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The Indo-Pacific Stingray Genus *Brevitrygon* (Myliobatiformes: Dasyatidae): Clarification of Historical Names and Description of a New Species, *B. manjajiae* sp. nov., from the Western Indian Ocean †

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Abstract: Members of the genus *Brevitrygon* are small, locally abundant tropical stingrays (family Dasyatidae) occurring in soft sedimentary habitats of inner continental shelves of the Indo-West Pacific from the Red Sea to Indonesia. Formerly members of the genus *Himantura*, whose members lack dorsal and ventral skin folds on the tail (typical of most dasyatid genera), folds are present or rudimentary in some *Brevitrygon*. Important to artisanal fisheries and known to consist of at least five species, these fishes are possibly the most frequently misidentified of all stingrays. Most were inadequately described in the 19th century, and they are often taxonomically confused due to morphological similarity, ontogenetic variability, and sexual dimorphism. Their nomenclatural history is complex with four of the known species represented within the type series of one species, *B. walga* (Müller & Henle). Also, the type of the species with which *B. walga* is most often confused, *B. imbricata* (Bloch & Schneider) from off southern India and Sri Lanka, is in very poor condition. A lectotype has been designated for *B. walga* (confined to the Bay of Bengal). The genus also contains *B. heterura* (Bleeker) from the Indo-Malay Archipelago, *B. javaensis* (Last & White) from off southern Indonesia, and a new species, *B. manjajiae* sp. nov., from the western Indian Ocean. The former species are redescribed and redefined based largely on a combination of morphometrics, tail morphology, squamation, and molecular data. Molecular divergences were detected within lineages of *B. heterura*, *B. walga* and *B. manjajiae* sp. nov., requiring further investigation.

Keywords: Chondrichthyes; Elasmobranchii; systematics; taxonomy; diversity; review of genus; nomenclatural discussion; redescriptions; morphology; genetics; NADH2

Citation: Last, P.R.; Weigmann, S.; Naylor, G.J.P. The Indo-Pacific Stingray Genus *Brevitrygon* (Myliobatiformes: Dasyatidae): Clarification of Historical Names and Description of a New Species, *B. manjajiae* sp. nov., from the Western Indian Ocean. *Diversity* **2023**, *15*, 1213. https://doi.org/10.3390/d15121213

Academic Editor: Bert W. Hoeksema

Received: 12 October 2023
Revised: 26 November 2023
Accepted: 5 December 2023
Published: 12 December 2023

1. Introduction

The Indo-West Pacific stingray genus *Brevitrygon* (Last, Naylor, & Manjaji-Matsumoto) was erected in 2016 based on a combined morphological and molecular study of the family Dasyatidae [1]. Its members, formerly and most recently placed in the genus *Himantura* (Müller & Henle, 1837 (e.g., [2–4])), have been amongst the most frequently misidentified stingray species. The taxonomic confusion has arisen largely because of their basic morphological similarity, overt sexual dimorphism, ontogenetic variability, and nomenclatural complexity. All species are small rays (adults typically smaller than 25 cm

disc width [DW]) and some are amongst the most numerically abundant stingrays in the regions in which they occur [5]. The group presently contains four valid nominal taxa, *B. heterura* (Bleeker, 1852), *B. imbricata* (Bloch & Schneider, 1801), *B. javaensis* (Last & White, 2013), and *B. walga* (Müller & Henle, 1841), but additional species are known to occur in the Indo-Pacific region [6].

The existence of taxonomic issues in this group has been discussed recently [1,7,8], but the underpinning nomenclatural decisions have not been fully explained. The nomenclature has been further complicated by serious errors in the literature and the widespread misattribution of two names, *B. imbricata* and *B. walga,* and these are discussed in sections below. The unique type of *B. imbricata*, a dry-mounted adult male specimen (ZMB 7585), collected from the Coromandel Coast (India), is in poor physical condition and has not been formally linked to either of the two species occurring further south in the Bay of Bengal (Northern Indian Ocean). The type series of *B. walga* contains four valid species, which are collectively distributed across the entire geographic range of the genus, and a lectotype needs to be designated [9]. One of the syntypes in the type series remains unnamed, and this is addressed below.

Original descriptions of these old nominal taxa were inadequate for discriminating between species so in the following review of the genus *Brevitrygon*, the nomenclature is clarified, these historical species are redescribed and rediagnosed, and the new species is formally described. A key is provided to members of the genus.

2. Materials and Methods

The morphological methods largely follow standards proposed by Manjaji [3] for whiprays and are based on Compagno & Heemstra [10] and Last & Stevens [11]. Last et al. [12] redefined some of these including some new descriptive characters (i.e., morphology of the disc and its attributes and squamation). Measurements were typically taken point-to-point with one notable exception, snout length, which was taken both directly and horizontally (distance along the longitudinal axis from the snout tip to a perpendicular line joining the eyes); these measurements have been used extensively in the literature, so both methods were recorded for comparative purposes. Lengths and widths were taken selectively for thorns of the central disc and tail. Also, the height of the mid-scapular denticle was excluded in the measurement of disc thickness. Dorsal and ventral skin folds may be present (weak or as low fleshy ridge) or absent on the tail depending on the species. These folds and ridges grade into the dorsal and ventral surfaces of the tail so their start and end positions are usually hard to identify. Measurements were taken in millimetres (mm). Morphometric data are expressed as proportions of DW.

Meristic data for types of the new species were obtained from radiographs taken by J. Pogonoski (CSIRO). Counts, which follow Compagno & Roberts [13], include some minor modifications/considerations as follows: the first enlarged anterior element of the pelvic fin (with 2–4 distal segments fused at their bases) is counted as one; elements of the first synarcual were not included in vertebral counts; intermediate pectoral-fin radial elements were assigned to a pterygial unit based on the relative level of overlap with each of the adjacent units; distal propterygial and metapterygial elements were considered to form part of the main pterygial skeleton and were not incorporated into counts; the notochord of the tail was excluded from counts; delineation of the last monospondylous and first diplospondylous centra was difficult in some specimens, which might have created minor counting errors; tooth rows for both upper and lower jaws were counted from vertical rows (following [14]); and corners of the jaws had to be dissected apart in selected material to make tooth rows and oral papillae fully visible for counting.

The developmental stages of the dorsal denticles in the genus *Himantura* (which formerly included *Brevitrygon*) are extremely useful for distinguishing species [3,12]. The sequence and extent of their development usually varies between species with few species displaying all possible stages of development. Clarification of the terminology for the

enlarged, spine-like denticles and thorns in the scapular region and along the dorsal midline of the tail is needed. The term 'denticle' is herein used to refer to the small or medium-sized placoid scales of the denticle band, typically less than 4 mm in diameter, and enlarged scales exceeding 4 mm in size are referred to as 'thorns' (following [3]). Any oversized denticles in the scapular region are referred to as 'mid-shoulder or scapular denticles' and those on the dorsal midline of the tail as 'enlarged denticles' or 'thorns'. The terms 'sting(s)' are often used herein as optional abbreviations for the caudal sting(s) or stinging spine(s) and the regions of the tail preceding (i.e., 'pre-sting') and distal to (i.e., 'post sting') the origin of the first sting.

