Research article

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FIRST RECORD OF *PAO PALEMBANGENSIS* (TETRAODONTIFORMES: TETRAODONTIDAE) FROM THE TAPI RIVER BASIN, SOUTHERN THAILAND, WITH SOME BIOLOGICAL OBSERVATIONS AND NOTES ON ITS DISTRIBUTIONAL RECORDS

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ABSTRACT

Specimens of the Southeast Asian freshwater pufferfish *Pao palembangensis* (Tetraodontiformes: Tetraodontidae) were collected from the Phunphin Stream, Tapi River drainage, Surat Thani Province, southern Thailand, representing the first record of the species from the Tapi River basin based on voucher specimens. Detailed morphological descriptions of the specimens are provided with some biological observations on fresh and live specimens, including the remarkably arched anterior portion of the spine and an ability of closing eye openings which are reported for the first time. Additionally, previous published distributional records of the species in Indochina (excluding Malaysia) are also reviewed. As a result, all records of the species north to the present record (the Tapi River basin) are considered to be misidentifications of other tetraodontids.

Keywords: distribution, *Pao*, *Pao palembangensis*, Tapi River, Tetraodontidae

INTRODUCTION

The Southeast Asian freshwater pufferfish *Pao palembangensis* was originally described as *Tetraodon palembangensis* by BLEEKER (1851) from rivers in Palembang, Sumatra, Indonesia. It can be characterized by: Sides and entire abdomen with well-defined wide-meshed dark networks (reticulations), 3–18 of the meshes enclosing one, sometimes two, rounded spots or ocelli; depressed head; and body spines often in dermal pits hidden under dermal papillae (DE BEAUFORT & BRIGGS, 1962; DEKKERS, 1975; ROBERTS, 1989; KOTTELAT *ET AL.*, 1993). The species has been reported under different generic names (*Crayacion, Monotreta, Pao, Tetraodon, Tetrodon*) from Indochina (Laos [Mekong River basin]; Thailand [Mekong, Chao Phraya and Bang Pakong river basins; Songkhla Lake; Toh Daeng Peat Swamp]; Peninsular Malaysia [Perak and Pahang river basins]), Sumatra (Wampu, Kampar, Indragiri, Batang Hari, Banyuasin, and Musi river basins), Borneo (Kapuas and Mahakam river basins), Belitung Island, and Java (BLEEKER 1865–69; VOLZ, 1903, 1904; SUVATTI, 1950; 1981; DE BEAUFORT & BRIGGS, 1962; DEKKERS, 1975; ROBERTS, 1989; KOTTELAT *ET AL.*, 1993; KOTTELAT, 1995, 1989; SIRIMONTAPORN,1999; KHAN *ET AL.*, 1996; KOTTELAT & WIDJANARTI, 2005; TAN & KOTTELAT, 2009; VIDTHAYANON, 2002, 2017; NG *ET AL.*, 2019; PANITVONG, 2022). However, the distribution of the species in Indochina has been unclear. Although some workers

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have recognized that the species is widely distributed in the region, including the Mekong basin in Laos and the Chao Phraya basin in Thailand (e.g., DE BEAUFORT & BRIGGS, 1962; DEKKERS, 1975; KOTTELAT, 1989; ROBERTS, 1989; KOTTELAT *ET AL*., 1993; RAINBOTH *ET AL*., 2012; DANIELS, 2020; DOI *ET AL*. 2022), it was absent in recent surveys of fresh and brackish water fishes in the two basins and adjacent areas (e.g., RAINBOTH, 1996; KOTTELAT, 2001; RAINBOTH *ET AL*., 2012; YOSHIDA *ET AL*., 2013; TAKI *ET AL*., 2021; the present author's unpublished data). During an ichthyological survey in the Tapi River and its tributaries in Surat Thani Province, southern Thailand, in March and May 2024 by the author, three specimens of a pufferfish with unique color patterns were collected (Fig. 1). Subsequently the pufferfish was identified as *Pao palembangensis,* and represents the first record of the species from the Tapi River basin based on voucher specimens. The specimens are described here in detail along with some biological observations. Additionally, previous published distributional records of the species in Indochina are also reviewed.

MATERIALS AND METHODS

Methods of counts and measurements follow DEKKERS (1975) except for the following: postorbital head length was measured from the posterior eye margin to the lowermost edge of gill opening (the posterior point for measuring "head length" in DEKKERS [1975: 90]); preorbital and postorbital head depth were measured at the anterior and posterior eye margins, respectively; preorbital and postorbital head width were measured at the anterior and posterior eye margins, respectively. Rostrum (about anterior 3/4 portion of the snout, naked [without spinules]) length was measured from the tip of snout to the anterior-most junction between the rostrum and the rest of the snout on the lateral side. Rostrum width was measured at the widest point of the rostrum base at the junction between rostrum and the rest of the snout in dorsal view. Distance between nasal organs was measured as the shortest distance between the inner edges of the right and left nasal organ bases. Caudal peduncle length was measured from the posterior end of anal fin base to the mid-lateral posterior edge of the hypural plate. Caudal peduncle width was measured at the most constricted (narrow) portion of the caudal peduncle in lateral view. Fin rays were counted with a binocular microscope or taken from radiographs. Vertebral counts were taken from radiographs, including urostyle, and follow the methods of ROBERTS (1989). Fin-ray lengths were determined by measurement from the embedded base. Several spinules were observed by cutting a part of dorso-lateral portion of dermal skin of a specimen (THNHM-F 023969, right side) in a triangle shape (each side ca. 1 cm long) and stained with Alizarin Red powder dissolved in ca. 5% potassium hydroxide (KOH) solution for one day then dissected and observed under a dissecting microscope. Standard, total and head lengths are abbreviated as SL, TL and HL, respectively. Sex determination follows NUGRAHA *ET AL*. (2011) and recognizes "single genital hole" as male and "two genital holes" as female. The posterior genital hole was topologically recognized as the anus in the present study. Definition of "Indochina" follows POYARKOV *ET AL*. (2021) in excluding Peninsular Malaysia. Reference data (morphological description, photographs, drawings, etc.) of each reference were examined to check correctness of identification. Voucher specimens of the records and their accompanying data were also examined in some cases, if needed. Institutional codes mentioned in the present study are as follows: the Academy of Natural Sciences of Philadelphia, USA (ANSP); Natural History Museum, London, UK (BMNH); California Academy of Sciences, USA (CAS); Muséum national d'Histoire naturelle, Paris, France (MNHN); Fish collection, Inland Fisheries Research and Development Division, Department of Fisheries, Bangkok, Thailand (NIFI); Naturhistorisches Museum Basel, Switzerland (NMB); Naturalis Biodiversity Center, Leiden,

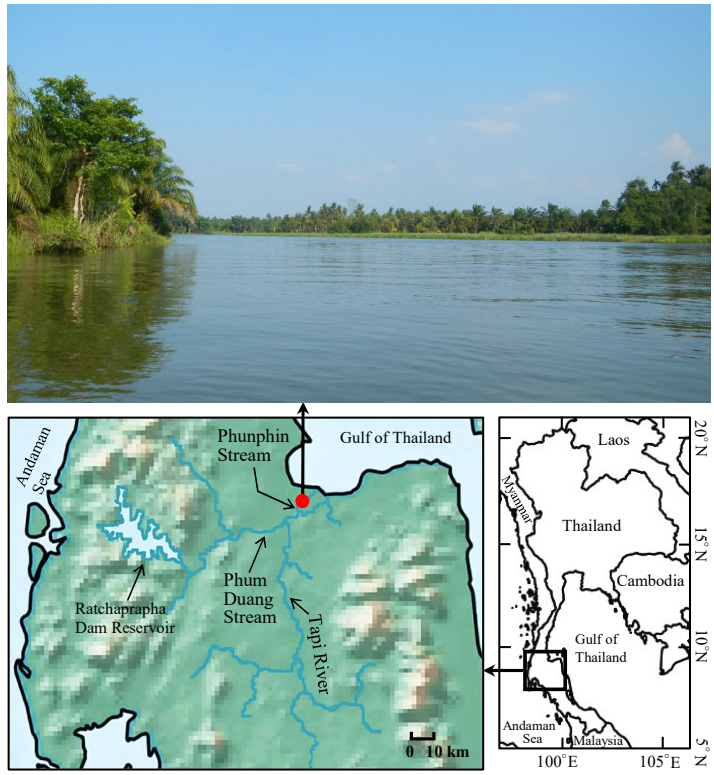

Figure 1. Collection locality of specimens of *Pao palembangensis* examined in the present study (the solid red circle) in the Phunphin Stream at Si Wichai Sub-district, Phunphin District, Surat Thani Province, southern Thailand (9°08′22.99″N, 99°13′30.25″E, 6.2 m alt.) on the lower left map showing the Tapi River basin, and a view upstream of the Phunphin Stream at the collection locality (upper photo). Photograph by the author.

Netherlands (RMNH); Research Laboratory of Ichthyology, Faculty of Fisheries, Kasetsart University, Bangkok, Thailand (RLIKU); Thailand Natural History Museum, National Science Museum, Pathum Thani, Thailand (THNHM); University of Michigan Museum of Zoology, Ann Arbor, USA (UMMZ); and Zoölogisch Museum, Universiteit van Amsterdam, Netherlands (ZMA).

RESULTS

Pao palembangensis (Bleeker, 1851)

(Figs. 2–6, 7A–B, 8, 9; Table 1)

Material examined: THNHM-F 023968, 137.1 mm SL, female, Phunphin Stream (Khlong Phunphin) (tributary of the Tapi River), lower Tapi River basin, Si Wichai Sub-district, Phunphin District, Surat Thani Province, Thailand (9°08′22.99″N, 99°13′30.25″E, 6.2 m alt), 24 Mar. 2024, a local fisherman and Prachya Musikasinthorn; RLIKU 10303, 138.5 mm SL, male, data as for THNHM-F 023968, 27 May 2024, a local fisherman; THNHM-F 023969, 120.4 mm SL, male, data as for RLIKU 10303.

DESCRIPTION

Meristic and morphometric characters of examined specimens are shown in Table 1. Dorsal-fin rays 11 or 12 (unbranched 1 or 2, branched 10). Anal-fin rays 11 (unbranched 1 or 2, branched 10). Pectoral-fin rays 22–24 (unbranched 2 or 3, branched 20 or 22). Principal caudal-fin rays 5/5. Total vertebrae 20 or 21, abdominal + caudal = 10+10 or 11.

