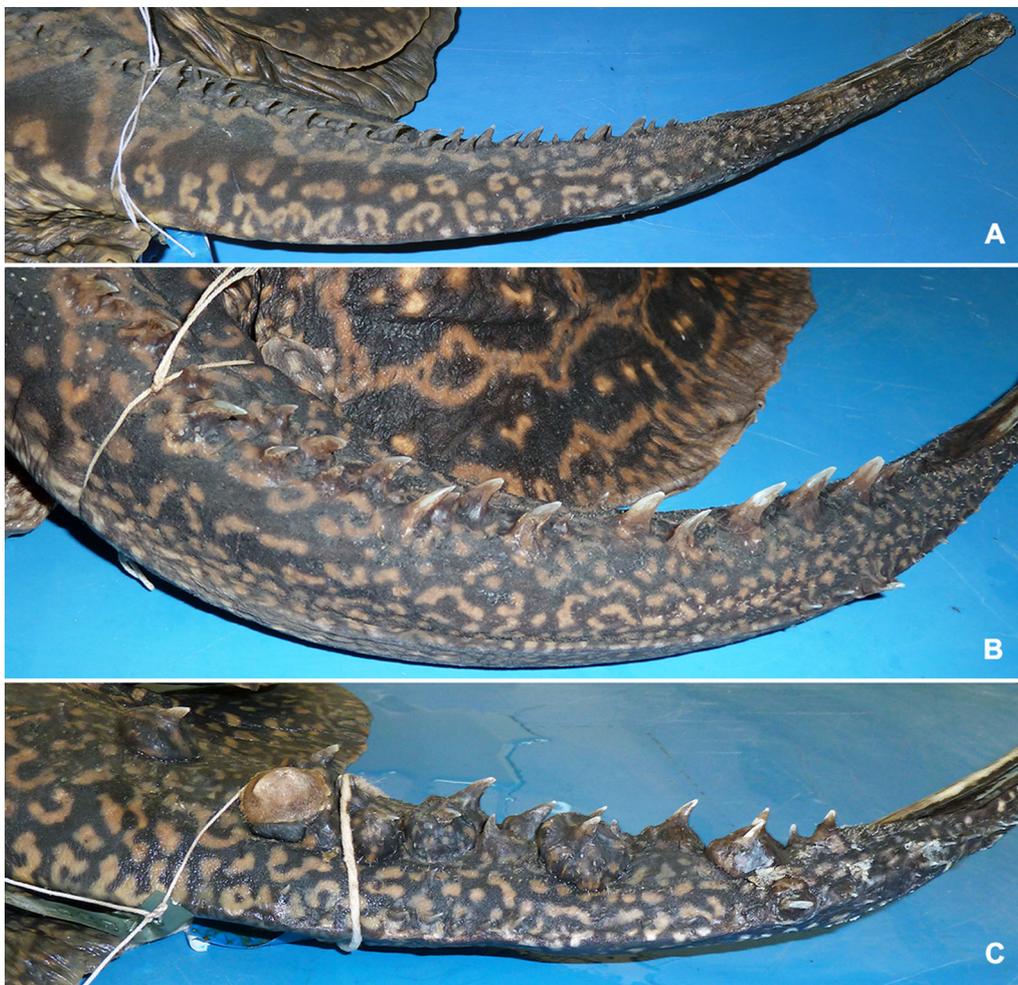


FIGURE 40. Dorsolateral view of tail of *Potamotrygon jabuti*, **sp. nov.**, showing development and arrangement of tail thorns. A) MZUSP 105023 (holotype, rio Jamanxim, 739 mm TL); B) MZUSP 25578 (paratype, near São Luiz rapids, 700 mm TL); C) MZUSP 103920 (Pimental, 810 mm TL).

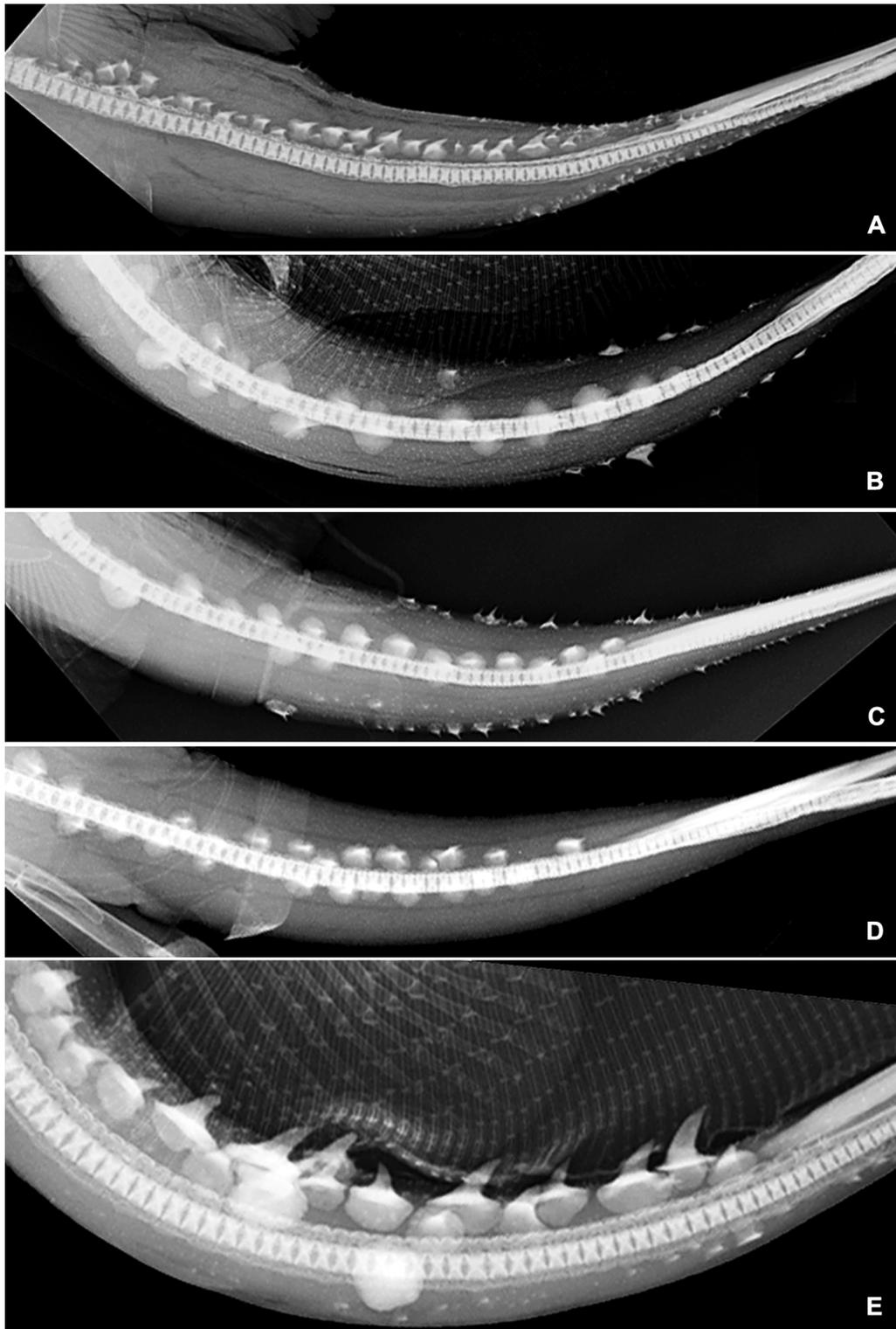


FIGURE 41. Dorsal view of tail in radiographs of *Potamotrygon jabuti*, **sp. nov.**, showing organization of tail thorns; all specimens adult males. A) MZUSP 105023 (holotype, 739 mm TL); B) MZUSP 25578 (700 mm TL); C) MZUSP 103921 (693 mm TL); D) MZUSP 105013 (507 mm TL); E) MZUSP 25580 (596 mm TL).