DNA was extracted using the E.Z.N.A Tissue DNA Kit (Omega Bio-Tek, Inc., Norcross, GA, USA). Extracted total DNA was stored at −20 °C until used for amplification of the NADH dehydrogenase subunit 2 (NADH2) region of the mitochondrial DNA via polymerase chain reaction (PCR). A single set of universal primers [15] designed to bind to the ASN and ILE tRNA regions of the mitochondrial genome were used to amplify the target fragment. PCR reactions were generally carried out in 25 µL volume comprising 0.3 µM primers, 2.5 mM $MgCl_2$, 200 µM each dNTP, 10X Ex Taq buffer (20 mM Tris-HCl pH 8.0, 100 mM KCl, 0.1mM EDTA, 1mM DTT, 0.5% Tween 20, 0.05% Nonidet P-40, 50% Glycerol), 0.25 U TaKaRa Ex Taq (Takara, Mountain View, CA, USA), and 50–100 ng template DNA. The reaction mixture was denatured at 94 °C for 3 min, after which it was subjected to 35 cycles of denaturation at 94 °C for 30 s, annealing at 48 °C for 30 s and extension at 72 °C for 90 s. PCR products were purified with ExoSAP-IT (USB, Cleveland, OH, USA) and bi-directionally sanger sequenced using BigDye® Terminator chemistry on an ABI 3730xl genetic analyzer (Applied Biosystems®, Life Technologies, Grand Island, NE, USA) at Retrogen Inc. Custom DNA Sequencing Facility (San Diego, CA, USA). DNA sequences were edited using Geneious® Pro v. 6.1.7 (Biomatters Ltd., Auckland, New Zealand. Available at http://www.geneious.com). The edited sequences were translated to amino acids and aligned with corresponding NADH2 sequences from representatives of closely related species using the MAFFT module within the Geneious Package (Biomatters Ltd., Auckland, New Zealand). The aligned amino acid sequences were translated back, but in frame, to their original nucleotide sequences to yield a nucleotide alignment. The full protein-coding alignment was 1044 nucleotides long. A maximum likelihood tree was constructed from the aligned NADH2 sequences (1044 bp) using a General Time Reversible model accommodating invariant sites and gamma distributed rate variation GTR+I+G. All analyses used the model test application built into the software package PAUP* 4.0. Sequence data were deposited in GenBank (https://www.ncbi.nlm.nih.gov/genbank/ (accessed on 29 November 2023)) under accession numbers OR882017–OR882069.

Specimens referred to in this paper include those deposited in the Australian National Fish Collection, Commonwealth Scientific and Industrial Research Organisation Marine Laboratories, Hobart (CSIRO), and loaned from or observed at the following collections: Bishop Museum, Honolulu, HI, USA (BPBM); Stanford University collection (SU), which was subsequently incorporated into the California Academy of Sciences, San Francisco, USA (CAS); Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium (IRSNB); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Museum of Fisheries Science, Tokyo University of Fisheries, Japan (MTUF); Muséum National d'Histoire naturelle, Paris, France (MNHN); Muzium Sabah/Sabah Museum, Kota Kinabalu, Sabah, Malaysia (MUS); Bogor Zoological Museum/Museum Zoologicum Bogoriense, Cibinong, West Java, Indonesia (MZB); Pisces Collection, National Museum of Marine Biology and Aquarium, Pingtung, Taiwan (NMMBP); Natural History Museum, London, UK (BMNH); Natural History Museum of Los Angeles County (LACM); National Museum of Nature and Science, Zoology Department, Division of Fishes, Tsukuba, Japan (NSMT); Museums and Art Galleries of the Northern Territory, Darwin, Australia (NTM); Phuket Marine Biological Centre, Phuket, Thailand (PMBC); Naturalis Biodiversity Center—previously Rijksmuseum van Natuurlijke Historie. Leiden, The Netherlands (RMNH); the Smithsonian Institution National Museum of Natural History, Washington, DC, USA (USNM);

Universiteit van Amsterdam, Faculty of Science, Zoölogisch Museum, Amsterdam, The Netherlands (ZMA); the Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin, Germany (ZMB); and the Zoological Museum Hamburg (ZMH). Institutional acronyms follow [16].

The following specimens were measured in full: *Brevitrygon imbricata* (BMNH 2013.4.14.3, *BPBM 27597(1), *BPBM 27597(2), MNHN 2438, MNHN 2439(1), MNHN 2439(2), MNHN 7932, NTM S-13160-009, USNM 222552, USNM 222529-1, USNM 222529-2, USNM 222529-3); *Brevitrygon walga* (BMNH 1889.2.1.4196, CAS 141045, *CSIRO H8667-01, *CSIRO H8668-01, *CSIRO H 8666-01, *CSIRO H8669-01, MNHN 2431, MTUF 29999); *Brevitrygon heterura* (BMNH 1867.11.28.158, CSIRO H4426-11, *CSIRO H4924-05, CSIRO *H4924-04, CSIRO H4924-14, CSIRO H4426-11, CSIRO H4924-10, CSIRO H4924-02, CSIRO H4924-11, *CSIRO H4924-01, *CSIRO H4924-13, CSIRO H4927-04, CSIRO H4924-06, CSIRO H4924-07, CSIRO H4924-09, *CSIRO H4924-12, CSIRO H4924-03, H4924-08, *CSIRO H4927-04, *CSIRO H5473-01, *CSIRO H5473-02, CSIRO H5474-02, *CSIRO H5474-20, CSIRO *H5474.01, *CSIRO H5471-07, CSIRO H5584-09, *CSIRO H5474-19, *CSIRO H5471-06, *CSIRO H5471-05, *CSIRO H5471-04, CSIRO H5473-01, CSIRO H5473-01, CSIRO H5474-18, CSIRO H5474-17, *CSIRO H5584-08, CSIRO H5584-07, *CSIRO H5474-16, *CSIRO H5474-14, *CSIRO H5474-15, CSIRO H6131-01, CSIRO G443 unreg., CSIRO KA351 unreg., *MTUF 29998, MTUF 29999, *PMBC unreg., UMS MMKK11); *Brevitrygon javaensis* (*CSIRO H 5859-01, CSIRO H 5859-03, *CSIRO H 5860-08, *CSIRO H 5860-11, *CSIRO H 6129-01, MZB 21461); *Brevitrygon manjajiae* sp. nov. (*BPBM 33199, CSIRO H *7627-02, *CSIRO H 7627-03, *LACM 38129-83(2 of 3), MNHN 7924, *USNM 222555, *USNM 470881(1 of 2), *USNM 470881(2 of 2), USNM 222585(1 of 4), USNM 222624(1 of 4), USNM 222624(2 of 4), USNM 222624(3 of 4), USNM 222624(4 of 4), *MCZ 59269(1 of 5); data based on newly acquired measurements, partial remeasures from Manjaji [3] and extracted from Last & White [17]. Other morphometric data were taken selectively from additional material for the diagnoses of species. Meristics were obtained from radiographs of some of the above (designated with an asterisk), as well as the following additional material: *B. imbricata* USNM 222564(2); *B. walga* CAS 141045; *B. javaensis* CSIRO H 5860-12, CSIRO H 5860-14, CSIRO unreg C46, 47, 52; and *B. manjajiae*, CSIRO H 7625-04, CSIRO H 7627-01, LACM 38129-83(1 of 3), LACM 38129-83(3 of 3), LACM 38130-60(1 of 4), LACM 38130-60(2 of 4), LACM 38130-60(3 of 4), LACM 38130-60(4 of 4), LACM 38134-37, LACM 38314-24, MCZ 59269(2 of 5), MCZ 59269(3 of 5), MCZ 59269(4 of 5), MCZ 59269(5 of 5).

Nomenclatural Acts: the electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix https://zoobank.org/ (accessed on 4 December 2023). The LSID for this publication is urn:lsid:zoobank.org:pub:EEE4F179-9E86-441A-83CA-D9DBB0AEC366. The electronic edition of this work was published in a journal with an ISSN and has been archived and is available from the following digital repositories: CLOCKSS, Swiss National Library (Helveticat).

3. Results

3.1. Genus Brevitrygon Last, Naylor & Manjaji-Matsumoto, 2016

Type species *Dasyatis javaensis* (Last & White, 2013) by original designation.