Body moderately elongate, rounded dorsally and ventrally in cross-section (maximum body depth and width 39.2–44.9 and 38.1–44.6%SL, respectively), tapering posteriorly to laterally compressed caudal peduncle. Body deepest between pectoral fins (often bump-like, more obvious or distinctively elevated in female) and widest at around between anterior edges of gill-openings (Figs. 2, 3). Dorsal contour of body from the highest portion of body to the anterior insertion of dorsal fin base slightly concaved in the female specimen. Dorsal fin rounded, 7th dorsal-fin ray longest, dorsal-fin origin largely anterior to vertical through the origin of anal fin (predorsal and preanal length 77.1–79.0 and 83.2–85.3, respectively). Anal fin rounded, somewhat smaller than dorsal fin, 5th or 6th anal-fin ray longest, anal-fin origin just below 8th to 9th ray of dorsal fin. Pectoral fin fan-shaped, 6, 7, 8 or 9th pectoral-fin ray longest, dorsal end of pectoral fin base at level slightly below center of eye. Caudal fin rounded. Gill opening descending anteriorly, its slit extending ventrally from level of center of eye to around 2/3 down to the pectoral fin base.

Head relatively depressed in lateral view (preorbital and postorbital head depth 21.3–23.5 and 27.3–28.9%SL, respectively). Chin moderately prominent or indistinct. Mouth small (11.7–14.2%SL, 24.1–29.3%HL), terminal. Lips thick, surface smoothed. Nasal organ long (3.0–3.2%SL, 6.1–6.7%HL), situated in a small depression, with two divided medium-size flat skin flaps, inner flap somewhat larger than outer flap (Figs 4A). Eye large (7.1–8.9%SL, 14.6–17.8%HL), spherical, and laterally situated. The upper margin of orbit slightly above the dorsal contour of the head in lateral view. The lower margin of orbit at level of middle of gill opening. Circularly wrinkled thick skin at orbit rims; eye openings can be completely closed by converging of the skin around the eyes and retracting the eye balls (Figs. 8C, 9A). Interorbital region wide (21.8–24.9%SL, 43.8–51.5%HL), slightly concave in lateral view. Snout moderately long (15.9–17.7%SL, 31.8–36.5%HL), shorter than postorbital head length (24.7–28.2%SL, 51.2–56.3%HL), dorsolaterally concaved, and moderately and strongly concaved in lateral and dorsal view, respectively. Rostrum portion of snout moderately long (10.7–11.6% SL, 21.4–24.0%HL), occupying about anterior 3/4 portion of the snout, without spinules.

Two main lateral lines on head and side of body (Fig. 5). The dorsal-most lateral line encircles the eye, with a preopercular branch terminating at level of middle of anal fin base at around below an anterior origin of the gill opening, and a posteriorly directed branch coursing along the dorso-lateral side of body from mid-posterior part of eye to a midlateral portion of caudal peduncle dropping abruptly at above a posterior end of anal fin base then running through middle of caudal fin base, with a dorsally directed branch above an area just anterior to gill opening almost meeting in midline with its counterpart from the other side of body. The ventral lateral line originates an area just above the corner of mouth on a naked area of the snout running posteriorly almost parallel to body and dropping down just before an anterior border of spinuled area and then courses along a ventrolateral portion of body to below pectoral fin base.

Dorsal, lateral and ventral surfaces of body densely covered with sharply pointed five or six-rooted (asterisk-shape base) spinules (Fig. 5, 6, 9): from between nasal organs to middle of adpressed last dorsal-fin ray, on dorsal side; from anterior edges of nasal organs bases to a posterior end of anal fin base on lateral side; and, from an area slightly anterior to

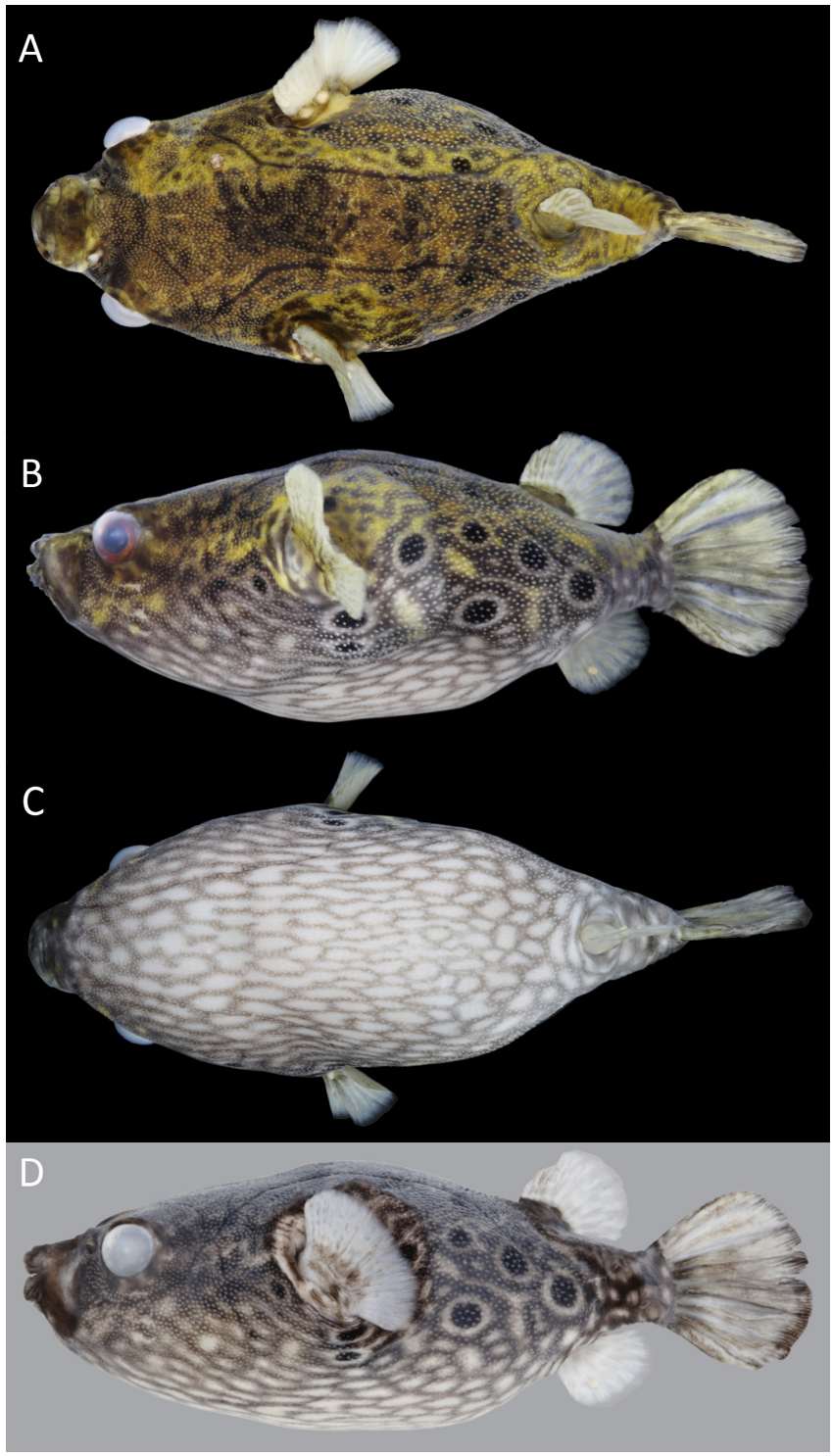

Figure 2. *Pao palembangensis*, RLIKU 10303, 138.5 mm SL, male, Khlong Phunphin (Tapi River drainage), Surat Thani Province, Thailand. Fresh condition: Dorsal (A), lateral (B), and ventral (C) views. Preserved condition (D) in lateral view. Photographs by the author.

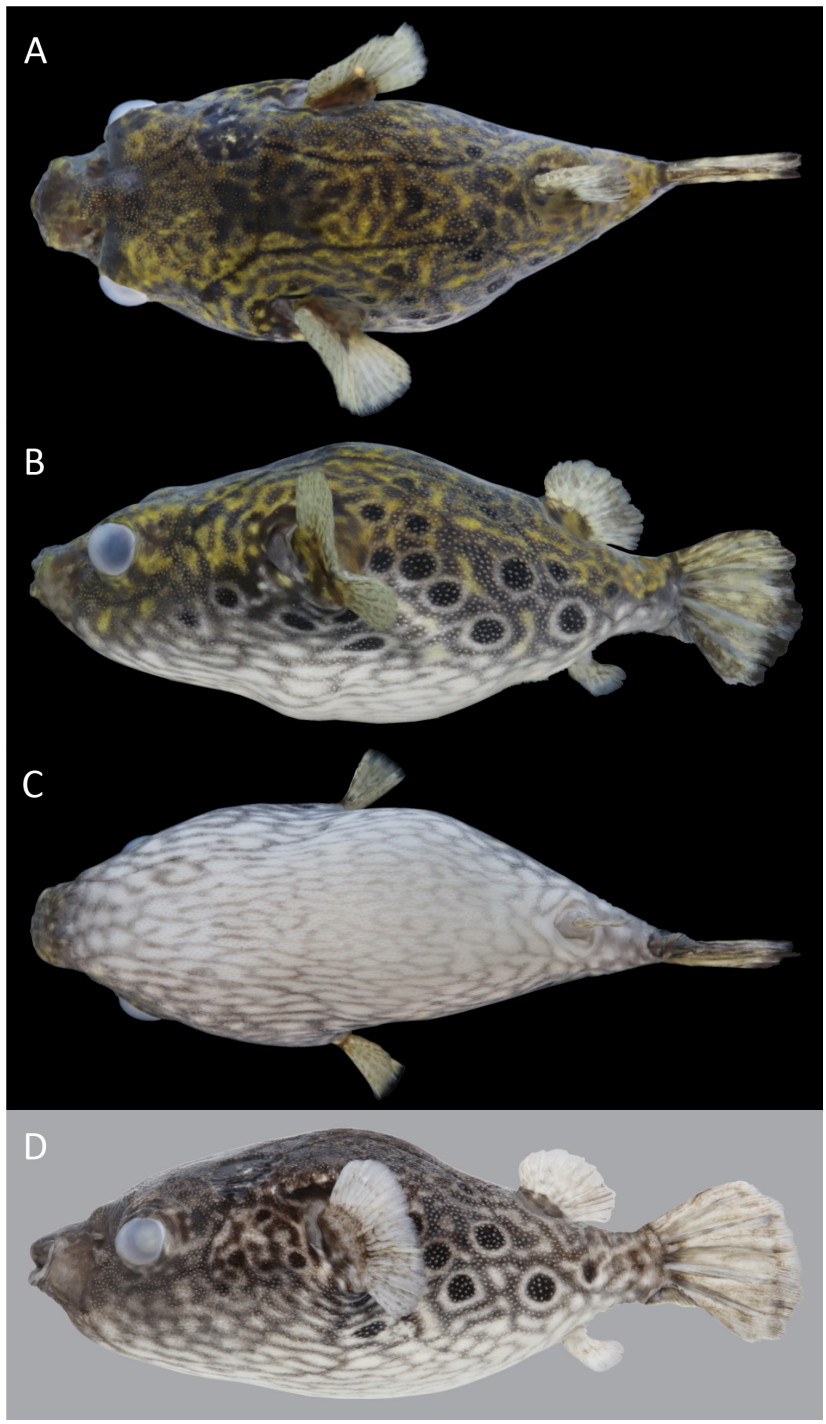

Figure 3. *Pao palembangensis*, THNHM-F 023968, 137.1 mm SL, female, Khlong Phunphin (Tapi River drainage), Surat Thani Province, Thailand. Fresh condition: Dorsal (A), lateral (B, right side reversed), and ventral (C) views. Preserved condition (D) in lateral view. Note distinctively elevated dorsal profile above pectoral fins in lateral view (B, D) and intensively reticulated patterns on dorsal side of head and body (A). Note that a posterior portion of anal fin and a lower portion of caudal fin are wanting. Photographs by the author.