FIGURE 42. Base of tail region of *Potamotrygon jabuti*, **sp. nov.**, in dorsal view, showing anterior rows of dorsal tail thorns and dorsal clasper morphology in adult males. A) MZUSP 105011 (702 mm TL); B) MZUSP 105019 (520 mm TL).

Intraspecific variation. Specimens of *P. jabuti* from Pimental, near the São Luiz rapids, at the most downriver part of its distribution, tend to have more developed dorsal tail thorns that are usually much taller than those from rio Jamanxim, and distributed in irregular double rows at least posteriorly, closer to caudal stings (material from rio Jamanxim, in contrast, tend to have an irregular single row of tail thorns). Many of these specimens also have hypertrophied bucklers (with greatly expanded and tall bases, and sharp crowns) and/or hypertrophied tubercles (with expanded but flat bases and sharp crowns) on the tail and even on the disc (usually posterior disc) (Fig. 40c), structures that are also lacking from specimens from rio Jamanxim (e.g. Figs. 40a, 41a). A few specimens examined from rio Cururu (in IRSNB), just downriver from the confluence of rios Juruena and Teles Pires (upper rio Tapajós), also have enlarged tubercles, marking the farthest upriver occurrence of these structures. Other species of *Potamotrygon* from the lower Tapajós, in the mouth-lake or even closer to Itaituba, also have bucklers and tubercles on disc and tail (discussed below), such that these features are considered to vary intraspecifically in *P. jabuti*. Furthermore, specimens from the lower part of the range of *P. jabuti* are slightly larger, but this may be an artifact of sampling.

born in captivity, and resemble neonates of *P. motoro*; field collected neonate specimens of *P. jabuti* are like those in Fig. 38a, as are late-term embryos aborted by gravid females upon capture, although neonate specimens that have ocelli with yellow centers are sometimes present. But after a few months, the complex marbled pattern of *P. jabuti* becomes apparent—the aquarium specimens in Fig. 38b are almost five months old (R. Hardwick, pers. comm.) and had color patterns identical to those in Fig. 38a, highlighting the typical transformations in color pattern that are present even in specimens of *P. jabuti* with very complex designs as adults (e.g. Figs. 22–35, 37). Specimens of *P. motoro* undergo far less dramatic transformations in color, maintaining their ocellated patterns as adults.

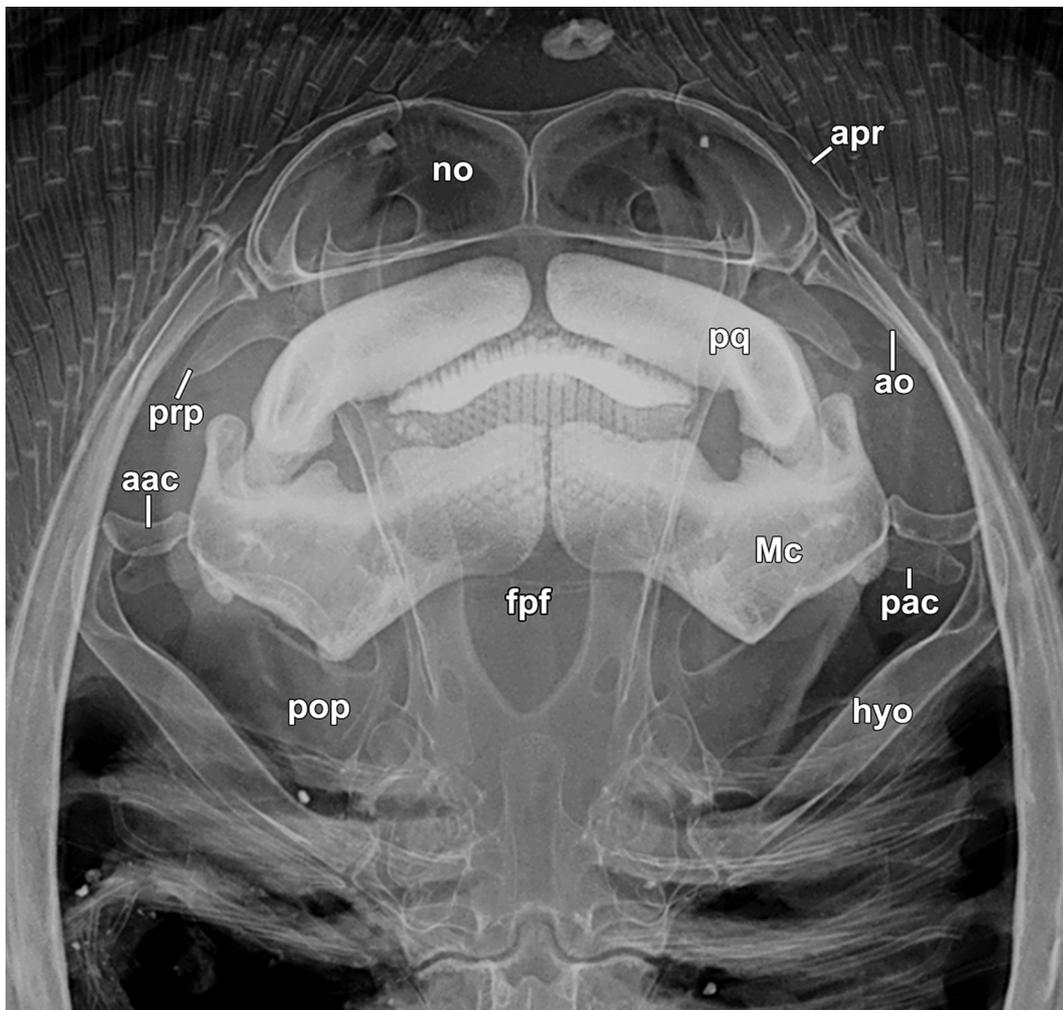


FIGURE 44. Radiograph of head skeleton of *Potamotrygon jabuti*, **sp. nov.** (MZUSP 25578, 700 mm TL). Abbreviations: **aac**, anterior angular cartilage; **ao**, antorbital cartilage; **apr**, anterior segment of propterygium; **fpf**, frontoparietal fontanelle; **hyo**, hyomandibula; **Mc**, Meckel's cartilage; **no**, nasal opening (nasal aperture); **pac**, posterior angular cartilage; **pop**, postorbital process; **pq**, palatoquadrate; **prp**, preorbital process.