Definition. Small stingrays of the family Dasyatidae (adults typically 16–25 cm DW) characterized by the following: disc oval to suboval, strongly depressed with pectoral-fin apex broadly rounded (Figure 1); snout acutely angular and elongate (1.9–3.6 times combined orbit and spiracle length) with variably concave anterior margin; eye small, not protrusible; nasal curtain broadly rectangular to weakly skirt-shaped (Figure 2); mouth with

0–4 oral papillae (Figure 2); tail shape and length typically sexually dimorphic (Figure 3), usually shorter (0.6–2.1 times DW), semi-rigid, and often expanded distally in adult females, more elongate (0.9–2.2 times DW) and filamentous distally in juvenile females and males; dorsal and ventral folds usually rudimentary or absent (low fleshy folds present in *B. imbricata*); caudal stings 1–3 (usually 2), very elongate (when undamaged, length of first 17–32%, second 22–35% DW), inserted relatively close to tail base (distance from cloaca to sting base 2.1–3.2 times interspiracular width); pelvic fins small to medium-sized (length 17–27% DW), protruding slightly beyond disc; clasper of adult male with pseudosiphon; secondary denticle band on disc present in adults (Figure 4), variably developed with edges sharply defined, skin on rest of disc naked; secondary denticle band on tail preceding caudal sting narrow (discontinuous in *B. javaensis*) (Figure 5); thorns absent on disc or with 0–3 scapular thorns and up to 8 slightly enlarged median scapular denticles (Figure 6); denticles and thorns on tail larger than on disc when present, rarely with denticles on post-sting tail; dorsal disc coloration largely plain; ventral disc predominately white, margin often dark edged; post-sting tail plain or with pale lateral stripe; marine, Indo–West Pacific.

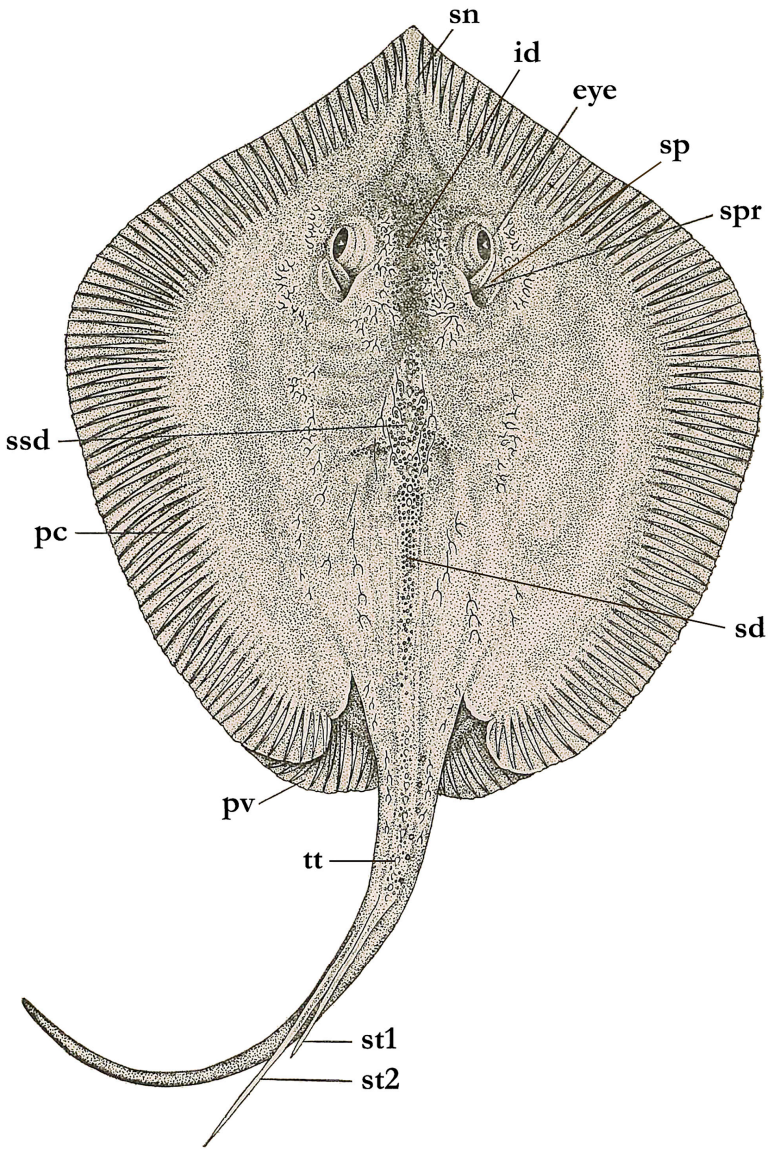

Figure 1. Representative member of the genus *Brevitrygon* highlighting key features of the dorsal disc and tail, modified after Chandy (1957). Abbreviations: id = interorbital denticles, pc = pectoral fin, pv = pelvic fin, sd = secondary denticle band, sn = snout, sp = spiracle, spr = inner ridge of spiracular pit, ssd = scapular denticles, st1 and st2 = caudal stings, tt = tail thorns.

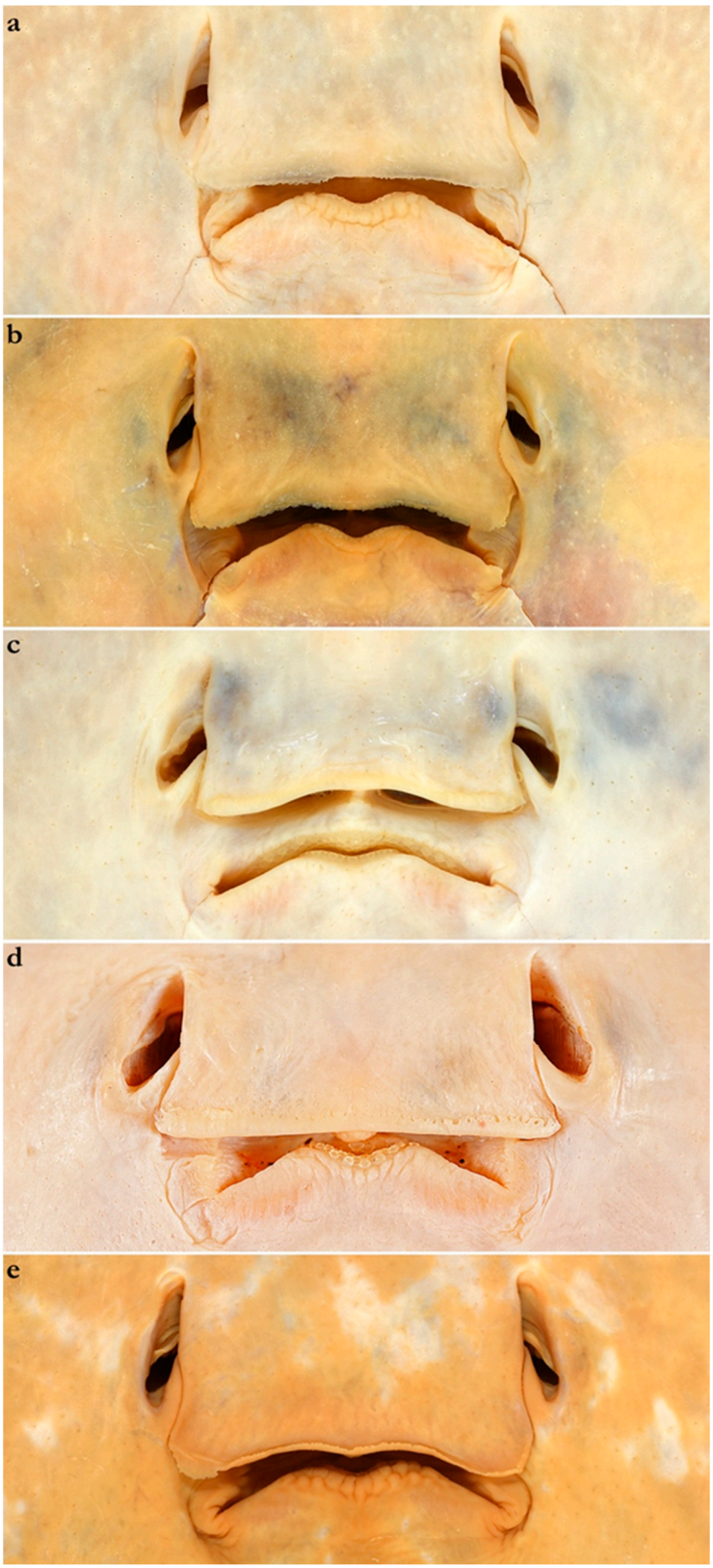

Figure 2. Oronasal region of (**a**) *Brevitrygon imbricata*, non-type NTM S 13160-009, female 186 mm DW, Sri Lanka (preserved); (**b**) *B. walga*, non-type CSIRO H 8666-01, female 233 mm DW, Myanmar (preserved); (**c**) *B. heterura*, non-type CSIRO H 5584-07, female 200 mm DW, Sabah, Malaysia (preserved); (**d**) *B. javaensis*, holotype MZB 21461, female 164 mm DW, Cilacap, Indonesia (preserved); (**e**) *B. manjajiae* **sp. nov.**, holotype USNM 222555, adult male 231 mm DW, Pakistan (preserved).