Table 1. Meristic and morphometric characters of *Pao palembangensis* examined in the present study (see Material examined).

Characters	THNHM-F 023969	THNHM-F 023968	RLIKU 10303	Dekkers (1975)[1]
Sex*	Male	Female	Male	
Total length (TL) in mm	152.6	171.9	171.8	45–232
Standard length (SL) in mm	120.4	137.1	138.5	36–194
Head length (HL) in mm	58.2	66.4	69.3	-
Meristic characters:				
Dorsal fin rays: total (unbranched)	12 (ii)	11 (i)	12 (ii)	12–14 (i–iii)
Anal fin rays: total (unbranched)	11 (i)	3+?** (i)	11 (ii)	10–12 (i–ii)
Pectoral fin rays: total (unbranched)	23 (iii)	24 (ii)	22 (ii)	21–23 (i–ii)
Principal caudal-fin rays: upper lobe/lower lobe	5/5	5/?5**	5/5	-
Total vertebrae	21	20	21	-
Abdominal vertebrae	10	10	10	-
Caudal vertebrae	11	10	11	-
Round spots (ocelli) on body sides	11 (R), 11 (L)	14 (R), 8 (L)	12 (R), 10 (L)	3–18
Morphometric characters (% SL [in SL]):				
Maximum body depth	39.2 (2.6)	43.2 (2.3)	44.9 (2.3)	(2.1–3.5)
Maximum body width	38.1 (2.6)	42.2 (2.4)	44.6 (2.2)	(2.1–3.2)
Body depth at dorsal-fin origin	23.8 (4.2)	26.0 (3.9)	28.5 (3.5)	-
Body width at dorsal-fin origin	25.8 (3.9)	24.9 (4.0)	30.5 (3.3)	-
Body depth at anal-fin origin	19.1 (5.2)	19.8 (5.1)	22.8 (4.4)	-
Body width at anal-fin origin	18.9 (5.3)	22.6 (4.4)	24.7 (4.1)	-
Body depth at pectoral fin base	38.7 (2.6)	41.7 (2.4)	43.3 (2.3)	(2.3–3.5)
Body width at pectoral fin base	38.4 (2.6)	42.7 (2.3)	44.9 (2.2)	(2.1–2.9)
Body depth at end of dorsal-fin base	14.8 (6.8)	14.3 (7.0)	16.9 (5.9)	(5.8–9.1)
Body width at end of dorsal-fin base	17.9 (5.6)	18.9 (5.3)	21.3 (4.7)	-
Body depth at end of anal-fin base	12.5 (8.0)	13.5 (7.4)	13.6 (7.3)	-
Body width at end of anal-fin base	15.3 (7.8)	16.2 (8.5)	18.2 (7.6)	-
Snout to dorsal-fin origin	77.1 (1.3)	77.4 (1.3)	79.0 (1.3)	-
Snout to anal-fin origin	83.8 (1.2)	83.2 (1.2)	85.3 (1.2)	-
Head length	48.3 (2.1)	48.4 (2.1)	50.0 (2.0)	(1.9–2.2)
Postorbital head length	24.7 (4.0)	26.6 (3.8)	28.2 (3.6)	-
Preorbital head depth	21.9 (4.6)	23.5 (4.3)	21.3 (4.7)	-
Preorbital head width	24.0 (4.2)	24.6 (4.1)	24.6 (4.1)	-
Postorbital head depth	27.3 (4.4)	28.9 (4.7)	28.9 (4.8)	-
Postorbital head width	31.1 (3.2)	32.2 (3.1)	32.5 (3.1)	-
Snout length	17.1 (5.8)	17.7 (5.7)	15.9 (6.3)	-
Rostrum length	11.6 (8.6)	11.1 (9.0)	10.7 (9.3)	-
Rostrum width	16.7 (2.9)	15.7 (3.1)	15.6 (3.2)	-
Mouth width	14.2 (7.1)	11.7 (8.6)	12.2 (8.2)	-
Upper lip depth	2.2 (45.6)	2.6 (38.8)	3.1 (31.8)	-
Lower lip depth	2.2 (44.9)	2.0 (50.4)	3.1 (32.2)	-
Nasal organ to tip of snout	12.3 (8.1)	12.1 (8.3)	11.3 (8.9)	-

Table 1 (continued).

Characters	THNHM-F 023969	THNHM-F 023968	RLIKU 10303	DEKKERS (1975)[1]
Nasal organ to eye	5.8 (17.2)	6.2 (16.1)	5.3 (18.8)	-
Distance between nasal organs	11.0 (9.2)	9.8 (10.2)	8.3 (12.1)	-
Nasal organ diameter	1.1 (94.0)	1.3 (79.7)	0.9 (109.0)	-
Nasal organ length	3.0 (33.3)	3.2 (31.0)	3.1 (32.7)	-
Horizontal eye diameter	7.6 (13.2)	7.1 (14.2)	8.9 (11.3)	-
Interorbital width (fleshy width)	21.8 (4.6)	24.9 (4.0)	21.9 (4.6)	-
Longest dorsal-fin ray	13.6 (7.3)	10.8 (9.2)	11.6 (8.6)	(8.3–11.0)
Longest anal-fin ray	11.8 (8.5)	9.6 (10.4)	13.1 (7.6)	(8.7–10.6)
Shortest unbranched dorsal-fin ray	4.8 (21.0)	5.3 (18.8)	5.2 (19.2)	(18–25)
Longest pectoral-fin ray	12.5 (8.0)	14.3 (7.0)	12.0 (8.3)	(8.3–11.6)
Caudal-fin length	26.3 (3.8)	26.1 (4.1)	24.6 (4.1)	-
Caudal-peduncle depth	10.5 (9.5)	10.8 (9.3)	11.1 (9.0)	-
Caudal-peduncle length	13.8 (7.3)	14.9 (6.7)	15.5 (6.5)	-
Length of dorsal-fin base	9.1 (11.0)	8.6 (11.7)	9.3 (10.7)	(8.7–12.6)
Length of anal-fin base	6.9 (14.5)	9.6 (18.6)	6.3 (15.8)	(12.5–17.7)
Length of pectoral-fin base	12.3 (8.1)	12.9 (7.8)	12.9 (7.8)	(7.1–10.3)
Gill opening length	9.8 (10.0)	12.0 (8.4)	11.0 (8.9)	-
Caudal-peduncle length/caudal-peduncle depth	1.3	1.4	1.4	-
Morphometric characters (% HL [in HL]):				
Postorbital head length	51.2 (2.0)	55.0 (1.8)	56.3 (1.8)	-
Preorbital head depth	45.3 (2.2)	48.5 (2.1)	42.7 (2.3)	-
Preorbital head width	49.7 (2.0)	50.8 (2.0)	49.2 (2.0)	-
Postorbital head depth	56.6 (1.8)	59.7 (1.7)	57.9 (1.7)	-
Postorbital head width	64.4 (1.6)	66.5 (1.5)	65.1 (1.5)	-
Snout length	35.5 (2.8)	36.5 (2.7)	31.8 (3.1)	(2.7–3.1)
Rostrum length	24.0 (4.2)	23.0 (4.3)	21.4 (4.7)	-
Rostrum width	34.7 (2.9)	32.4 (3.1)	31.3 (3.2)	-
Mouth width	29.3 (3.4)	24.1 (4.1)	24.5 (4.1)	(2.9–4.6)
Upper lip depth	4.5 (22.0)	5.3 (18.8)	6.3 (15.9)	(9.8–18.0)
Lower lip depth	4.6 (21.7)	4.1 (24.4)	6.2 (16.1)	(12.2–40.0)
Nasal organ to tip of snout	25.5 (3.9)	24.9 (4.0)	22.6 (4.4)	(3.3–5.7)
Nasal organ to eye	12.0(8.3)	12.8 (7.8)	10.6 (9.4)	(8.0–11.8)
Distance between nasal organs	22.5 (4.4)	20.2 (5.0)	16.6 (6.0)	-
Nasal organ diameter	2.2 (45.4)	2.6 (38.6)	1.8 (54.5)	-
Nasal organ length	6.2 (16.1)	6.7 (15.0)	6.1 (16.4)	(12.4–31.0)
Horizontal eye diameter	15.7 (6.4)	14.6 (6.9)	17.8 (5.6)	(4.5–9.3)
Interorbital width (fleshy width)	45.1 (2.2)	51.5 (1.9)	43.8 (2.3)	(1.7–2.5)

* Determined from NUGRAHA *ET AL*. (2011); ** damaged.

[1] Including Bleeker's specimens which contain the presumed holotype (see DEKKERS [1975: 107]; KOTTELAT [2013: 480]).