Potamotrygn jabuti and *P. motoro* have other features in common, not just the color pattern of neonates (data on *P. motoro* from Loboda, 2010; Loboda & Carvalho, 2013). Both species typically have a relatively robust head (somewhat wide interorbital, interspiracular and interbranchial regions; similar also in other proportions), a similar extent of the darker grayish to brownish ventral color on outer disc and posterior pelvic fins (small beige, yellow to light orange spots and vermiculate shapes also present in *P. jabuti*, grayish mottling in some specimens of *P. motoro*, e.g. from rio Negro), absence of labial grooves, teeth on upper jaw with monognathic heterodonty as intermediate lateral tooth rows have larger hexagonal teeth forming a crushing surface, with slightly undulated tooth bands (more developed in *P. motoro*), two angular cartilages of similar proportions (anterior angular usually slightly greater), and a relatively broad frontoparietal fontanelle (e.g. Fig. 44). The broad frontoparietal fontanelle seems to vary slightly among specimens of *P. jabuti*, but less so in specimens of *P. motoro*. The hexagonal

intermediate tooth rows in the upper jaws are also present, but to a lesser degree, in *P. brachyura*, *P. ocellata*, and *P. rex*, species that also have two well developed angular cartilages, but that do not share a closer relationship (except *P. ocellata*, which is closely related to *P. motoro* and may even be synonymous with it; *P. rex* belongs to the black stingray group, and the relationships of *P. brachyura* are largely unknown). Some of the characters listed above are more general, present in other congeneric species (head proportions, similarities in ventral color, lack of labial grooves), but the similarities in the dorsal color pattern of neonates may be derived for *P. jabuti* and *P. motoro*. Further comparisons are underway.

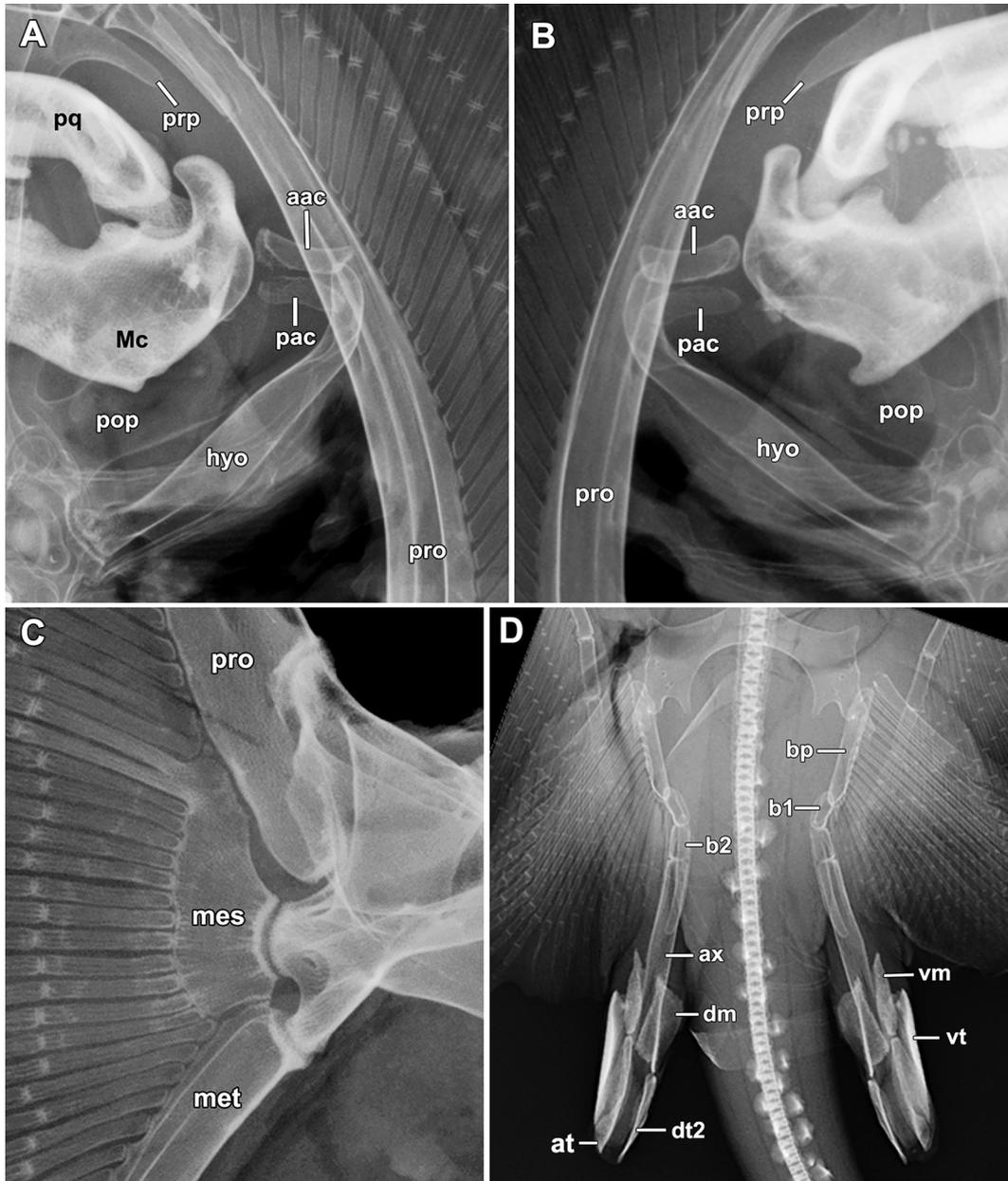


FIGURE 45. Skeletal features of *Potamotrygon jabuti*, sp. nov., from radiographs, in dorsoventral view. A) Head region of holotype (MZUSP 105023, 739 mm TL); B) Head region of MZUSP 105011 (702 mm TL); C) Basal cartilages and their articulation with scapulocoracoid (holotype MZUSP 105023); D) Base of tail region, showing distribution and development of dermal denticles and thorns, and clasper skeleton (MZUSP 105013, 507 mm TL). Abbreviations: **aac**, anterior angular cartilage; **at**, accessory terminal cartilage; **ax**, axial cartilage; **b1**, basal (intermediate) segment 1; **b2**, basal (intermediate) segment 2; **bp**, basipterygium; **dm**, dorsal marginal cartilage; **dt2**, dorsal terminal 2 cartilage; **hyo**, hyomandibula; **Mc**, Meckel's cartilage; **mes**, mesopterygium; **met**, metapterygium; **pac**, posterior angular cartilage; **pop**, postorbital process; **pq**, palatoquadrate; **pro**, propterygium; **prp**, preorbital process; **vm**, ventral marginal cartilage; **vt**, ventral terminal cartilage.