Figure 3. Lateral (**a**,**b**,**d**,**f**,**h**) and dorsal (**c**,**e**,**g**,**i**) views of the post-sting tail of females of *Brevitrygon* species. (**a**) *B. imbricata* non-type BPBM 27597 (1 of 2), female 202 mm DW, Kerala, India (preserved) showing a shortened tail with obvious dorsal and ventral skin folds; (**b**,**c**) *B. walga* non-type CSIRO H 8666-01, female 233 mm DW, Nabule, Myanmar (preserved); (**d**,**e**) *B. heterura* non-type CSIRO H 5584-07, female 200 mm DW, Sabah, Malaysia; (**f**,**g**) *B. javaensis* holotype MZB 21461, female 164 mm DW, Cilacap, Indonesia; (**h**,**i**) *B. manjajiae* **sp. nov.** paratype LACM 38134-37, female 207 mm DW, Sindh, Pakistan (preserved).

Descriptive features. Disc subequal to slightly longer than wide, length 1–1.1 times DW; barely more robust on cranial and mid-scapular regions than through abdomen; preorbital snout angle 101–118°, usually slightly broader in females than males; margin of snout deeply concave; lateral apices of disc very broadly rounded (making maximum width difficult to determine accurately), posterior margin broadly convex, free rear tip narrowly rounded. Pelvic-fin subtriangular, protruding slightly beyond posterior disc; lateral margin almost straight, apex narrowly or broadly pointed; free rear tip angular to narrowly rounded in females, merging with clasper in males. Clasper short, stout basally, tapering, depressed slightly, rounded distally; postcloacal length to 23% DW in adult males; hypopyle short, about 40–50% of length of clasper outer margin, without prominent anterior notch; lining of pseudopera smooth; pseudosiphon present, short, located on inner lateral margin beside origin of glans; pseudorhipidion weak or absent. Pre-sting tail usually depressed, tapering gradually and evenly toward sting but becoming less depressed below sting base. Post-sting tail of adult males and juveniles slender, semi-rigid to weakly filamentous; low or rudimentary cutaneous folds present or absent; typically, with weak to well-developed fleshy lateral ridges. Post-sting tail of adult females more expanded distally (often bulbous) and shorter than males. Caudal stings long and slender, second usually longest, to 35% DW. Snout broadly elongate, sharply pointed, very depressed; preorbital snout length 28–34% DW, often slightly longer in adult females than males; interorbital space almost

flat, weakly concave across preorbit; eye size variable, interorbital distance 1.2–2.8 times orbit diameter. Spiracles large (length 5–7% DW), subrectangular to suboval, situated dorsolaterally. Nostril length 2.4–3.0 in internasal distance; internasal distance 2.1–2.7 in prenasal length. Nasal curtain broad, width 1.6–2.2 times length. Mouth narrow, width 8–11% DW, 1.0–1.4 in internasal width; profile slightly to moderately arched, not obviously more so in males than females; upper jaw strongly double concave, dorsal to lower jaw; lower jaw notched near symphysis, largely concealing and slotting into symphysial knob of upper jaw; oronasal groove prominent, deep; skin along margin of lower jaw weakly papillose anteriorly, otherwise smooth*; B. javaensis* with 4 oral papillae, other species have 0 to 3. Teeth in weakly defined rows or in quincunx; broadly suboval to rhomboidal in adult males, usually slightly larger in upper jaw than lower jaw, weakly to moderately cuspid; acuspid or weakly cusped, and in dense quincunx in females; more tooth rows in lower jaw (to ~60) than upper jaw (to~46); number of tooth rows ontogenetically variable, increasing with size. Gill opening margins moderately S-shaped, smooth-edged; length of first gill slit 1.1–1.9 times length of fifth, 2.3–3.9 in mouth width; distance between first gill slits 1.8–2.4 times internasal distance, 36–44% of ventral head length; distance between fifth gill slits 1.1–1.6 times internasal distance length, 23–30% of ventral head length. Ontogenetic stages of squamation follow definitions of Manjaji [3], and the rates of development varies between species: *Stage 0* (~70–110 mm DW), disc and tail entirely naked or sometimes with 1–2 prominent embryological scapular denticles on dorsal disc (Figure 6); *Stage 1* (~90–140 mm DW), primary median denticle band poorly developed, band progresses rapidly into next stage; *Stage 2* (~90–140 mm DW), main stage of denticle band developed and occurring well before maturity, often early and interspecifically variable, continuous (sometimes disjunct in *B. imbricata*), denticles well-spaced and non-imbricated, smaller than embryological and primary denticles; *Stage 3* (~110–230 mm DW), band well developed in most species, present as median row of 1–10 enlarged denticles or small thorns on pre-sting tail probably progressing concurrently with *Stage 2* (Figure 4); *Stage 4* (~140–235 mm DW), secondary denticle band well developed, continuous, semi-symmetrical with mostly well-defined lateral margins, their extension and width interspecifically variable, typically broadest over scapulocoracoid and or mid-abdomen, usually constricted over branchial region, variably penetrating preorbital snout and dorsal surface of pre-sting tail, band narrow on dorsal tail or partly absent; *Stages 5, 6* inapplicable to *Brevitrygon*. Total pectoral-fin radials 98–108; propterygials 44–50, mesopterygials 9–17, and metapterygials 40–49. Total pelvic-fin radials 21–27 in females; 15–19 plus clasper in males. Total vertebral segments (excluding first synarcual centra) 84–100; monospondylous centra (excluding first synarcuals) 32–40; diplospondylous centra 46–64.

Coloration. Disc, pelvic fins, and pre-sting tail uniformly yellowish, brownish, or greyish on dorsal surface, lacking a defined pattern; outer portion of dorsal disc often paler. Uniformly whitish ventrally or with yellowish spots; disc margin often dusky or yellowish. Tail beyond sting similar to dorsal disc, pale or darker on either or both surfaces; lateral margins whitish in some species forming a stripe sandwiched between darker dorsal and ventral surfaces.

Species. *B. heterura* (Bleeker, 1852), *B. imbricata* (Bloch & Schneider, 1801), *B. javaensis* (Last & White, 2013), *Brevitrygon manjajiae* sp. nov., and *B. walga* (Müller & Henle, 1841).

Etymology. Derived from *brevis* (Latin), meaning short and *trygṓn* (Greek τρυγών), meaning stingray, in allusion to the short, semi-rigid tails of these stingrays.

Remarks. Recently erected [1] morphologically conservative genus containing five small species with nominal species previously placed in the genus *Himantura*. Manjaji [3], in a review of *Himantura*, placed two of the species (i.e., *H. imbricata* and *H. walga*) in a subgroup of the genus, the 'signifer' complex. This subgroup also contained *Fluvitrygon* species (i.e., *H. signifer* and *H. oxyrhyncha*) clustering as sister groups with *Brevitrygon* and subsequently placed in the subfamily Urogymninae (Last et al. [1]: Figures 3 and 5).

Figure 4. Squamation of the central disc in the genus *Brevitrygon*—secondary denticle band. (**a**) *B. imbricata*, non-type NTM S 13160-009, female 186 mm DW, Sri Lanka (preserved); (**b**) *B. walga*, non-type CSIRO H 8666-01, female 233 mm DW, Myanmar (preserved); (**c**) *B. heterura*, non-type CSIRO H 5584-07, female 200 mm DW, Sabah, Malaysia (preserved); (**d**) *B. javaensis*, holotype MZB 21461, female 164 mm DW, Cilacap, Indonesia (preserved); (**e**) *B. manjajiae* **sp. nov.**, holotype USNM 222555, adult male 231 mm DW, Pakistan (preserved).