R = right side; L = left side

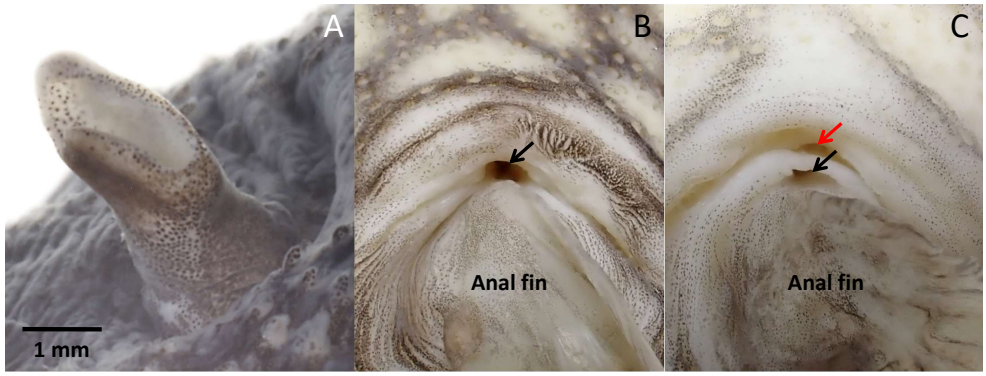

Figure 4. Some body parts of *Pao palembangensis*. A nasal organ (A) (THNHM-F 023968, 137.1 mm SL, female, right side reversed, dorsolateral view); and an anus in a male (B) (RLIKU 10303, 138.5 mm SL) and an anus and a genital hole in a female (C) (THNHM-F 023968, 137.1 mm SL) specimens in ventral view. Anuses and a genital hole indicated by black and red arrows, respectively. All specimens were in preserved condition. Photographs by the author.

chin to posterior end of anal fin base on ventral side (Fig. 5). Dorsal, pectoral, and anal fin bases (including narrow surrounding areas of genital hole and anus), and areas surrounding eyes and gill openings naked (without spinules) (Fig. 5). Each spinule is attached and partly covered at its anterior side by a tentacle-like organ with a round egg-shaped papilla at its top (Fig. 6A). Each tentacle-like organ is partly connected with the body proximally (Fig. 6A). Each spinule is usually stored in a round dermal pit with an exposed tip of the papilla of the tentacle-like organ (Fig. 6B). The spinules are exposed and erected only when the body is inflated (Figs. 6A, 9). Skin with thick dermal muscles on the belly and most areas of the body, including the interorbital region. A female genital hole located at just in front of anus in single specimen (THNHM-F 023968, 137.1 mm SL) (Fig. 4C). An anterior spine (the 1–9th anterior vertebrae) strongly arched upward and descending posteriorly, in maximum angles of ca. 45–55° to body axis, then running straight (horizontally) from the 10th vertebra to posterior end (urohyal) (Fig. 7A, B).

Color of fresh specimens (Figs. 2A–C, 3A–C).—Dorsal half of head and body covered by alternately dark brown and orangish-yellow vermiculations (more intensively vermiculated in the female specimen) and irregularly shaped dark brown spots which aggregate to compose a large dark irregular blotch, which often has an elongated pentagonal shape with concaved anterior and lateral margins, on posterior portion of head to anterior one-third of adpressed pectoral fins, and an additional smaller irregular dark blotch (about subequal to size of an eye ball) on dorsal side of body at an area between posterior tips of adpressed pectoral fin (not prominent in the female specimen). A posteriorly curved dark inter-orbital band at between anterior margins of right and left orbits. Most of a top of each of the tentacle-like organ partly pigmented. Ventrolateral portion of head and body covered by alternately black, dark brown or dark gray and pale white or orangish-yellow vermiculations and irregularly shaped spots. Abdominal portion of head and body covered by dense dark gray to black reticulations (meshes) in diverse shapes, the majority of them laterally elongated and elliptical (mesh lateral length 3.9–17.7%SL). Eight to 14 various sized (4.3–6.5%SL) black ocelli, each with a pale white or orangish-yellow outer ring scattered on each lateral side of body. Dorsal and anal fin pale white, with several scattered small-to-medium size dark brown spots. Dorsal fin base dull orangish-yellow with several medium size dark brown spots. Numerous small dark brown

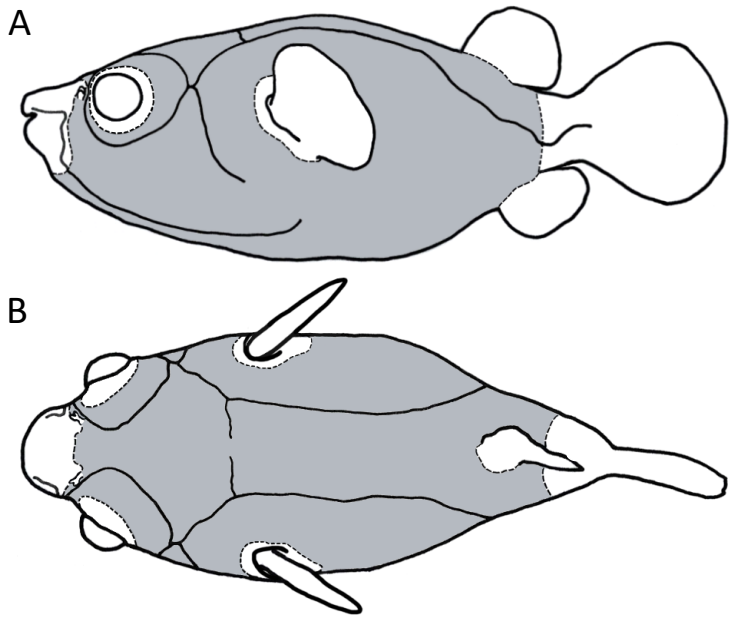

Figure 5. Schematic drawings of lateral line system and the area covered by spinules (in gray color with broken line borders) of *Pao palembangensis* (based on RLIKU 10303, 138.5 mm SL). A, lateral view; B, dorsal view. Drawings by the author.

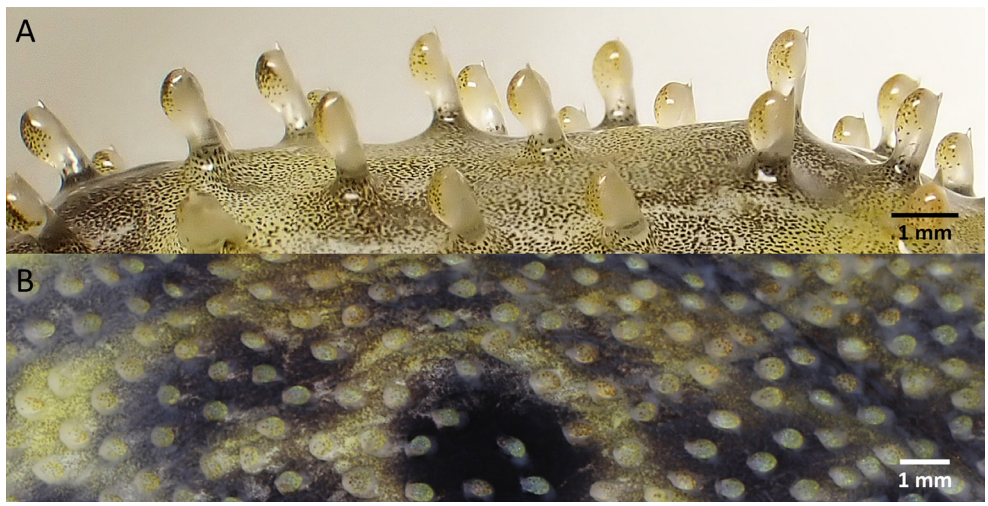

Figure 6. Appearance of spinules of *Pao palembangensis* in different conditions. A, Close-up of numerous erected spinules, each attached and partly covered by a tentacle-like organ with a round egg-shaped papilla at its top (RILKU 10303, 138.5 mm SL, male) (photographed in live condition when maximally inflated [left side, an area just before dorsal fin, lateral view]) (see also Fig. 9, and while uninflated [Fig. 8]). B, Spinules stored in their holes or dermal pits with exposed tips of papillae of tentacle-like organs (the same specimen, photographed in uninflated and fresh condition [left side, a dorso-lateral portion below dorsal fin, lateral view]). Photographs by the author.

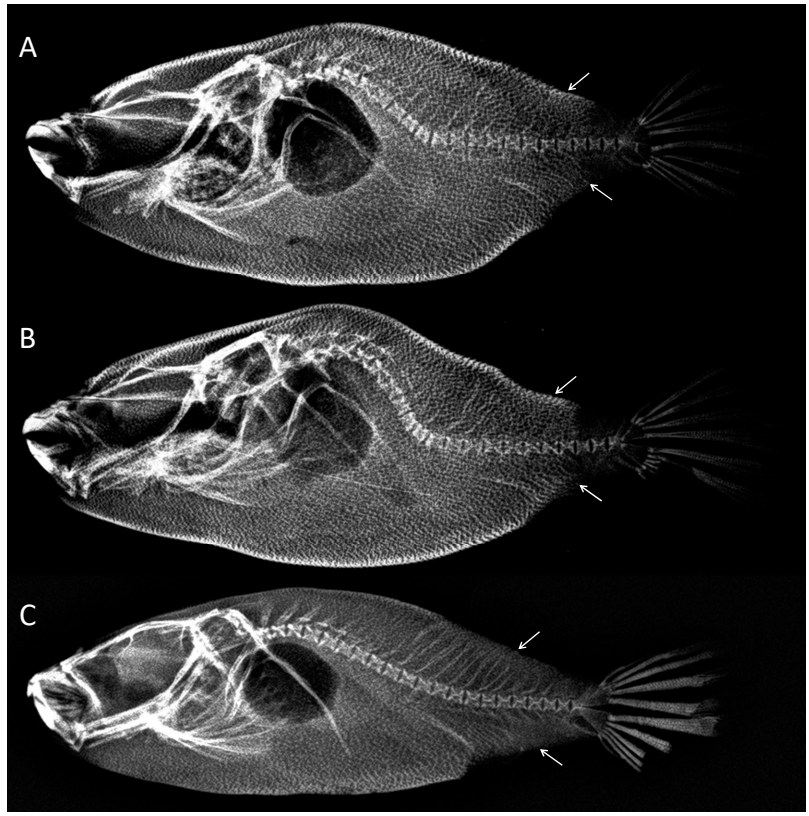

Figure 7. Radiographs (lateral view) of *Pao palembangensis* (A, RLIKU 10303, male, 138.5 mm SL ; and B, THNHM-F 023968, female, 137.1 mm SL) and *Pao* cf. *leiurus* (C, RLIKU 10304, 119.3 mm SL) as s representative of other members of the genus *Pao* examined in the present study for comparison: Specimens of *P. palembangensis* showing a strongly arched anterior portion of spine (vertebrae), which is more prominent in the female (probably resulting from the more strongly humped back in the female than in the male), compared to that of *P.* cf. *leiurus*; depressed anterior portions of crania (heads); and areas of body covered by spinules. White arrows indicate posterior ends of dorsal (above) and anal (below) fin base of each specimen.

spots scattered on pectoral fins, mainly on their rays. Proximal portion and base of pectoral fins dull yellow to dull orangish-yellow with several medium-to-large irregular dark brown blotches scattered on them. Caudal fin mottled pattern of dark brown and pale yellow, dark gray to black at margins. A dark upside-down horseshoe-shaped black band covers the upper half of the caudal fin base, both tips bending anteriorly at around middle of caudal fin base, terminating at around middle of caudal peduncle. Iris ruby red. Several (ca. 6) radially situated dark brown bands on circularly wrinkled thick skin around eyes (Figs. 8C, D, 9A). Dorsal side of rostrum portion dull yellow, with scattered variously-sized dark brown blotches. Ventral side of rostrum portion dark gray to black, with several scattered small yellow spots. Two distinct small black blotches on each side of upper lip and each side of lip corners, with less distinct smaller small black blotches on lower lip (Figs. 8B–D).