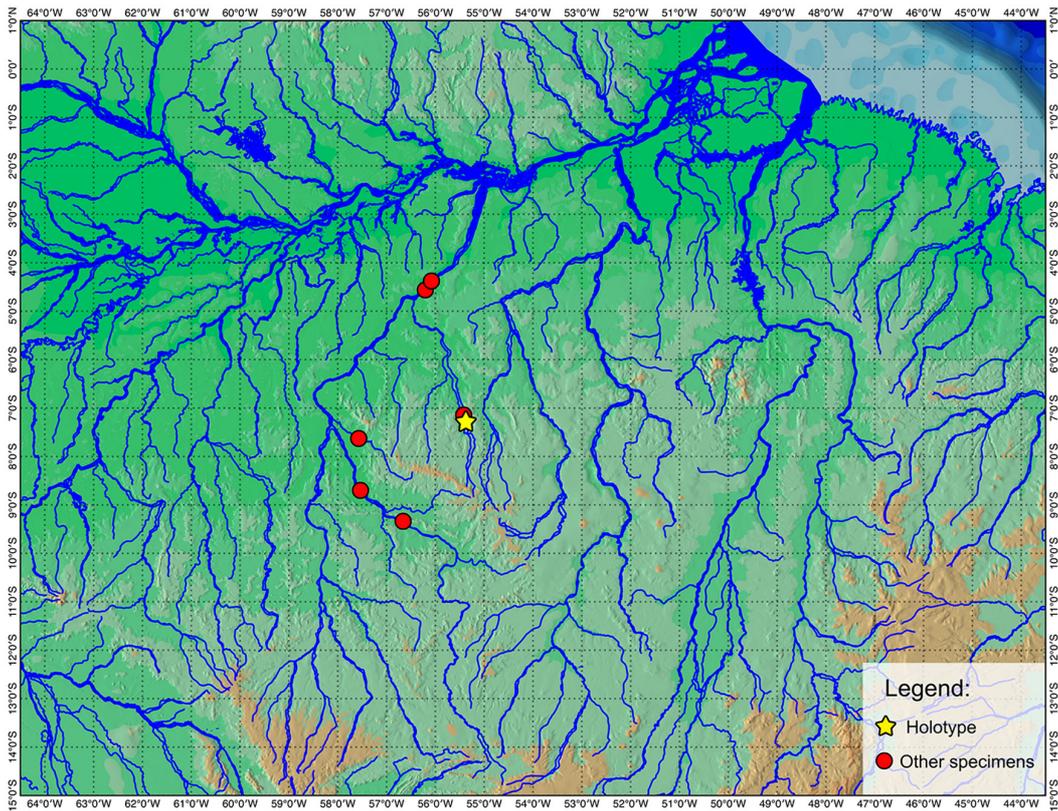


FIGURE 46. Map showing distribution of *Potamotrygon jabuti*, **sp. nov.**, in the middle and upper rio Tapajós. Symbols may indicate multiple specimens.

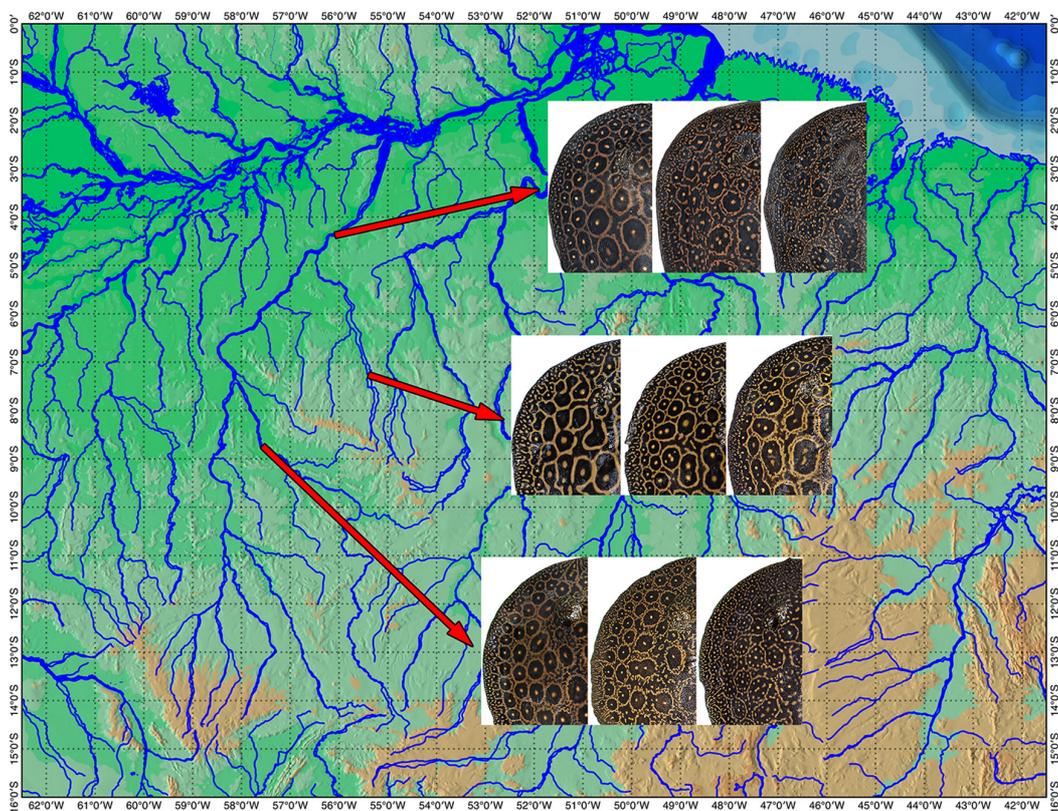


FIGURE 47. Map showing distribution of dorsal color patterns of *Potamotrygon jabuti*, **sp. nov.**, based on specimens sampled at three major collecting sites in the middle and upper rio Tapajós.

The presence of two angular cartilages of more or less similar width also occurs in *P. falkneri*, *P. tatianae*, *P. brachyura*, *P. boesemani*, *P. motoro*, *P. ocellata*, *P. yepezi*, *P. rex*, *P. henlei*, *P. leopoldi*, and in *P. albimaculata* described above (Rosa *et al.*, 2008; Carvalho *et al.*, 2011; Silva & Carvalho, 2011a; Loboda & Carvalho, 2013; Carvalho, 2016). Two developed and similar angulars may not define a monophyletic species group within *Potamotrygon*, but there are more specific similarities in angular cartilage morphology among certain species. The posterior angular is clearly more slender than the anterior in *P. falkneri* and *P. tatianae*, species that doubtlessly form a monophyletic group; *P. albimaculata*, however, also has a more slender posterior angular and is not particularly closely related to these two species (*P. albimaculata* forms a group with other black stingrays). The angulars in *P. jabuti* and *P. motoro* are very similar in shape and proportions, but whether this is additional evidence of their closer affinity needs further scrutiny.