Figure 5. Squamation in the genus *Brevitrygon*—dorsolateral view of pre-sting tail. (**a**) *B. imbricata*, non-type NTM S 13160-009, female 186 mm DW, Sri Lanka (preserved); (**b**) *B. walga*, non-type CSIRO H 8666-01, female 233 mm DW, Myanmar (preserved); (**c**) *B. heterura*, non-type CSIRO H 5584-07, female 200 mm DW, Sabah, Malaysia (preserved); (**d**) *B. javaensis*, holotype MZB 21461, female 164 mm DW, Cilacap, Indonesia (preserved); (**e**) *B. manjajiae* **sp. nov.**, holotype USNM 222555, adult male 231 mm DW, Pakistan (preserved).

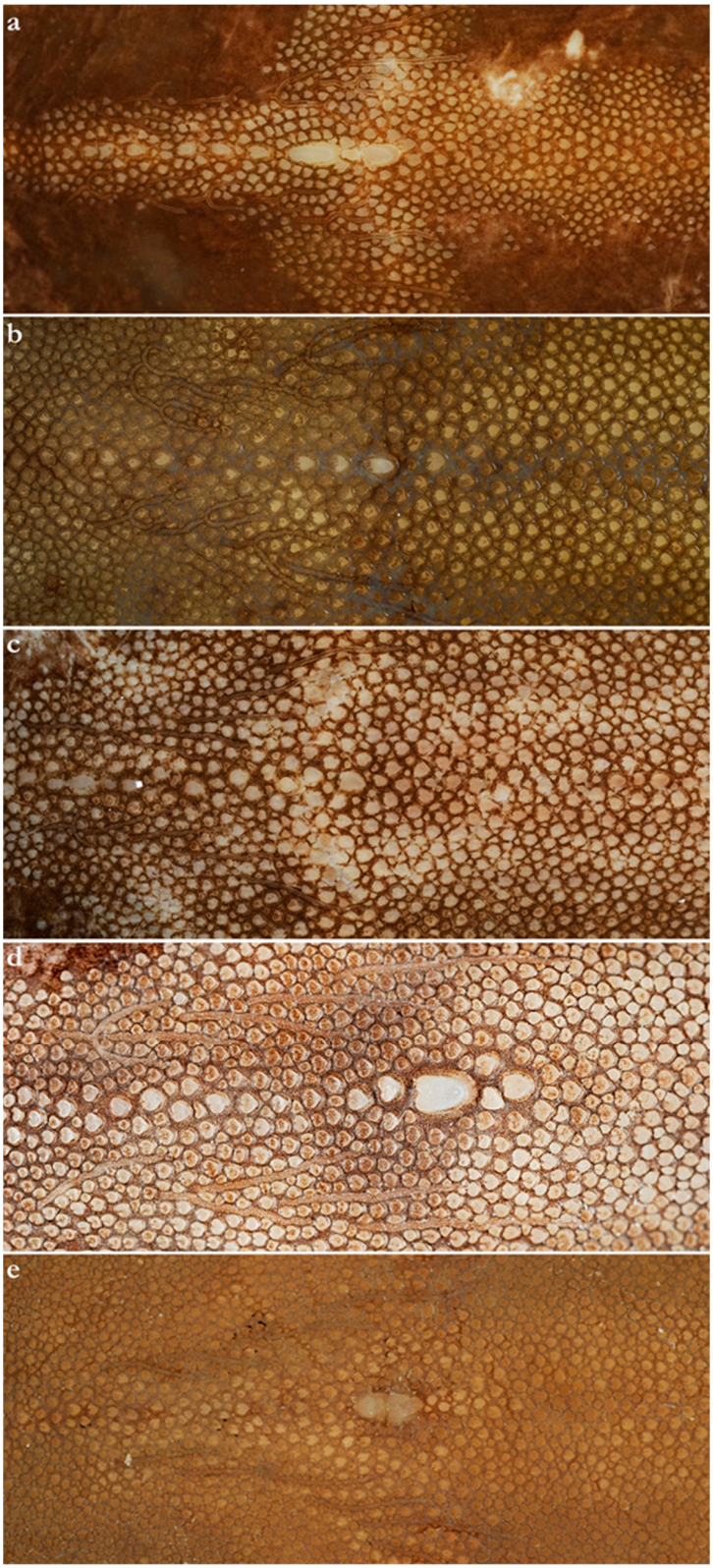

Figure 6. Squamation in the genus *Brevitrygon*—scapular denticles. (**a**) *B. imbricata*, non-type NTM S 13160-009, female 186 mm DW, Sri Lanka (preserved); (**b**) *B. walga*, non-type CSIRO H 8666-01, female 233 mm DW, Myanmar (preserved); (**c**) *B. heterura*, non-type CSIRO H 5584-07, female 200 mm DW, Sabah, Malaysia (preserved); (**d**) *B. javaensis*, holotype MZB 21461, female 164 mm DW, Cilacap, Indonesia (preserved); (**e**) *B. manjajiae* **sp. nov.**, holotype USNM 222555, adult male 231 mm DW, Pakistan (preserved).

The alpha taxonomy of *Brevitrygon* has been confused with four of the species in the type series of a single taxon, *B. walga*. The problem of misidentification has been compounded as specimens of the oldest nominal species are among the syntypes, and a lectotype for the remaining species has never been designated [9]. The current confusion over the identities of the four species has been further exacerbated by errors in the literature, including in two recent guides to rays of the Indo-Pacific region [6,18], where outdated information was inadvertently incorporated into the manuscripts. In Last et al. [6], the correct description of *B. imbricata* was inadvertently swapped with the treatment of *B. walga*; distributional information and the figure for *B. imbricata* now apply to the redefined definition of *B. walga*. *Brevitrygon walga*, by designation of the lectotype, applies to a ray commonly collected by naturalists in the 19th century and confined to the Bay of Bengal (as figured in Last et al. [6], p. 534). *Brevitrygon heterura* is adopted as the correct name of a common western Pacific species, formerly widely misidentified as *Himantura walga* (e.g., [2,19,20]). *Brevitrygon imbricata*, which was once thought to be confined to the western Indian Ocean, is now confirmed to occur off southern India and Sri Lanka and possibly the northwestern Pacific based on material observed herein. A *Brevitrygon* (i.e., *B. manjajiae* sp. nov., also present in the type series of *B. walga*) from the Arabian Sea and further west, remains undescribed. The validity of nominal species, and the undescribed species listed above, has been confirmed through a combination of recent molecular and morphological investigations (see Section 4 below).

3.2. Species Treatments

Last & Compagno [2], without insights from a detailed examination of the types, suggested that records of *Brevitrygon* (as *Himantura*) *walga* in the Indian Ocean might be *B.* (as *H.*) *imbricata*, due to the confusion between these species and the occurrence of the former in the Western Pacific. Hence, resolution of the nomenclature within *Brevitrygon* is initially dependent on the delineation of the two oldest nominal taxa, *B. imbricata* and *B. walga*, based on an examination of the types, as these names have been loosely applied to populations across the entire range of the genus (i.e., Western Indian Ocean to the Eastern Pacific).

As discussed above, types of these taxa revealed that the oldest taxon, *B. imbricata*, exists in the type series of *B. walga*. In addition, as multiple species exist in the type series of *B. walga*, a lectotype needs to be selected, and the selection of this specimen affects the nomenclature of the other three species in the type series. Given the nomenclatural importance of these old nominal taxa, they are treated below sequentially followed by more recent taxa in order of their ages. A brief redescription is provided for each due to the paucity of relevant information in their original treatments and ongoing confused morphological diagnoses. A synonymy is included for each species, which constitutes updates of the synonymies from the unpublished doctoral thesis of Mabel Manjaji-Matsumoto [3]. Descriptions below also incorporate some reassessed morphometric and meristic data from this thesis.

3.2.1. *Brevitrygon imbricata* (Bloch & Schneider, 1801)

[Coromandel Whipray]

(Figures 2–15 and 39; Table 1)

Raja imbricata Bloch & Schneider 1801: 366, 553, Tranquebar [Tharangambadi], Coromandel Coast, India. Holotype (not designated): ZMB 7585 (dry mounted), adult male ~150 mm DW, damaged (original description) [21].