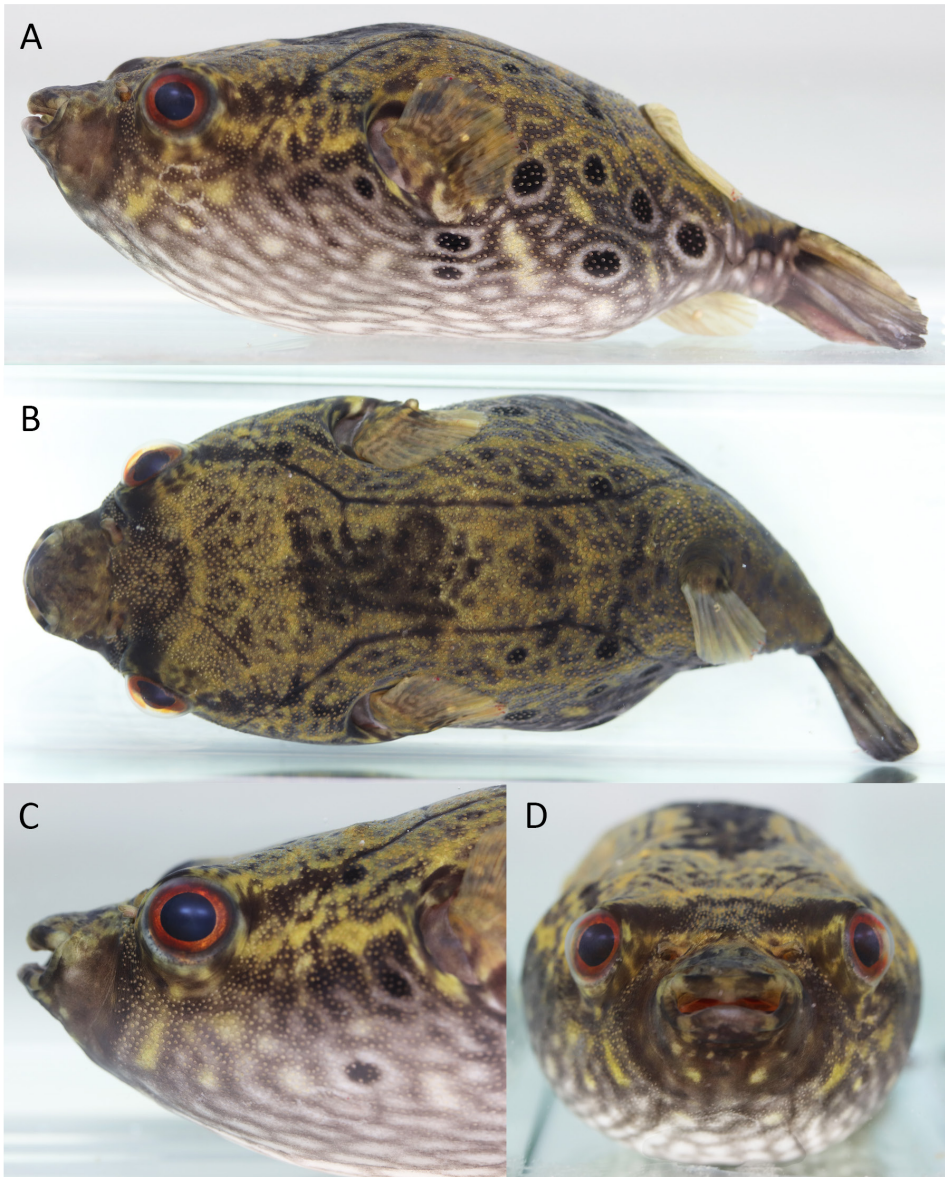

Figure 8. *Pao palembangensis*, RLIKU 10303, 138.5 mm SL, male, in live and uninflated condition. Lateral (A), dorsal (B), close-up of lateral side of head (right side reversed) (C), and front (D) views. Note black spots on upper and lower lips. Photographs by the author.

Color when alive (Figs. 6A, 8, 9).—Similar to fresh coloration, but all colors more vivid and brighter (changed by situation). Dorsal half of head and body covered by alternately dark brown and goldish yellow or goldish-orange vermiculations. Ventrolateral and abdominal portions of head and body covered by dense brownish gray reticulations.

Color in alcohol (Figs. 2D, 3D, 4).—Similar to fresh coloration, but all reddish, orangish, and yellowish colors on head, body, and fins lost or becoming white. Dark color patterns on head and body turn to slightly purplish dark brown.

Notes on ecology and indigenous knowledge.—The present examined specimens of *P. palembangensis* were collected with a casting net by a fisherman near the shore in the Phunphin Stream (Tapi River system) with gentle flow, ca. 2–3 m depth, in relatively muddy water and muddy bottom, and with thick vegetation at shoreline (Fig. 1). The collection location of the specimens is about 10 km from the mouth of the stream to the Gulf of Thailand. According to local fishermen, the water of the stream is fresh to somewhat or mildly brackish

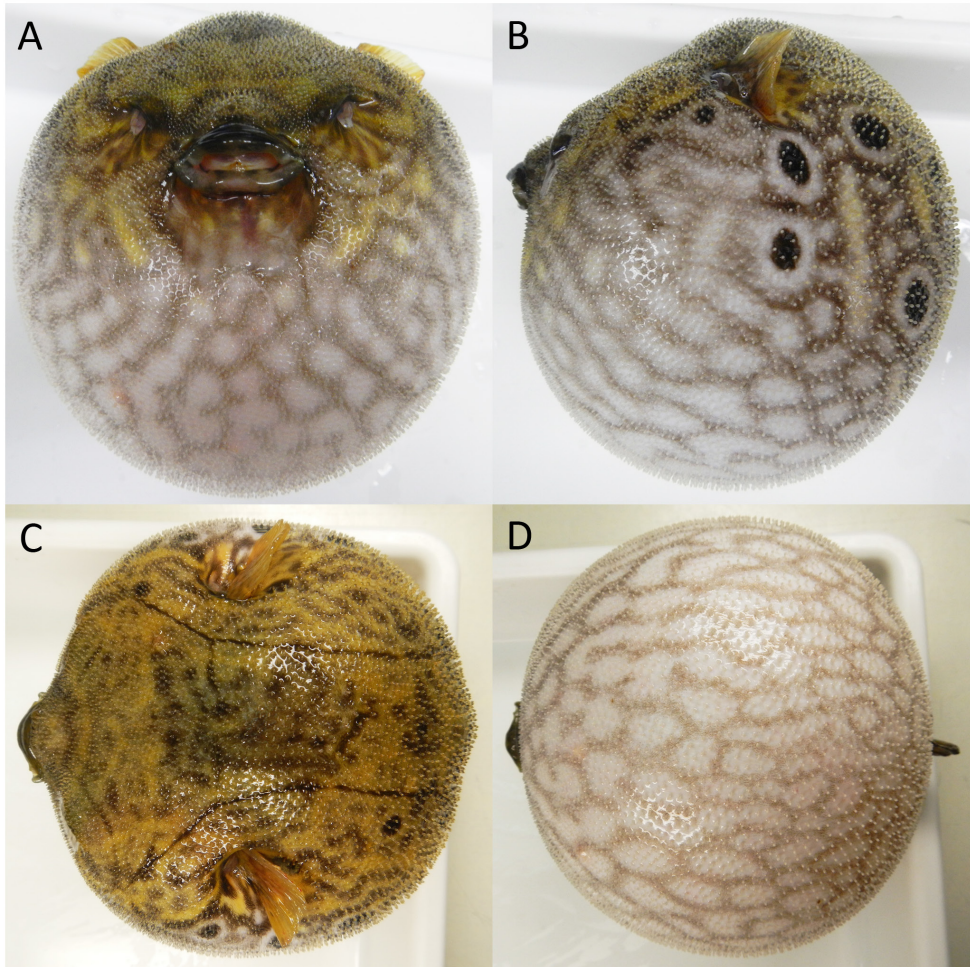

Figure 9. A maximally inflated state of a live individual of *Pao palembangensis* (RLIKU 10303, 138.5 mm SL, male) in live condition in air: Front (A), lateral (B), dorsal (C), and ventral (D) views. Note numerous fully exposed and erected spines around the head and body; deeply retracted eye balls and largely shrunken (nearly closed) eye openings (A); and expanded ocelli on lateral sides of central to posterior portions of the body (B, C). Photographs by the author.

as influenced by the tides and seasons. Other fish species collected together at the collection locality were: *Ambassis vachellii* (juvenile), *Brachygobius* sp., *Butis butis* (juvenile), *B. gymnopomus* (juvenile), *Clupeichthys* sp., *Cyclocheilichthys apogon*, *C. heteronema*, *Doryichthys boaja*, *D. deokhatoides*, *Hemibagrus* sp., *Mystus singaringan*, *Osphronemus goramy* (juvenile), *Pao* cf. *leiurus*, *Parachela johorensis*, *Rasbora aurotaenia*, and *Toxotes chatareus*. The fishermen who live at the bank of the stream about 1 km downstream from the collection locality reported that *P. palembangensis*, called "pla pao" (a general local name for all freshwater and marine pufferfishes), is most frequently found in the area in the dry season (around March–May) when the stream water is more brackish, and is rarer in the rainy season when the water is less brackish. The fish are more abundant and frequently caught downstream where the water is more brackish. Fishermen also mentioned that *P. palembangensis* reaches at least about 25 cm in total length, and like all other freshwater and marine pufferfishes, it is not eaten as a food by locals in the area, since they believe it is poisonous or makes eaters get "drunk".

Review of Distributional Records of *P. palembangensis* in Indochina

In Indochina, *P. palembangensis* was first reported from "Siam (present Thailand)" by GÜNTHER (1870) as "*Tetrodon palembangensis*" based on a stuffed specimen (BMNH 1859.7.8.9, ca. 7.7 cm SL) collected by the French explorer Henri Mouhot during his Indochinese expedition during 1858–1861. From the date of cataloging of the specimen (8 July 1859), the specimen was probably collected from the Chao Phraya River basin during Mouhot's first visit to central Thailand during 19 October–December 1858 (see KOTTELAT & TAN [2018]). Photographs of the specimen were reexamined by me (Fig. 10). It had no meshed reticulation patterns on the lateral and ventral sides of body, spinules on the dorsal side were distributed far beyond the dorsal-fin base posteriorly, and the snout length was subequal to the post orbital head length. The specimen is clearly not *P. palembangensis*, and from its overall appearance, including a faint large ocellus-like marking and the other characters mentioned above, it is tentatively identified here as *P. cochinchinensis* (sensu TAKI *ET AL.*, 2021).