Other specimens examined. (66 specimens). MZUSP 25489, juvenile female, Comunidade Pimental, right bank of rio Tapajós, Pará state, Brazil, 04°36'00"S, 056°16'00"W, 31.i.1979, col. J.C. Oliveira; MZUSP 25579, 6 late-term pups (1 c&s), left bank affluent, rio Tapajós, at km 69 of highway BR 230, 04°31'00"S, 056°16'00"W, Pará state, Brazil, 31.i.1979, col. J.C. Oliveira; MZUSP 25580, adult male, data as in MZUSP 25579; MZUSP 97631, rio Jamaxim, near Novo Progresso, Pará state, Brazil, 07°03'52"S, 055°26'28"W, col. J. Birindelli, L. Sousa & A. Netto-Ferreira; MZUSP 97632, same data as MZUSP 97631; MZUSP 100030, Mato Grosso state, Brazil, 9°18'42"S, 056°46'47"W, col. L. Sousa & A. Netto-Ferreira; MZUSP 103919, Comunidade Pimental, right margin of rio Tapajós, Pará state, Brazil, 4°33'05"S, 056°16'43"W, 11.x.2005, col. M.R. de Carvalho, M. Cardoso, M.L.G. de Araújo & S.M.V. Melo (field no. TJ05.35); MZUSP 103923, Comunidade Pimental, right margin of rio Tapajós, Pará state, Brazil, 4°33'05"S, 056°16'43"W, 11.x.2005, col. M.R. de Carvalho, M. Cardoso, M.L.G. de Araújo & S.M.V. Melo (field no. TJ05.40); MZUSP 103925, just downriver from Comunidade Pimental, in rapids, rio Tapajós, Pará state, Brazil, 4°33'06"S, 056°16'38"W, 11.x.2005, col. M.R. de Carvalho, M. Cardoso, M.L.G. de Araújo & S. Mello (field no. TJ05.44); MZUSP 103927, just upriver from Comunidade Pimental, rio Tapajós, Pará state, Brazil, 12.x.2005 (field no. TJ05.46); MZUSP 105000, near Pousada Santa Rosa, left bank of rio Teles Pires, rio Tapajós basin, Mato Grosso state, Brazil, 08°46'45"S, 057°27'55"W, col. M.R. de Carvalho, F. Marques, M. Carvalho & A. Datovo (field no. MT05.01); MZUSP 105004, data as in MZUSP 105000 (field no. MT05.07); MZUSP 105009, adult female, data as in MZUSP 105000 (field no. MT05.12); MZUSP 105012, data as in MZUSP 105000 (field no. MT05.17); MZUSP 105014, data as in MZUSP 105002 (field no. MT05.19); MZUSP 105015, data as in MZUSP 105002 (field no. MT05.20); MZUSP 105017, data as in holotype (field no. MT05.22); MZUSP 105018, data as in holotype (field no. MT05.23); MZUSP 105019, data as in holotype (field no. MT05.24); MZUSP 105020, data as in holotype (field no. MT05.25); MZUSP 105021, data as in holotype (field no. MT05.26); MZUSP 105022, data as in holotype (dissected for lateral line) (field no. MT05.27); MZUSP 105023, data as in holotype (field no. MT05.28); MZUSP 105024, data as in holotype (field no. MT05.29); MZUSP 105025, data as in holotype (field no. MT05.30); MZUSP 105026, data as in holotype (field no. MT05.31); MZUSP 105027, data as in holotype (field no. MT05.32); MZUSP 105028, data as in holotype (field no. MT05.33); MZUSP 105029, data as in holotype (field no. MT05.34); MZUSP 105030, data as in holotype (field no. MT05.35); MZUSP 105031, data as in holotype (field no. MT05.36); MZUSP 105032, data as in holotype (field no. MT05.37); MZUSP 105033, data as in holotype (field no. MT05.38); MZUSP 105034, data as in holotype (field no. MT05.39); MZUSP 105035, data as in holotype (field no. MT05.40); MZUSP 105036, data as in holotype (field no. MT05.41); MZUSP 105037, data as in holotype (field no. MT05.42); MZUSP 105039, data as in holotype (dissected for lateral line) (field no. MT05.44); MZUSP 106682–106686, 5 specs., from aquarium trade, rio Tapajós (no further data); MZUSP 116092, data as in MZUSP 103919 (dissected for brain) (field no. TJ05.41); MZUSP 116093, rio Tapajós, no further data (dissected for brain); MZUSP 117801, Comunidade Pimental, right bank of rio Tapajós, Pará state, Brazil, 04°33'41"S, 056°15'12"W, 9.x.2005, col. M.R. de Carvalho, M. Cardoso, M.L.G. de Araújo & S.M.V. Melo (field no. TJ05.31); MZUSP 117802, data as in MZUSP 117801 (field no. TJ05.32); MZUSP 117803, juvenile male, 398 mm TL, data as in MZUSP 117801 (field no. TJ05.34); MZUSP 102449., from aquarium trade, rio Tapajós (no further data); MZUSP uncat. (6 juvenile specimens from aquarium trade); IRSNB 17885, 4 large specimens (one with aborted embryo), station 129, arm of rio Cururu downstream of the Franciscan mission of Cururu, upper Tapajós, State of Pará, Brasil, 21.xi.1964, col. J.-P. Gosse; IRSNB 17898, 2 neonates, same data as IRSNB 17885 (photographs only).

Stingrays of the Tapajós basin

The following potamotrygonid species were collected in the lower rio Tapajós: *P. motoro*, *P. humerosa*, *P. orbignyi*, *Potamotrygon* sp., and *Paratrygon aiereba* (Figs. 48–50). Although not collected, *Plesiotrygon iwamae* is possibly present in the lower rio Tapajós mouth-lake, perhaps closer to the confluence with rio Amazonas. In the mid and upper Tapajós the two endemic species *P. albimaculata* and *P. jabuti* co-occur to some extent with *P. orbignyi* and *P. aiereba* and another species herein called *P. cf. scobina* (see below) at least in the region of the São Luiz rapids, just upriver from Itaituba. Therefore, at least seven species of potamotrygonids occur in rio Tapajós based on material collected and specimens currently in collections, or eight if *Plesiotrygon* is present in its lowermost areas as expected. *Heliotrygon* specimens may also occur in the Tapajós mouth-lake, given their distribution and presence in the lower parts of many major Amazonian affluents (Carvalho & Lovejoy, 2011; Carvalho & Shibuya, 2013). *Potamotrygon scobina*, which has a wide occurrence in lower parts of many right bank Amazonian tributaries (Fontenelle, 2013), has not been collected in the lower rio Tapajós (nor in the lower rio Xingu), but this is probably due to sampling. In any case, rio Tapajós has one of the most diverse potamotrygonid assemblages, almost as great as rio Tocantins (Carvalho, 2016), but will equal or even surpass it if *Plesiotrygon*, *Heliotrygon*, or *P. scobina* are found there. River basins with diverse stingray assemblages, such as the Tapajós, Negro and Tocantins-Araguaia systems, have 8–10 stingray species, a number likely to increase with greater sampling in their lowermost areas.

Specimens collected in the lower rio Tapajós (in the mouth-lake, below Itaituba) were remarkable in having an intense pattern of enlarged bucklers and tubercles on dorsal and lateral tail, and dorsal disc regions (Figs. 48, 49). These were found in *P. motoro* and *P. orbignyi*, and slightly less in *P. humerosa* and *Potamotrygon* sp. *Potamotrygon humerosa* is a particularly prickly species (Silva & Carvalho, 2015) with many thornlets on lateral tail, but specimens collected in the Tapajós had fewer bucklers and tubercles that were generally smaller than those in *P. orbignyi*; collected specimens of *Paratrygon aiereba* lacked these structures (Fig. 48). Above river from Itaituba, in the middle Tapajós, specimens of *P. jabuti* also have bucklers and tubercles, even in material from rio Cururu, but these structures are lacking in specimens of *P. jabuti* that occur even farther upriver (rios Teles Pires and Jamanxim). The presence of bucklers and tubercles in the middle (*P. jabuti*) and lower (particularly *P. motoro* and *P. orbignyi*) Tapajós is puzzling, especially concerning the latter two species. *Potamotrygon motoro* and *P. orbignyi* are widespread in the greater Amazonian foreland basin (e.g. in Peru, Ecuador, Bolivia), lowland Amazonian basin (Brazil), the Orinoco system (Venezuela, Colombia), in some rivers draining the Guiana Shield (*P. orbignyi*), in rio Mearim (*P. motoro*), and in the Paraná-Paraguay system (*P. motoro*), without presenting bucklers or tubercles as developed as in the Tapajós specimens (one exception is a specimen of *P. orbignyi*, MZUSP 51681, which also has bucklers but lacks locality data). *Potamotrygon constellata* (Vaillant, 1880), described from near Tefé in the mid rio Solimões, was partly based on the presence of large bucklers on its disc margins and tail (as was its junior synonym, also from Tefé, *P. circularis* Garman, 1913). This seldomly reported species is similar in most details to *P. orbignyi* and may even be its junior synonym; nonetheless, it highlights that bucklers and tubercles occur not just in the Tapajós basin.