Trygon walga (non Müller & Henle): MNHN 2438, MNHN 2439 (former syntypes of *T. walga*).

Trygon dadong Bleeker 1856: 355, Rio, Bintan Island, Indonesia. Holotype: RMNH.PI SC.7446, female 158 (originally 163) mm DW (original description) [22].

Trygon (Himantura) dadong: Duméril 1865, 591, Bintan, Indonesia (brief description) [23].

Trygon (Himantura) polylepis (non Bleeker): Günther 1870, 475, Ceylon [=Sri Lanka] (brief description based on skin of adult male, determination Manjaji [3]) [24].

Leiobatis (*Himantura*) *dadong*: Boeseman 1983, pl. 557 Figure 1a,b (Plagiostom. Pl. 35 of Bleeker, 1877) (illustration of holotype, new combination) [25].

Dasybatus (Himanturus) imbricatus (non Bloch & Schneider): Garman 1913, 379, East Indies (description, likely misidentification) [26].

Dasyatus (*Amphotistius*) *imbricatus* (non Bloch & Schneider): Fowler 1956, 43, Red Sea and Southern Arabia, brief description (misidentification) [27].

Dasyatis (*Amphotistius*) *imbricata*: Chandy 1957, India, anatomical study (new combination) [28].

Himantura imbricata (non Bloch & Schneider): Compagno & Roberts 1982, 325 (new combination, likely misidentification in part) [13].

Dasyatis imbricata (non Bloch & Schneider): Dor 1984, 17 [29]; Mohsin & Ambak 1996, 75, as *imbricatus* with author as Schneider [30]; Fricke 1999, 30–31, as *imbricatus*) (new combination, misidentification) [31].

Amphotistius imbricatus (non Bloch & Schneider): Rainboth 1996, 52, Cambodia (new combination, likely misidentification) [32].

Brevitrygon imbricata (non Bloch & Schneider): Last et al. 2016, 360 (new combination, misidentification in part) [1].

Brevitrygon sp. 1: Fernando et al. 2019, 207–08, Figures 2B and 6C,D [33].

Holotype. ZMB 7585, adult male ~150 mm DW, Tranquebar [Tharangambadi], Coromandel Coast, India (Figure 7).

Material examined. BPBM 27597(2), female 202 mm DW, adult male 205 mm DW, Kerala fishing harbor, India, 9 February 1980; MNHN 2438 (syntype of *T. walga*), adult male 159 mm DW, Pondicherry, India; MNHN 2439 (2, syntypes of *T. walga*), female 138 mm DW, female 173 mm DW (Figure 8a), Coromandel, India; NTM S13160–009, female 186 mm DW, Chilaw fish market, Sri Lanka, 17 September 1991; RMNH.PISC.7446 (holotype of *Trygon dadong*), female 163 mm DW, Bintan Island, Indonesia; USNM 222564(2), immature male 120 mm DW, female 88 mm DW, Lunawa, Sri Lanka, 6 December 1969; SAM (LJVC collection 517), mature male 185 mm DW, SAM (LJVC collection 518), mature male 174 mm DW, SAM (LJVC collection 519), mature male 166 mm DW, Taiwan, Taiwan Straits, 6 October 1975.

Other material. Global Cestode Database (elasmobranchs.tapewormdb.uconn.edu; Caira et al., 2018), SL5, 30, 35, 36, 37, 48, 49, 73, 74; Tree of Life for Chondrichthyan fishes project: GN14701, TK77, Tuticorin. India; GN14702, K17, Kollam, India; GN14703, K18, Kollam, India; GN14704, D52, Kollam, India; GN14705, D51, Kollam, India; GN 18380, Kollam, India; GN 19689, Trivandrum, India; GN 19704, Thoothukudi, India; GN 21024, Kollam, India; GN 21042, Tuticorin, India; GN 21046, Muttom, India.

Diagnosis. A species of *Brevitrygon* (to at least 22 cm DW) distinguished by the following combination of features: snout length 29–32% DW, angle 105–114°; disc noticeably longer than wide; orbit relatively large, diameter 6–8% DW; nostril length ~4% DW and internasal width 10–12% DW; tail relatively short, robust in both sexes (length 0.8–1.2 times DW); post-sting tail with prominent lateral ridges and prominent dorsal and ventral cutaneous folds (Figure 9); pelvic fins relatively large, length 18–23% DW; postcloacal length of clasper to 20% DW; disc mainly with one enlarged, spear-shaped scapular denticle or thorn, preceded by up to 8 slightly enlarged denticles; secondary denticle band poorly developed in adults, semi-truncate anteriorly and barely extending forward of orbits, expanded laterally to form a cruciate pattern over scapulocoracoid; band very narrow (sometimes broken) over branchial region and abdomen (width narrower than eye length), margins not converging posteriorly; tail of adults with very narrow band of similar size denticles preceding sting, and row of 0–7 enlarged median denticles or small thorns; dorsal disc uniformly pale brownish to yellowish; ventral disc white; tail forward of sting pale brownish dorsally and white ventrally; post-sting tail with dorsal and ventral surfaces, and

associated skin folds, darker brownish, lateral ridges paler; pectoral-fin radials 98–108; total vertebral count (excluding first synarcual centra) 89–97.