Subsequently, *P. palembangensis* was listed by KÁROLI (1881) as "*Tetrodon palembangensis*" from "Siam" based on specimen(s) obtained by Xantus János (specimen No. "Mus. 1606" [not available for the present study]) without description or figure. According to KORSÓS (2008), Károli's fish, amphibian, and reptile specimens deposited at the Hungarian Natural History Museum were lost during the fire caused by Russian bombs in 1956.

Later, SAUVAGE (1883) listed *P. palembangensis* as "*Tetraodon palenbengensis* [*sic*]" from "Mé-Nam" (Chao Phraya River, Thailand) based on specimen(s) collected by M. Harmand without any further information on the specimen(s) he examined. The specimen(s) was(were) probably lost (Jonathan Pfliger [MNHN], pers. comm.).

Later, TIRANT (1885) reported *P. palembangensis* as "*Tetrodon palembangensis* (Bleeker). Variété" from "Thu dau mot", southern Vietnam, which geographically belongs to the Mekong Delta with a description. The description of a 4 (or 4.2?) cm long (?TL) specimen includes some coloration which agrees well with that of females and immature individuals of *Carinotetraodon lorteti*, i.e., a back light olive with irregular dark brown longitudinal lines connecting and forming a network or narrow mesh all over; and a black crescent shape mark at dorsal and anal fin-base (see TAKI *ET AL.* [2021: 498]; RAINBOTH [1996: Plate XXVII, 213]), and clearly different from similar-size juvenile specimens of *P. palembangensis* (see "DISSCUSSION" bellow). KOTTELAT (1987), who reviewed and examined Tirant's materials stored in Musée des Confluences, Lyon (MHNL; formerly Musée d'Histoire Naturelle de Lyon

Figure 10. Photographs of "*Tetrodon palembangensis*", BMNH 1859.7.8.9, a stuffed specimen, ca. 7.7 cm SL, in lateral (bottom), dorsal (top), and front (left) views. The specimen was collected by the French explorer Henri Mouhot from "Siam" during 1858–1861 and reported by GÜNTHER (1870). The specimen was identified as *Pao cochinchinensis* (sensu TAKI *ET AL*. 2021) in the present study. Photographs courtesy of the Trustees of the Natural History Museum, London.

[MGHNL]), France, noted that the materials that Tirant identified as "*Tetrodon palembangensis* (Bleeker). Variété" were actually females of *C. lorteti*, and the conclusion is also followed by the present study.

Several decades later, HORA (1923) reported *P. palembangensis* as "*Tetraodon palembangensis*" based on specimens collected by Malcolm Smith from "Nontaburi" (also spelled as "Nonthaburi") which is geographically included in the Chao Phraya River basin, central Thailand. He wrote "In very young individuals about 45 mm. in length, the sides of the body are covered with a network of wide brown meshes. The upper surface is marked with transverse bands, while the under surface is much lighter in colour and is speckled with brown patches. In specimens about 50 mm. and upwards the whole of the body assumes more or less a grey tint while the under surface is a little lighter. The caudal fin is black with a light hinder margin." Later, HORA (1924), reported *P. palembangensis* as "*Tetraodon palembangensis*" based on "five young examples" (the smallest specimen was 8 mm in TL)

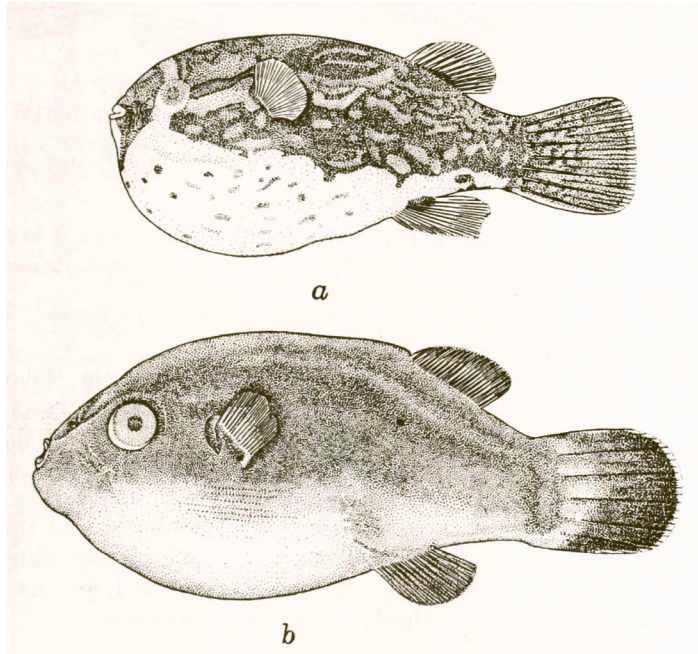

Figure 11. Drawings of specimens of "*Tetraodon palembangensis*" from Thailand in HORA (1924: 499, Fig. 9). The drawings show typical external morphology including coloration of female (a, 45 mm TL) and male (b, 50 mm TL) of *Carinotetraodon lorteti* (See RAINBOTH, 1996; TAN 1999; TAKI *ET AL*. 2021; EBERT 2001; KOTTELAT *ET AL*., 1993 for photographs and descriptions of *C*. *lorteri*). This Hora's misidentification including the drawings probably influenced subsequent workers.

Figure 12. Photograph of a drawing of *Crayacion palembangensis* (= *Pao palembangensis*) in BLEEKER (1865: Plate 208, Fig. 3) deposited in "Iconographia Zoologica", the Special Collections of the University of Amsterdam. Source: https://en.wikipedia.org/wiki/Pao_palembangensis

collected by Nelson Annandale from "fresh water near Lampam" in the vicinity of "inner lake" (Thale Luang) of the "Talé Sap" (the Songkhla Lake or the Songkhla Lagoon system in Peninsular Thailand) with description, which partly quoted his 1923 description of the species, and drawings (Fig. 11). From descriptions and drawings in his 1923 and 1924 papers, it can be assumed that the species he recognized as "*Tetraodon palembangensis*" was actually *Carinotetraodon lorteti,* as already pointed out by Dekkers (1975: 94 and 97, as *Tetraodon lorteti*) since most of the information, including drawings, agrees well with its features (e.g., a distinct reticulate pattern on dorsal and lateral sides of the body with plain ventral side in females [Hora, 1924: 499, Fig. 9a] [Fig. 11, top]; a uniformly colored body and a caudal fin with white edge in males [Hora, 1924: 499, Fig. 9b] [Fig. 11, bottom]) (See Rainboth, 1996; Tan 1999; Taki *et al*. (2021), Ebert (2001), Kottelat *et al*. (1993) for photographs and descriptions of *C. lorteri*).

Later, Chevey (1932) listed *P. palembangensis* as "*Tetrodon palembangensis*" in his inventory of fish fauna of Indochina as a species inhabiting freshwater without further information.

Later, Fowler (1934) reported *P. palembangensis* as "*Tetrodon palembangensis*" from "Kratt" (presently Trat or Trad of eastern Thailand) with the length (44 mm SL) and a drawing of the specimen (ANSP 60239). From the general appearance, including coloration (a large ocellus under dorsal fin and at candal fin bas of the drawing, it was reidentified as *Dichotomyctere ocellatus* by me. However, Dekkers (1975: 132) examined and reidentified the specimen as his new species *Tetraodon steindachneri* (now a junior synonym of *D. ocellatus*).

Later, Fowler (1935) reported *P. palembangensis* as "*Tetrodon palembangensis*" from "Srisawat" (a district included in the Mae Klong River basin in mountainous areas of Kanchanaburi Province, western Thailand) with a length of 61 mm SL, which is now probably lost (Mark Sabaj, pers. comm.).

Later, Smith (1945) correctly reported that a 19-cm long specimen of "*Tetraodon palembangensis*" (= *P. palembangensis*) with large black meshes on a yellow background (some of the meshes enclosing black spots) collected by "Masya and Suvatti" on 28 September 1927 from "the Tale Noi" (= Thale Noi), the northern most freshwater lake of the Songkhla Lagoon system, Peninsular Thailand.

Later, Suvatti (1950) listed *P. palembangensis* as "*Tetraodon palembangensis*" from "Upper Bangpakong River" and "Thale Noi" of Thailand without further information.

In the description of *P. palembangensis* as "*Tetraodon palembangensis*", de Beaufort & Briggs (1962), the first modern taxonomic comprehensive work on the species, stated its distribution in mainland Southeast Asia as "Siam, Indochina".

A few years later, Aubenton & Blanc (1966), in their taxonomic study of tetraodontiform fishes in Cambodia, mentioned and reported specimens of *P. palembangensis* as "*Monotreta cutcutia palembangensis*" collected from "Luang-Prabang, Laos", in collections of MNHN in "Remarks" on their new species *Monotreta tiranti* (now a junior synonym of *Carinotetraodon lorteti*) with a black and white drawing of the species, an apparent replication of a color drawing of *P. palembangensis* (as "*Crayacion palembangensis*") published in Bleeker (1865) (Fig. 12). Photographs of the two specimens deposited as "*Tetraodon palembangensis*" at MNHN (MNHN-IC-1939-0266 and MNHN-IC-1939-0267) from "Laos" (Collectors: "Delacour, Greenway et Blanc") presumably mentioned in the study were examined by me. The two tetraodontid specimens were in relatively poor condition but their body color patterns were still visible. In MNHN-IC-1939-0266 (75 mm SL), the ventral side of body possessed relatively fine white reticulate patterns on a brown background (typical coloration of *P. fangi*, see Taki *et al*. [2021: 504]), the absence of spinules on the snout and the dorsal side of the

caudal peduncle, and snout length was clearly shorter than post orbital head length. In MNHN-IC-1939-0267 (60 mm SL), the dorsal and lateral sides of body were brown, the ventral side of body white without any markings, and spinules on the dorsal side of body extended posteriorly at least to the middle of the dorsal side of caudal peduncle, and snout length was subequal to post orbital head length. They are apparently not *P. palaembangensis*, and were tentatively identified as *P. fangi* and *P. cochinchinensis* by me, respectively, by following TAKI *ET AL*. (2021).

Later DEKKERS (1975), in his review of the freshwater puffers of the genus *Tetraodon* in Asia, stated the distribution in Indochina of *P. palembangensis* (as "*Tetraodon palembangensis*") as "Thailand, Laos" and reported a specimen of the species collected by H. Bernatzik (NMB 5176, 147 mm SL) from "Tale Luang" (= Thale Luang), an inner lake of the Songkhla Lake [Songkhla Lagoon system] which is primarily freshwater but turn to be brackish during a peak of dry season (SIRIMONTAPORN *ET AL*., 1999: 3079), in a list of materials examined of a redescription of the species.