The presence of these structures in specimens from the lower and mid Tapajós, however, is necessarily a local phenomenon. Contaminated sediments from heavy mining efforts that employed mercury amalgamation, especially in the 1980s but presently resurging (Anon., 2014), and which have likely accumulated downriver in the mid Tapajós and in its mouth-lake, may somehow be related. Chapman (1984) notes that fishes, especially bottom-dwelling ones, have greater rates of dermal tumors when sediments are contaminated, even when water quality is acceptable, and potamotrygonids are in constant interaction with bottom sediments. Based on completed taxonomic revisions, however, there is presently no reason to regard these heavily armored specimens of *P. motoro* and *P. orbignyi* from rio Tapajós as distinct, although some distinctions are present in comparison to material from other regions of their wide distributions (Loboda, 2010; Silva & Carvalho, 2015; Loboda & Carvalho, unpubl.).

Potamotrygon motoro is the most morphologically variable potamotrygonid species in the lower rio Tapajós as different color patterns have been collected (Fig. 48), consisting of: (i) numerous, elaborate designs on dorsal disc composed of a central, very small ocellus surrounded by lighter colored spots forming a rosette-like pattern (Fig. 48b); (ii) large ocelli on dorsal disc with faint grayish and very broad outer ocelli outlines (Fig. 48a), but very similar to the previous pattern; and (iii) the typical *P. motoro* pattern (e.g. of the lectotype; Loboda & Carvalho, 2013), with tricolored ocelli (innermost color yellowish, intermediate color orange, and outermost color blackish-

brown), more or less evenly distributed on dorsal disc, and usually just larger than spiracle on central disc, with concentric rows of smaller and sometimes fused ocelli and spots on outer disc margins (Figs. 48c, d). These are the most conspicuous patterns; intermediate designs are also present. These specimens varied less in their ventral coloration, with a grayish to brownish central blotch present near coracoid bar, and outer disc margins and posterior pelvic fins grayish to brown, as well as in the pattern of dorsal tail thorns (single irregular row of mostly erect and well developed thorns). Characters that distinguish rio Tapajós *P. motoro* from specimens occurring in other regions are the hypertrophied bucklers and/or tubercles on disc and tail (but, as mentioned, these structures also occur in other species from the same region) and a slightly more elongated tail, not enough to consider specimens of *P. motoro* from the lower Tapajós as a separate species (Loboda & Carvalho, unpubl.).

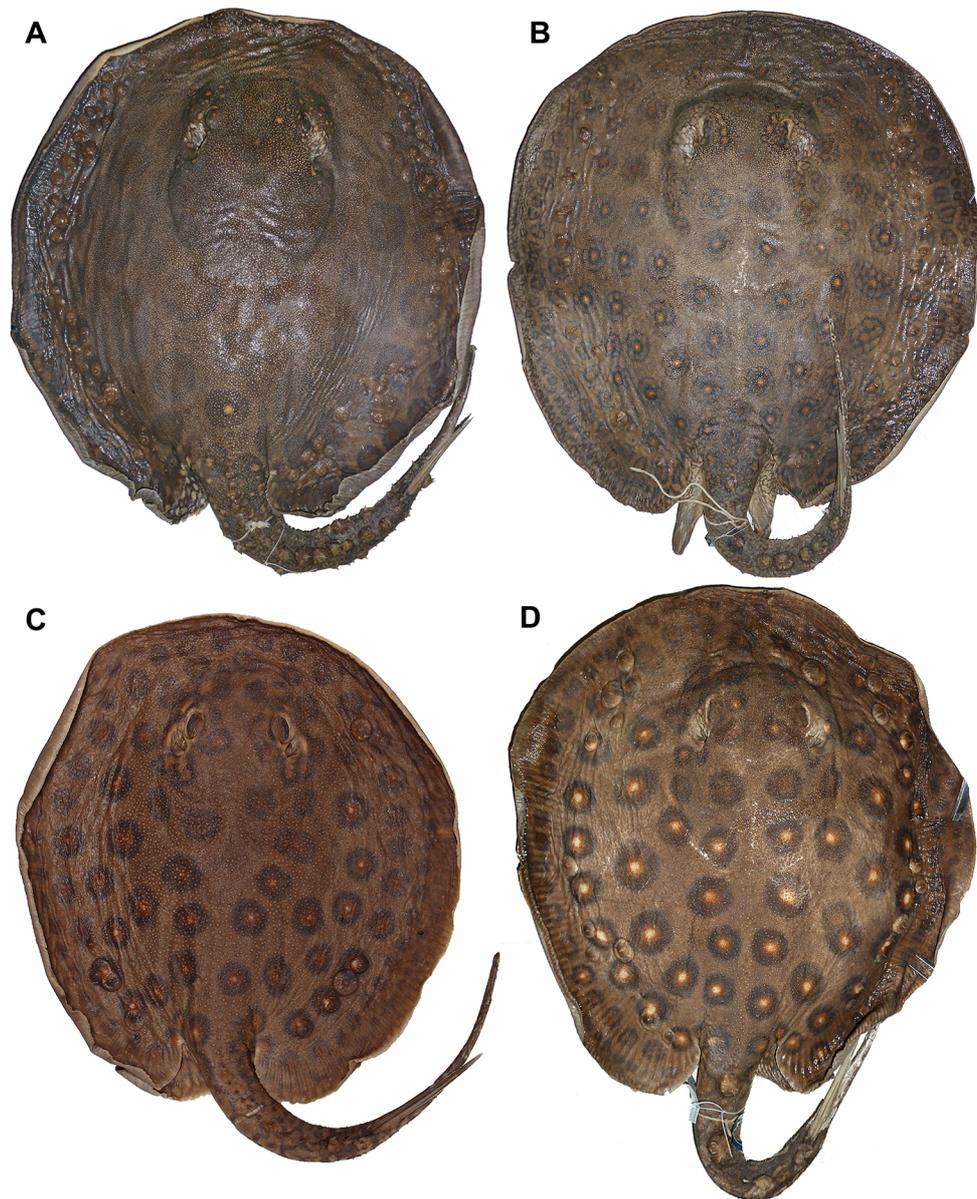


FIGURE 48. Specimens of *Potamotrygon motoro* collected in lower rio Tapajós. A) MZUSP 103895 (515 mm DW); B) MZUSP 103897 (594 mm DW); C) MZUSP 82468 (238 mm DW); D) MZUSP 103914 (346 mm DW).