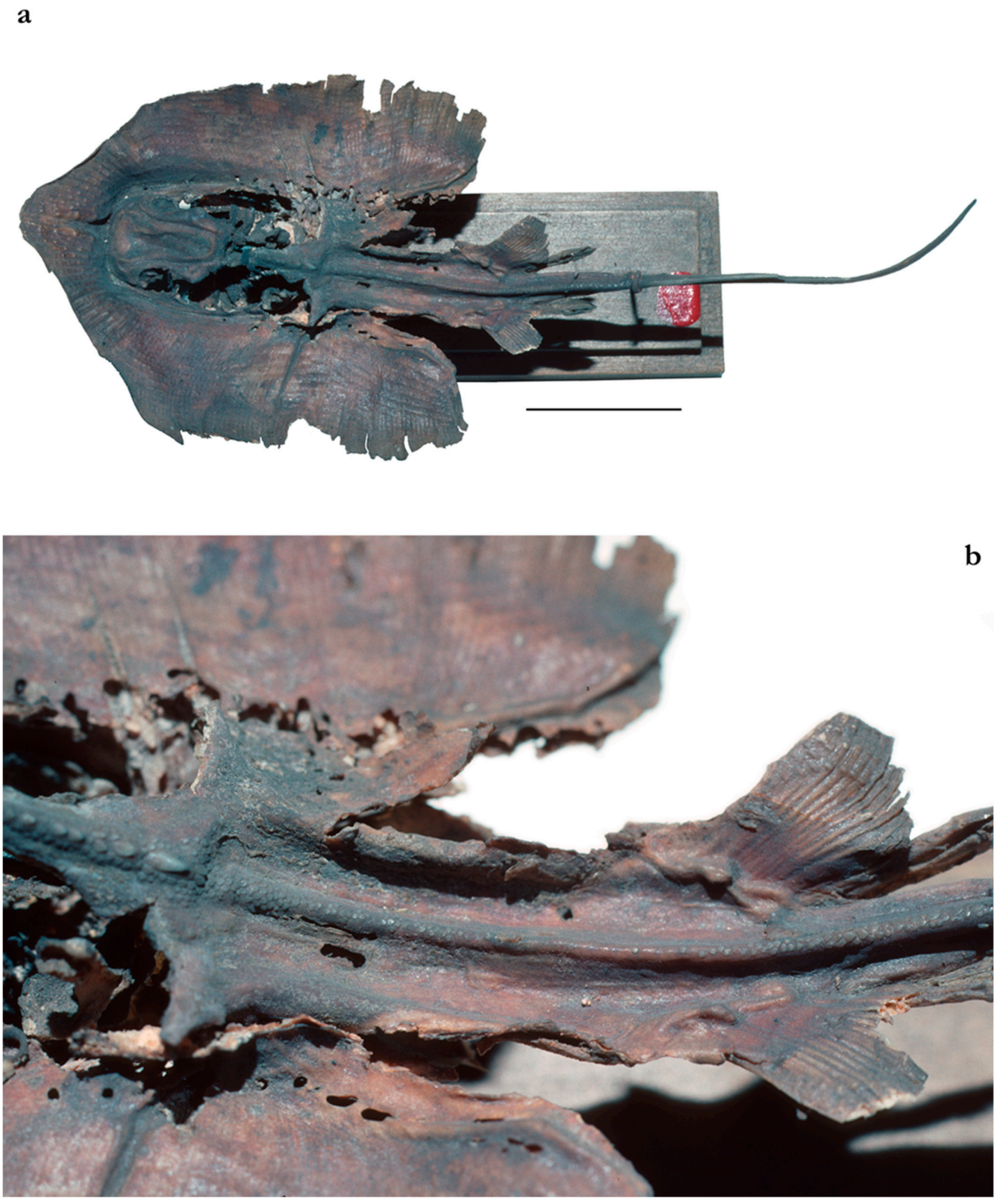

Figure 7. *Raja imbricata* Bloch & Schneider (=*B. imbricata*), holotype ZMB 7585, adult male ~171 mm DW, Tharangambadi, India: (**a**) dorsal surface, dry mounted; (**b**) close up of the typically narrow secondary denticle band on the disc and anterior tail. Scale bar: 5 cm.

Figure 8. Dorsal surfaces of (**a**) *Trygon walga* not Müller & Henle (=*B. imbricata*), syntype MNHN 0000-2439 (1 of 2), female 173 mm DW, Coromandel, India; (**b**) *Trygon dadong* Bleeker (=*B. imbricata*), holotype RMNH.PISC.7446, female 163 mm DW, Bitan Island, Indonesia.

Description. Morphometric data provided in Table 1, based on recent material (adults and adolescents). Disc suboval and pointed anteriorly (Figures 10 and 11), width 0.88–0.94 (n = 11) times disc length (DL); proportion to total length similar in both sexes, 1.87–1.99 times DW in males (1.98 in male holotype ZMB 7585), 1.70–2.08 times DW in females. Snout broader in females (angle forward of preorbit 108–114°, n = 6) than males (angle 105–108°, n = 5); disc width 1.84–2.34 and distance from snout tip to pectoral-fin insertion 1.91–2.33 times distance from snout tip to point of maximum width, respectively. Pelvic-fin length 18.1–22.6% DW; width across base in adult males 15.5–18.2% DW, in

females 17.1–20.3% DW, combined sexes 0.97–1.38 in pelvic-fin length. Clasper postcloacal length 18.4–20% DW in adult males. Tail of adult male slender, semi-rigid beyond sting, relatively short, length 0.94–1.11 times DW, 1.02–1.18 times precloacal length; more robust and often very short in adult female, length 0.77–1.16 times DW, 0.82–1.27 times precloacal length; tapering gradually and evenly from base toward sting, then constricted with very weak taper beyond sting to finely pointed tail tip in males, often expanded slightly and broadly rounded at tip in females; base relatively broad, moderately depressed, its width 1.29–1.96 times its height; slightly less depressed below sting base; distance from cloaca origin to sting 2.56–3.12 in precloacal length, 28–33% DL; dorsal cutaneous fold similar in both sexes, variably developed, with narrow apex, originating as a rudimentary ridge beneath mid or distal portion of sting, becoming taller (<1 mm high) near midlength of post-sting tail, then continuing as low fleshy ridge along distal tail; ventral fold long-based, low with narrow apex, originating as a rudimentary ridge approx. below base of sting, becoming taller (<1.5 mm high) from below sting and along anterior portion of post-sting tail, then continuing as low fleshy ridge to tail tip; lateral ridges prominent, margins broadly rounded. Preoral snout length 2.74–3.25 times mouth width, 2.56–3.22 times internarial distance, 1.23–1.44 times distance between first gill slits; direct preorbital snout length 2.49–2.76, 2.68–3.18 times interorbital length in males and females, respectively; distance from snout tip to maximum disc width 43–52% DW, slightly higher in females; eye small, length 1.20–1.70 in spiracle length; orbit diameter 0.80–1.15 in spiracle length, interorbital distance 1.62–1.96 (1.34 in MNHN 2439, 1) times orbit, intereye distance 2.45–2.66 (1.97 in MNHN 2439, 1) times orbit. Spiracles large, length 5.7–6.7% DW. Nostril length 2.38–3.00 in internasal distance; internasal distance 2.08–2.67 in prenasal length. Nasal curtain width 1.79–2.08 times length. Mouth narrow, width 9.3–10.9% DW, 1.04–1.22 in internasal width. Teeth of adult female (NTM S–13160-009) with much larger cusps in upper jaw than in lower jaw; upper jaw teeth broadly suboval to rhomboidal, in strong quincunx, largely acuspid; more densely packed in lower jaw; teeth rows ~40 in upper jaw, ~60 in lower jaw. Floor or mouth with 2 well-developed, simple, elongate oral papillae (in NTM S–13160-009); situated well apart. Gill opening margins moderately S-shaped, smooth-edged; length of first gill slit 1.06–1.49 times length of fifth, 2.54–3.59 in mouth width; distance between first gill slits 1.95–2.29 times internasal distance, 0.39–0.44 of ventral head length; distance between fifth gill slits 1.18–1.28, 1.34–1.42 times internasal distance length in males and females, respectively, 0.23–0.28 in ventral head length.

Squamation. Ontogenetic stages 0, 2, and 4, evident from type series, stages 1 and 3 likely applicable but not observed, stages 5 and 6 appear to be inapplicable; denticle development rate unknown, no obvious sexual dimorphism; body naked outside secondary denticle band. Secondary denticle band weakly developed in adults (Figure 4), covering most of interorbit, greatly expanded over scapulocoracoid, characteristically constricted over branchial and abdominal regions, narrow on tail, and with sharply defined margins; 0–1 small thorns (length to 6 mm), and 0–7 variably enlarged, median denticles on tail; large scapular denticles or thorns 1–3 (mainly 1) and up to 6 slightly enlarged nuchal denticles; enlarged denticles lanceolate to seed-shaped, length 3–19 mm, longest 1.4–12% DW, their distance from edge of spiracle 18–20% DW. Secondary denticle band barely extending forward of orbits, distance from snout tip 26–33% DW; covering most of interorbit, width 0.7–11% DW; constricted over gills, narrowest width preceding scapular region 0.9–2.9% DW, band discontinuous in female 138 mm DW (MNHN 2439, 1); very broad across scapulocoracoid (forming a cross), width at scapulocoracoid in adults 9–20% DW; band constricted over posterior disc, width across mid-abdomen 2.8–4.6% DW (absent in males and females smaller than 170 mm DW); on midline of tail very narrow, width at pectoral-fin insertion 0.7–2.9% DW (band absent in males and females smaller than 146 mm DW). Caudal sting(s) long, narrow and pungent; usually with 2, undamaged first sting 17–32% DW (n = 6), undamaged second sting 22–35% DW (n = 6); stings often missing or broken in material examined.