Later, SIRIMONTAPORN (1984) reported *P. palembangensis* as "*Tetraodon palembangensis*" from the "mouth of Songkhla Lake" and "the area from Hua Kao Deng to Ko Yo" (the Songkhla Lagoon system), Peninsular Thailand, with a color photograph of a specimen (ca. 56 mm SL) (page 91, No. 325). The photograph was reidentified by me as *Dichotomyctere ocellatus* from its general appearance and coloration (a large occellus at around base of dorsal and candal fins with a plain white abdomen).

Later, SIRIMONTAPORN (1990) reported *P. palembangensis* as "*Tetraodon palembangensis*" correctly from "Thale Noi" of the the Songkhla Lagoon system with a description (in Thai), its distributional data within the Songkhla Lake region or the Songkhla Lagoon system, and a black and white photograph in fresh or live condition (the same description and photograph [in color] were duplicated and published also in SIRIMONTAPORN *ET AL*. [1999]).

SAITANU & PARIYAWONGSKUL (1991) and SAITANU *ET AL*. (1991) obtained and reported specimens of "*Tetraodon palembangensis*" from the Mekong River basin in Nakhon Ratchasima and Udon Thani provinces, northeastern Thailand, respectively, with sex, length, weight, and toxicity of the specimens.

VIDTHAYANON (2002) reported *P. palembangensis* as "*Monotrete palembangensis*" from "Toh Daeng Peat Swamp" in Narathiwat Province, Peninsula Thailand, which belongs to the Golok River basin, with a color photo in fresh condition and a description (page 121) (The identification was confirmed in the present study).

Most recently, before the present report, LHEKNIM (2019) reported "*Pao palembangensis*" from "Thale Noi" of the Songkhla Lagoon system, southern Thailand, in his list of collected fish species in the lake during 1982–1983.

DISCUSSION

The three specimens of *Pao palembangensis* collected from the Phunphin Stream (Tapi River drainage) examined in the present study agree well with descriptions including meristic and morphometric characters and coloration provided in DEKKERS (1975), which included the presumed holotype of the species (Table 1) as well as BLEEKER's 1851 original description of the species, and a color drawing (Fig. 12) and a description in BLEEKER (1865–69) published later on except for the total number of pectoral-fin rays which was one more than the published range, which should be considered as infraspecific variation due to insufficient numbers of specimens used in previous studies. However, the two short anterior branches

of the dorsal-most lateral line encircling the eye and the posterior portion of the ventral lateral line above anal fin base which were shown in TYLER (1980: 296, Fig. 222) were not observed in the three specimens from the Tapi River basin and photographs of 13 specimens of *P. palembangensis* from Sumatra and Borneo examined in the present study. Detailed direct observations on additional specimens from more localities were needed to verity the variability of these characters. The three specimens of *P. palembangensis* can be readily distinguished from all the other 10 members of the genus *Pao* presently recognized as valid by FRICKE *ET AL.* (2024) (*P. abei*, *P. bailayi*, *P. barbatus*, *P. bergii*, *P. cochinchinensis*, *P. fangi*, *P. hilgendorfii*, *P. leiurus*, *P. ocellaris*, and *P. suvattii*) as follows: entire abdomen with very well-defined wide-meshed dark networks (reticulations) (vs. absent in all other congeners). Further, the present specimens of *P. palembangensis* can be distinguished from other congeners as follows: clearly shorter snout than post orbital head length (snout length 78.5–86.2% of post orbital head length) (vs. subequal in *P. abei*, *P. bergii*, *P. baileyi*, *P. barbatus*, *P. cochinchinensis*, *P. leiurus*, *P. ocellaris*, and *P. suvatti*), the presence of spinules on the mid-dorsal surface of the snout (vs. absent in *P. abei* and *P. fangi*); anteriorly-directed mouth (vs. up-turned mouth in *P. suvattii*); and, the absence of finger-like cutaneous outgrowths on head and body (vs. present in *P. baileyi*) (data used in the comparisons from POPTA [1905, 1906] [as *Tetrodon*]; KLAUSEWITZ [1957] [as *Tetraodon*]; DEKKERS [1975] [as *Tetraodon*]; KOTTELAT *ET AL.* [1993] [as *Tetraodon*]; KOTTELAT [1995] [as *Tetraodon*]; EBERT [2001] [as *Tetraodon*]; TAN & KOTTELAT [2001, 2009] [as *Monotrete*]; TAKI *ET AL.* [2021]; SAENJUNDAENG *ET AL.* [2013a, b] [as *Tetraodon*]; GRUDPAN *ET AL.* [2023]; and the present study).

From a preliminary survey of available data, there is a possibility that the strongly arched anterior portion of the spine (Fig. 7A, B) of *P. palembangensis* found in the present study is unique among members of the genus *Pao* (the same state of the spine was also observed in radiographs of all specimens of the species collected from Sumatra and Borneo examined in the present study). Although data of some species were not available in the comparison, the strongly arched anterior portion of spine was not observed in all specimens of congeners examined in the present study (*Pao abei*, *P. barbatus*, *P. baileyi*, *P. cochinchinensis*, *P. fangi*, *P.* cf. *leiurus*, *P. suvatti*). These had the same state as the specimen of *Pao* cf. *leiurus* shown in Figure 7C, i.e., the anterior portion of the spine gently sloping (also somewhat bending ventrally in some specimens) to the end of spine (urohyal) with maximum angles of only ca. 15–25° to body axis (vs. ca. 45–55° in *P. palembangensis*). A further investigation is needed to evaluate this interesting state of a character of *P. palembangensis* by comparisons to all members of the genus *Pao* and other genera and species of the family Tetraodontidae.

Some species of the family Tetraodontidae have been known to possess an ability of closing eye openings by having the skin around the eye converge toward the center of the iris with simultaneous retraction of the eyeball away from the surface, which is initiated just before the skin of the eye begins to move. This is an extraordinary feature among vertebrates and appears to have been acquired independently in the Tetraodontidae (OGIMOTO *ET AL.*, 2021). However, this peculiar ability was observed and recorded in only five species (*Takifugu flavipterus, T. niphobles*, *T. paradalis*, *T. rubripes*; and *Torquigener albomaculosus*) of the family. No freshwater tetraodontid species has been reported to have this ability before the present study (OGIMOTO *ET AL.*, 2021). Complete closing of eye openings was observed while a live individual of *P. palembengensis* (RLIKU 10303) was inflating shortly after being picked up out of the water from a bucket by the author with bare hands (Fig. 9A, see Fig. 8 for comparison to normal opened eye condition). It is unknown if closing of the eye openings of *P. palembengensis* is always performed together with inflation of the body, or whether it can be performed independently.

From the review of distributional records of *P. palembangensis* above, it can be concluded that most of previous records of the species in Indochina with morphological data or voucher materials are misidentifications of other species of pufferfishes (GÜNTHER, 1870; TIRANT, 1885; HORA, 1923, 1924; FOWLER, 1934; AUBENTON & BLANC, 1966). A possibility of coloration of juveniles of *P. palembangensis* different largely from that of adults can be rejected, since from observations in the present study, juvenile specimens of *P. palembangensis* from 58.9–108.3 mm SL (UMMZ 171710, 243442; CAS 217159) exhibited its unique coloration, generally similar but different only in detail, from sub-adults and adults (Fig. 13; see also KOTTELAT *ET AL.* [1993: Plate 84]). Hence, specimens of ca. 40–80 mm SL used in previous studies whose data, including drawings, photographs, and descriptions, were reexamined in this study are apparently not *P. palembangensis*.

In the records in which identifiable data or voucher specimens were not available in the present study (KÁROLI, 1882; SAUVAGE, 1883; FOWLER, 1935; SUVATTI, 1950; SAITANU & PARIYAWONGSKUL, 1991; SAITANU *ET AL.*, 1991), the collection localities given could have been uninhabitable by the species (e.g., mountainous or highland areas, upper reaches of rivers) except cases in which collection localities were only mentioned as vast areas such as "Siam" or "Mé-Nam" (Chao Phraya River). Based on reliable records of collection, the species is distributed primarily in rivers, marshes, lakes, swamps (including peat swamps), in lowland or plains near coastal areas, influenced by tidal water that is sometimes brackish (e.g., BLEEKER, 1865–69; DEKKERS, 1975; KOTTELAT & WIDJANARTI, 2005; SIRIMONTAPORN, 1999; KHAN *ET AL.*, 1996; KEIM *ET AL.*, 2021; VIDTHAYANON, 2002; the present study). The occurrence of fish species usually found in brackish to salt water environments (*Ambassis vachellii, Butis butis, B. gymnopomus*) (RAINBOTH, 1996; YOSHIDA *ET AL.*, 2013; TAKI *ET AL.*, 2021; personal observation) at the collection site of the Phunphin Stream, Tapi River basin, at the time the specimens of *P. palembangensis* were collected in the present study also suggests salt water influence of the location. Furthermore, *P. palembangensis* has not been recorded in recent ichthyofaunal surveys conducted in fresh and brackish waters of the Mae Klong, Chao Phraya, Bang Pakong, and Mekong river basins (e.g., JOHNSEN, 1963; THONGNOPHAKHUN, 1968; LEENANOND *ET AL.*, 1988; TERMVIDCHAKORN & HANGPONGKITTIKUL, 2008; SO *ET AL.*, 2013; YOSHIDA *ET AL.*, 2013; TRAN *ET AL.*, 2018; PRAXAYSOMBATH *ET AL.*, 2020; TAKI *ET AL.* 2021; GRUDPAN *ET AL.*, 2023; the present author's unpublished data), although the species has unique coloration and appearance which distinguish it from other tetraodontid species, and is also relatively large in size. Hence, many records are likely to be misidentifications of other tetradontid species inhabiting fresh and brackish waters.