Potamotrygon motoro was not collected from the mid and upper rio Tapajós and is not expected to occur there, repeating a pattern present in other Amazonian rivers draining the Brazilian Shield where it occurs only in their lowermost portions (rios Xingu and Tocantins-Araguaia; a single individual has been recorded from the Araguaia, but it may not be *P. motoro*; Loboda, 2010). If *P. jabuti* and *P. motoro* are closely related as alluded to above, then it may be hypothesized that *P. jabuti* branched off from their common ancestral stock to become isolated in the upper

Tapajós, possibly by a headwater capture event, while *P. motoro*, present in the nearby headwaters of rios Guaporé and Paraguai (very close to headwaters of the Tapajós), either expanded into Amazonian lowlands to eventually reach its present great distribution, or was previously already widespread. However, *P. jabuti* has not been recorded in the uppermost Juruena and Teles Pires (both very close to headwaters of the rio Paraguai system), but this may be due to a secondary reduction of its distribution.



FIGURE 49. Potamotrygonid specimens from the lower rio Tapajós. A) *Potamotrygon orbignyi* (MZUSP 103906, 335 mm DW); B) *Potamotrygon humerosa* (MZUSP 103913, 311 mm DW); C) *Paratrygon aiereba* (MZUSP 103907, 606 mm DW).

Paratrygon aiereba and *P. orbignyi* both occur in the lower and mid rio Tapajós (a pattern typical for both species in other basins, e.g. in the Xingu and Tocantins-Araguaia basins). No differences were evident in specimens of *P. orbignyi* from these regions, nor in comparison to specimens from throughout its range, other than the

constant presence of bucklers and tubercles (Silva & Carvalho, 2015) (Fig. 49a). *Paratrygon* specimens, on the other hand, varied slightly in color pattern between both segments of the Tapajós, with *P. aiereba* restricted to the lower segment (Fig. 49c) and a possibly distinct form (*P. cf. aiereba*) in the mid Tapajós, which is currently under study (Loboda, 2016; Loboda & Carvalho, unpubl.). *Potamotrygon humerosa* is distributed in Amazonian lowland areas, entering the lower portions of many affluents (Garman, 1913; Rosa, 1985; Silva & Carvalho, 2015), and was originally described from close to the mouth of rio Tapajós (Monte Alegre, its type locality, is just to the northeast of Santarém).

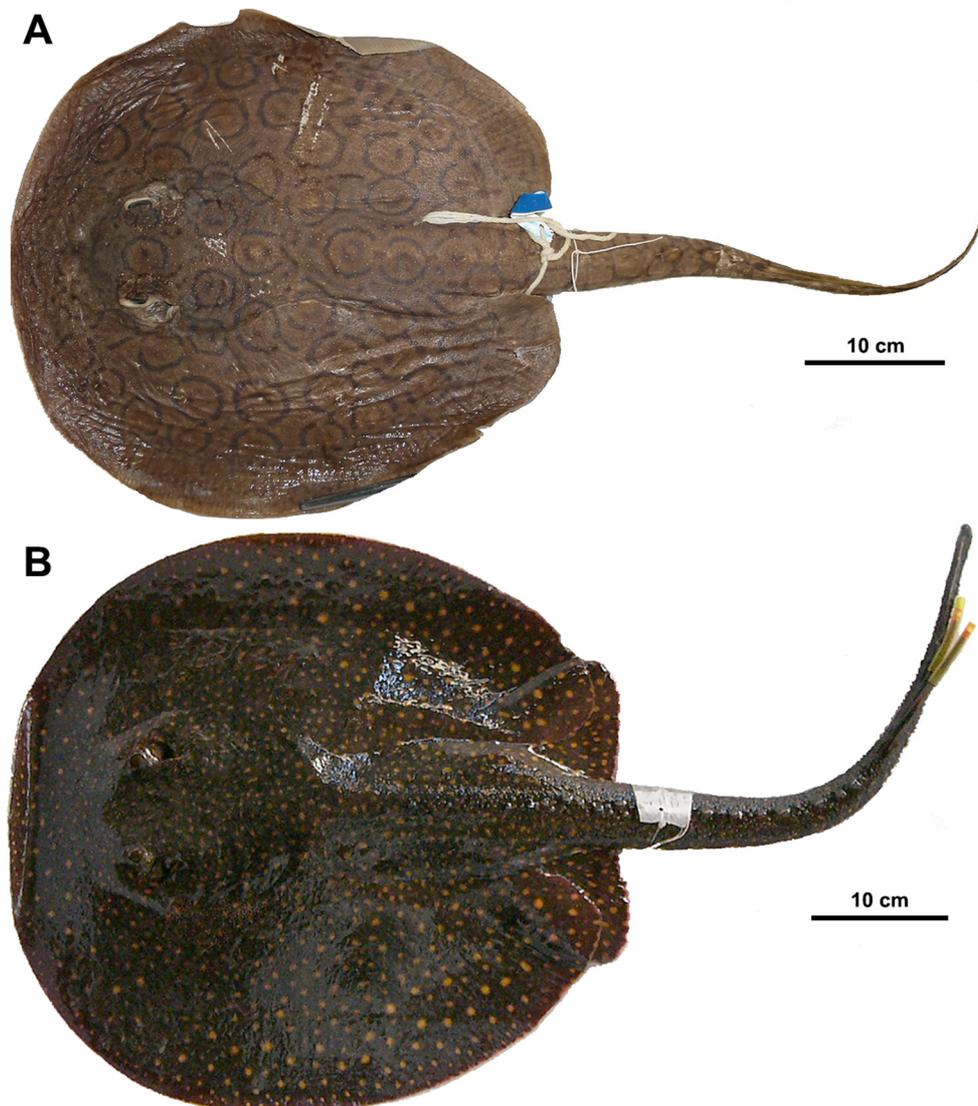


FIGURE 50. Specimens representing putative new species from the lower (A) and mid (B) rio Tapajós. A) *Potamotrygon* sp. (MZUSP 103904); B) *Potamotrygon* cf. *scobina* (MZUSP 103929, freshly collected).

Two species known from few individuals also collected in the Tapajós may represent additional new species (Fig. 50). *Potamotrygon* cf. *scobina* is known only from a single collected specimen (MZUSP 103929; Fig. 50b) from below the São Luiz rapids (and above Miritituba) in the lower Tapajós, which according to a local fisherman is the only place it occurs. This species resembles *P. scobina* in proportions, with an elongated tail, low head region, a single irregular row of low tail thorns, and slightly in its dorsal color, composed primarily of numerous small spots. But aspects of its color pattern are distinct (much darker, with yellow to orange spots forming poorly defined clusters), and it has two angular cartilages with the posterior angular similar in width to the more concave anterior angular (*P. scobina* has a reduced posterior angular and a small third angular element closer to hyomandibula; Fontenelle, 2013). The other species is known from a few small specimens from the lower Tapajós.

Potamotrygon sp. (Fig. 50a) has a light brown dorsal color pattern with numerous darker brown, circular rings that resemble a reticulate pattern (with smaller, poorly defined ocellate markings within rings), a light beige ventral color with a central coracoid blotch, a slender elongated tail, a single low row of dorsal tail thorns (more developed closer to caudal sting), dermal denticles stellate and evenly distributed on dorsal disc, and absence of labial grooves. In the collected specimen (MZUSP 103904) small, relatively low bucklers are present close to caudal sting. More material of both of these species is required before they can be properly identified.

The ecological dynamics of stingray species in the mid and upper rio Tapajós are being further impacted by hydroelectric power stations in construction or in planning that will interrupt its fast-flowing rivers (Teles Pires, Jamanxim) and result in more stagnant waters. The impact of these transformations on stingrays is poorly documented in other regions with similar environmental concerns, much less so in comparison to Neotropical migratory teleosts and bony fishes in general. One possible outcome is greater hybridization in the newly formed slow-moving system. However, the great distribution of potamotrygonids, which occur from small upland streams to the deeper troughs of large rivers over a vast geographical area, is no doubt partly due to their great resiliency. Species that are endemic to upland regions of single rivers are probably at greater risk than those widespread in lowland areas.

Key to the stingrays of rio Tapajós

The following key does not include the three above-mentioned putative new species presently being investigated (*Potamotrygon* sp., *P. cf. scobina*, and *Paratrygon cf. aiereba*). Information below on the dermal denticles of *P. humerosa* and *P. orbignyi* are from Silva & Carvalho (2015).

- 1a. Anterior margin of disc slightly indented at center; tail short in adults, much shorter than disc width, and slender at base; caudal stings close to tail base, not tail tip *Paratrygon aiereba*.
- 1b. Anterior margin of disc broadly rounded, not indented at center; tail longer and stouter at base, about three-fourths disc width; caudal stings located much closer to tail tip 2a.
- 2a. Dorsal disc blackish-brown with relatively small white to yellowish spots and faint ocelli; ventral color mostly dark brown with white or creamy areas usually only on ventral snout and central disc; multiple (at least five) rows of more or less evenly-spaced thorns spread over dorsal and lateral aspects of tail *Potamotrygon albimaculata*.
- 2b. Dorsal disc light to dark brown, and lacking white spots and ocelli; ventral color mostly creamy white to beige; thorn rows fewer (usually one or two), occupying a slender, discrete band on dorsal tail 3a.
- 3a. Dorsal disc light brown with reticulated darker brown pattern; labial grooves present at lower jaw corners 4.
- 3b. Dorsal color without dark brown reticulated pattern over light brown disc (instead with varied patterns of ocelli or a more complex marbled pattern); labial grooves absent. 5.
- 4a. Lateral tail region very prickly with numerous pointed thornlets and sharp dermal denticles; dermal denticles on disc inverted V-shaped with low number of crown ridges (usually 2) *Potamotrygon humerosa*.
- 4b. Lateral tail region less prickly, much more smooth, with far less intense covering of sharp denticles and lacking larger thornlets; dermal denticles on disc stellate with high number of crown ridges (usually 5) *Potamotrygon orbignyi*.
- 5a. Dorsal color usually brown to grayish-brown with varied patterns of clearly defined and evenly spread ocelli (usually with three colors, a yellow center, orange middle, and dark brown to blackish outer contour) *Potamotrygon motoro*.
- 5b. Dorsal color dark brown to greenish-brown with a complex marbled pattern with numerous yellow to golden spots, incomplete ocelli or irregular markings surrounded by a mesh-like reticulate golden pattern *Potamotrygon jabuti*.

Comparative material

Paratrygon aiereba. MZUSP 103896, rio Tapajós, near Comunidade Piauí, Pará state, Brazil, 02°17'03"S, 055°00'13"W, col. M.R. de Carvalho, M. Cardoso, M.L.G. de Araújo & S.M.V. Melo; MZUSP 103907, data as in MZUSP 103896; MZUSP 103916, Comunidade Pimental, rio Tapajós, Pará state, Brazil, 4°33'06"S, 056°16'38"W, col. M.R. de Carvalho, M. Cardoso, M.L.G. de Araújo & S.M.V. Melo; MZUSP 103917, same data as MZUSP 103916.

Potamotrygon humerosa. MZUSP 8472, lago Jacundá, Alter do Chão, Santarém, Pará state, Brazil, 02°30'S, 54°57'W; MZUSP 19198 (6 specimens), rio Tapajós, lake on island in front of Monte Cristo, Pará state, Brazil, 04°04'60"S, 055°37'00"W, Expedição Permanente à Amazônia; MZUSP 51425, datas as in MZUSP 19198; MZUSP 103913, rio Tapajós, near Comunidade Piauí, Pará state, Brazil, 02°17'03"S, 055°00'13"W, col. M.R. de Carvalho, M. Cardoso, M.L.G. de Araújo & S.M.V. Melo.

Potamotrygon motoro. MZUSP 14779–14786 (8 specimens), rio Tapajós, lake on island in front of Monte Cristo, Pará state, Brazil, 04°04'60"S, 055°37'00"W, Expedição Permanente à Amazônia; MZUSP 19197, same data as MZUSP 14779; MZUSP 22025, rio Tapajós, lagoa Santa Clara, Monte Cristo, Pará state, Brazil, 04°04'60"S, 055°37'00"W, Expedição Permanente à Amazônia; MZUSP 82468, rio Tapajós, 18.2 km doweriver from Lago Azul, Pará state, Brazil, 02°24'46"S, 054°53'30"W, M. Westneat; MZUSP 103895, rio Tapajós, near Comunidade Piauí, Pará state, Brazil, 02°17'03"S, 055°00'13"W, col. M.R. de Carvalho, M. Cardoso, M.L.G. de Araújo & S.M.V. Melo; MZUSP 103898, data as in MZUSP 103895; MZUSP 103899, data as in MZUSP 103895; MZUSP 103900, data as in MZUSP 103895; MZUSP 103901, data as in MZUSP 103895; MZUSP 103903, data as in MZUSP 103895; MZUSP 103905, data as in MZUSP 103895; MZUSP 103909, data as in MZUSP 103895; MZUSP 103910, data as in MZUSP 103895; MZUSP 103911, data as in MZUSP 103895; MZUSP 103912, data as in MZUSP 103895; MZUSP 103914, data as in MZUSP 103895.

Potamotrygon orbignyi. MZUSP 21983, Maranhãozinho waterfall, rio Tapajós, São Luiz, Pará state, Brazil, 04°28'S, 56°15'W, Expedição Permanente à Amazônia; MZUSP 25582, left margin of rio Tapajós River, opposite to igarapé Boa Vista (or Uruá), km 62 of BR-230, PARNA, Pará state, Brazil, 04°33'00"S, 56°16'59"W, J.C. Oliveira; MZUSP 103897, rio Tapajós, near Comunidade Piauí, Pará state, Brazil, 02°17'03"S, 055°00'13"W, col. M.R. de Carvalho, M. Cardoso, M.L.G. de Araújo & S.M.V. Melo; MZUSP 103902, data as in MZUSP 103897; MZUSP 103906, data as in MZUSP 103897; MZUSP 103908, data as in MZUSP 103897; MZUSP 103915, data as in MZUSP 103897; MZUSP 103924, Comunidade Pimental, rio Tapajós, Pará state, Brazil, 4°33'06"S, 056°16'38"W, col. M.R. de Carvalho, M. Cardoso, M.L.G. de Araújo & S.M.V. Melo; MZUSP 103928, same data as MZUSP 103924.

Potamotrygon cf. scobina. MZUSP 103929, rio Tapajós at São Luiz, Pará state, Brazil, col. M.L.G. de Araújo.

Potamotrygon sp. MZUSP 103904, rio Tapajós, near Comunidade Piauí, Pará state, Brazil, 02°17'03"S, 055°00'13"W, col. M.R. de Carvalho, M. Cardoso, M.L.G. de Araújo & S.M.V. Melo.

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