Therefore, the actual distributional range of *P. palembangensis* can be reconstructed from reliable sources based on presumably correctly identified specimens as follows: from the Tapi River basin, Thale Noi and Thale Luang (Songkhla Lagoon system), and Toh Daeng Peat Swamp (Golok River basin) of southern Thailand, Peninsular Malaysia (Perak and Pahang river basins including Tasek Bera) to Sumatra (Kampar River basin [Gunung Sahilan]; Indragiri River basin [Taluk]; Batang Hari River basin [Jambi]; and Musi River basin [Palembang]), Borneo (Singkawang; Kapuas River basin [Bunut, Kapuas Lakes, Pontianak, Putussibau, Semitau, Sintang]; and Mahakam River basin [Muyub Ilir, Perdana, Tering Lama]), Belitung Island (Tebat Rasau), and Java (Jakarta Bay) (BLEEKER, 1865–1869; DE BEAUFORT & BRIGGS, 1962; DEKKERS, 1975; ROBERTS, 1989; CHRISTENSEN, 1992 [including data of presumed voucher specimens: CAS-ICH 93399, 94563]; KHAN *ET AL.*, 1996; SIRIMONTAPORN *ET AL.*, 1999; VIDTHAYANON, 2002; KOTTELAT & WIDJANARTI, 2005; TAN & KOTTELAT, 2009; KOTTELAT, 2013; KEIM *ET AL.*, 2021 [as *P. hilgendorfii*]; present study). DEKKERS (1975: 107) noted that the record of *P. palembangensis*

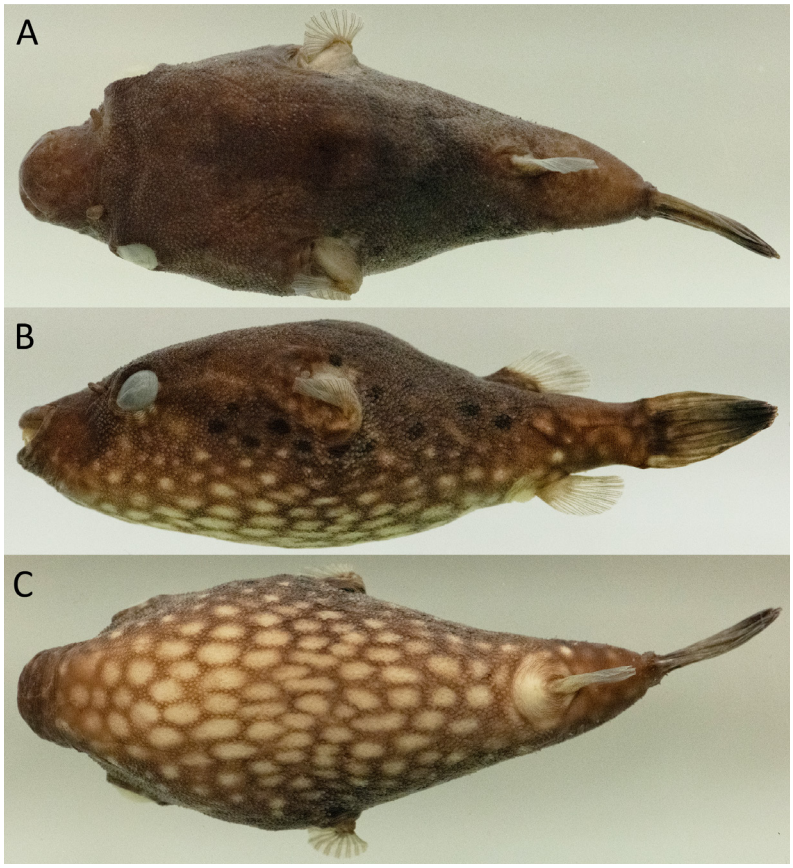

Figure 13. A juvenile alcohol-preserved specimen of *Pao palembangensis* (UMMZ 243442, 58.9 mm SL, sex undetermined) collected from Jambi, Sumatra, Indonesia: Dorsal (A), lateral (B), and ventral (C) views. Note black spots at lateral side of body which have not developed into ocelli yet; numerous white spots scattered on brown background at ventro-lateral to ventral side of body which will presumably develop into the meshed pattern of adults, a large irregular blotch which often has elongated pentagonal shape with concaved anterior and lateral margins and a smaller irregularly-shaped spot posterior to it on dorsal side of body which are similar to those in adults, and a large brown spot and a posteriorly indented large dark brown spot at each distal and middle of the most proximal portion of caudal fin, respectively, with small white spots scattered on brown backgroud in the area in between. Photographs by Juan Gabriel Albornoz-Garzón (UMMZ).

from "Bay of Djakarta" (= Jakarta Bay, Java, Indonesia) (ZMA 110.195 [presently relocated to RMNH]) seemed doubtful since other records which he examined were from freshwater and the specimen was sent from the Bogor Museum which at the time was not always accurate when labelling. But from the results of the present study, the species can possibly occur in brackish water environments such as mouth of rivers and no positive reasons to deny the record. Thus, in the present study, the record was recognized as a part of the distributional range of the species. The record of the species from the Tapi River basin in the present study represents its northernmost distribution as currently known. Although the entire area of the

Tapi River basin has not been sufficiently surveyed, *P. palembangensis* has not been recorded in previous fish surveys in the basin, including two comprehensive surveys in its upper and lower parts (DUANGSAWASDI & KRACHANGDARA, 1994; LHEKNIM, 2004). This probably reflects the fact that the species inhabits mainly the lower-most reaches of the river basin.

P. palembangensis is reported to be utilized as a food fish in Tasek Bera (Pahang River basin) in Peninsular Malaysia (HUA, 2002), the Kapuas Lake area of the Kapuas River basin in western Borneo (KOTTELAT & WIDJANARTI, 2005), and on Belitung Island in Indonesia (KEIM *ET AL.*, 2021[as *P. hilgendorfii*]). However, fishermen in the Phunphin Stream area, including one who caught the specimens examined in the present study, reported that villagers of the area avoid eating puffers, all of which all called as "pla pao", since it is believed that the fish will make eaters "drunk". The author experienced weak numbness and dull pain while handling live and fresh specimens of *P. palembangensis* with mucous with bare hands, presumably caused by toxic substance(s) such as tetrodotoxin (TTX) or saxitoxin (STX). These poisonous substances have been found in many fresh, brackish, and marine pufferfishes (NAGASHIMA *ET AL.*, 2015). Although the function of the tentacle-like organs attached to each spinule of *P. palembangensis* is unknown, from their gross structure, it is possible that they contain secretory cells which release alarm or poisonous substances such as TTX or STX when the fish molested, in combination with spinules which can sting or puncture the skin and enable the substances to enter the attacker's body. Many tetraodontids are known to secrete TTX from their skin, presumably to protect themselves from attackers when stimulated (KODAMA *ET AL.*, 1986; MATSUURA, 2015; NAGASHIMA *ET AL.*, 2015). Since previous reports of TTX toxicity of *P. palembangensis* specimens obtained from northeastern Thailand (SAITANU & PARIYAWONGSKUL, 1991; SAITANU *ET AL.*, 1991) most likely involve misidentifications of other freshwater puffer species (see above), toxicity examination of *P. palembangensis* should be conducted on correctly identified species in the future.

Interestingly, recent molecular analyses of Asian freshwater tetraodontids show remarkable distinctions and relatively deep divergence between *P. palembangensis* and some other members of the genus *Pao* (YAMANOUE *ET AL.* 2011; ZHU *ET AL.*, 2020; YAMADA *ET AL.*, 2021). Although some of these studies may have involved misidentifications, they suggest the possibility of the higher-level taxonomic distinction of *P. palembangensis* from other congeners, as previously suggested by TYLER (1980: 338). This possibility is also supported by several unique morphological and behavioral features observed in the species: relatively large body size (reaching ca. 250–300 mm TL), relatively large spinules each attached by a tentacle-like organ, strongly arched anterior portion of spine, and the ability to close eye openings by using surrounding skin and retraction of eye balls, which haven't been reported in other members of the genus so far. Further morphological (including osteology) and molecular observations on *P. palembangensis* and detailed comparison with other members of the genus *Pao* are needed to test this hypothesis.

Comparative materials: *Pao palembangensis*: UMMZ 171710, 4 specimens, 82.5–131.2 mm SL, Palembang, Sumatra, A. Thienemann (photographs and radiographs examined); UMMZ 243442, 2 specimens, 58.9–89.8 mm SL, Area of vicinity of Jambi, Batang Hari drainage, Jambi, Sumatra, Indonesia, H. H. Ng *et al*.; CAS 217159, 7 specimens, 53.7–127.6 mm SL, Fish market at Sintang (purchased), Kapuas River basin, Kalimantan Barat, Borneo, Indonesia, 19 July–1 August 1976, T. R. Roberts and S. Woerjoatmodjo (photographs and radiographs examined). *Tetraodon palembangensis*: MNHN-IC-1939-0266, 1 specimen, 75 mm SL, Laos, Delacour, greenway et blanc (photographs examined [reidentified as *Pao fangi* in present study]); MNHN-IC-1939-0267, 1 specimen, 60 mm SL, Laos, Delacour, Greenway et Blanc (photograph examined [reidentified as *Pao cochinchinensis* in

present study]). *Tetrodon palembangensis*: BMNH 1859.7.8.9, a stuffed specimen, ca. 7.7 cm SL, Siam, Henri Mouhot (photographs examined [reidentified as *Pao cochinchinensis* in present study]). *Pao abei*: CAS 91016 (holotype), 103 mm SL, Xe Bang Fai at Ban Geng Sahwan, Xe Bang Fai watershed, Mekong basin, Laos, Oct. 1996, Phouthalom Vongsay (photographs and radiograph examined). *Pao baileyi*: RLIKU 10306, 2 specimens, 78.0–103.8 mm SL, Pak Se, Laos, Dec. 2009, Prasert Suriwiyo. *Pao barbatus*: CAS 79100 (holotype), 72.4 mm SL, Huay Huang 30 km W of Chiang Khan, Loei Province, Thailand, 7 Apr. 1990, T. R. Roberts; (photographs and radiograph examined). *Pao cochinchinensis*: RLIKU 10447, 5 of 10 specimens, 108.7–119.9 mm SL, Pasak Chonlasit Dam reservoir, Manao Wan Sub-dist., Phatthana Nikhom Dist., Lopburi Prov., Thailand, 18 May 2019, Nantich Ngamtampong; RLIKU 10305, 2 specimens, 99.0–110.2 mm SL, Takeo, Cambodia, 20–22 Sept. 2000, Tyson R. Roberts. *Pao fangi*: RLIKU 5932, 1 specimen, 53.2 mm SL, A canal at Bang Khan Mok (Chao Phraya basin), Lopburi District, Thailand, 17 Jan. 2009; NIFI 04682, 1 specimen, 61.6 mm SL, Market near Tram Chim National Park, Vietnam, 28 May 2007, Chavalit Vidthayanon; NIFI 00624 (paratype of *Pao palustris*), 1 specimen, 91.1 mm SL, Tha Bo, Nong Khai, Thailand, 6 June 1977, Cheerawan Ratanathawee. *Pao* cf. *leiurus*: RLIKU 10304, 1 specimen, 119.3 mm SL, Phunphin Stream (tributary of the Tapi River), lower Tapi River basin, Si Wichai Sub-district, Phunphin District, Surat Thani Province, Thailand (9°08′22.99″N, 99°13′30.25″E, 6.2 m alt), 27 May 2024, a local fisherman. *Pao suvatti*: NIFI 03574, 5 specimens, 141.2–120.1 mm SL, Nong Han, Sakon Nakhon, 27 Mar. 1976.

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