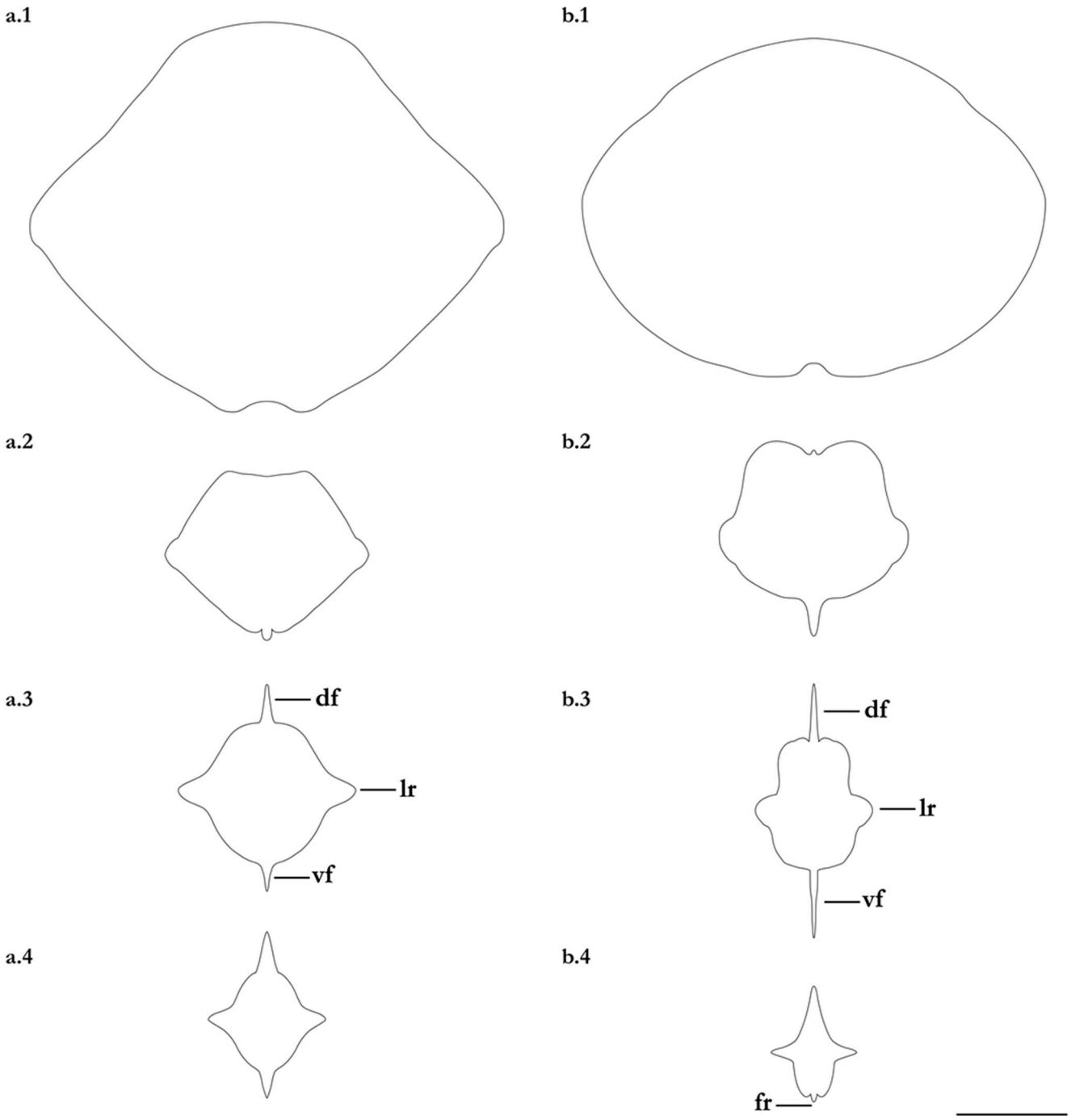

Figure 9. Schematic cross-sections of the post-sting tail of *Brevitrygon imbricata* for (**a**) non-type BPBM 27597, adult male 205 mm DW, Kerala, India; and (**b**) non-type NTM S 13160-009, female 186 mm DW, Sri Lanka. Sections taken at: 1. sting origin; 2. axis 25% from origin; 3. through midlength; and 4. axis 75% from origin. Abbreviations: df = dorsal cutaneous fold, fr = low fleshy ridge, lr = lateral ridge, vf = ventral cutaneous fold. Scale bar: 2 mm.

Table 1. Morphometric data for *Brevitrygon imbricata*: putative syntype of *Trygon walga* Müller & Henle (MNHN 2438), non-types from India and Sri Lanka, and 3 specimens from Taiwan. Measurements expressed as percentages of disc width (mm).

	Pondicherry, India	**Southern India and Sri Lanka**						**Taiwan**	
	MNHN 2438	**All Data (n = 11)**		**Males (n = 5)**		**Females (n = 6)**		**Males (n = 3)**	
		Min	**Max**	**Min**	**Max**	**Min**	**Max**	**Min**	**Max**
Disc, width (mm)	159	138	205	171	205	138	204	162	182
Total length	197.6	169.8	207.9	187.2	198.5	169.8	207.9	191.9	202.0
Disc, length (direct)	106.9	106.1	113.3	107.1	113.1	106.1	113.3	105.7	109.4
Disc, thickness	10.6	7.9	13.3	10.5	12.8	7.9	13.3	12.3	12.9
Snout to origin of cloaca	91.2	89.0	94.7	89.0	94.7	91.2	93.4	88.8	91.9
Cloaca origin to tail tip	106.4	76.6	116.5	94.4	105.4	76.6	116.5	100.9	110.7
Snout to pectoral insertion	98.6	95.0	103.8	95.7	103.8	95.0	103.2	95.4	98.9
Snout to maximum width	48.2	42.9	52.3	42.9	49.2	46.0	52.3	42.7	52.6
End of orbit to pectoral insertion	62.6	58.1	66.1	59.1	65.7	58.1	66.1	61.6	63.6
Snout, preorbital (direct)	30.5	29.0	31.9	29.7	31.1	29.0	31.9	28.1	31.8
Snout, preorbital (horizontal)	29.8	26.1	30.7	27.6	30.7	26.1	30.0	25.0	28.4
Orbit diameter	6.7	5.8	7.5	6.1	6.9	5.8	7.5	7.0	7.6
Eye diameter	4.7	3.8	5.0	3.8	5.0	4.0	4.5	4.2	4.4
Spiracle length	6.2	5.7	6.7	5.9	6.5	5.7	6.7	5.5	6.7
Orbit and spiracle length	10.0	9.7	11.1	10.4	11.1	9.7	10.8	10.1	11.3
Interorbital width	11.6	10.0	12.1	11.0	12.1	10.0	11.5	11.1	11.3
Intereye width	17.3	14.6	17.1	15.7	17.1	14.6	16.6	15.8	17.5
Distance between spiracles	15.5	15.5	16.6	15.5	16.6	15.6	16.4	16.8	17.9
Head length (direct)	57.0	55.2	58.6	56.5	58.6	55.2	57.8	55.7	59.1
Snout, prenasal (direct)	24.2	24.0	26.9	24.0	26.0	24.0	26.9	22.4	26.3
Nostril length	3.9	3.5	4.3	3.7	4.3	3.5	4.3	3.7	4.6
Nasal curtain, length	5.4	4.9	6.6	5.7	6.6	4.9	6.2	6.3	7.0
Nasal curtain, width	11.4	10.2	12.5	11.6	12.5	10.2	11.7	12.2	12.4
Distance between nostrils	11.8	10.1	12.1	10.7	12.1	10.1	10.9	12.3	13.1
Snout, preoral (direct)	30.6	29.8	32.4	29.8	31.7	30.0	32.4	27.3	32.0
Mouth width	9.8	9.3	10.9	9.6	10.9	9.3	10.5	8.4	9.4
Width, 1st gill slit	2.3	2.8	3.7	2.8	3.2	2.9	3.7	3.2	3.7
Width, 3rd gill slit	2.5	3.0	4.0	3.0	4.0	3.2	4.0	3.9	4.2
Width, 5th gill slit	1.7	2.3	2.7	2.3	2.7	2.4	2.7	2.5	2.6
Distance between 1st gill slits	23.2	22.0	24.4	23.1	24.4	22.0	24.3	23.9	24.7
Distance between 5th gill slits	14.9	13.5	15.3	13.6	15.3	13.5	15.3	14.6	15.4
Length pelvic fin	21.1	18.1	22.6	18.3	20.9	18.1	22.6	20.4	21.2
Width across pelvic fin base	14.7	15.5	20.3	15.5	18.2	17.1	20.3	16.4	17.1
Greatest width across pelvic fins	33.6	26.6	42.9	26.6	38.2	35.6	42.9	34.9	38.0
Tail width, axil of pelvics	8.1	7.3	9.8	8.2	9.8	7.3	9.1	7.8	9.7
Tail height, axil of pelvics	5.4	5.0	5.7	5.0	5.6	5.1	5.7	5.9	6.1
Tail width, base of sting	5.2	4.1	5.2	4.2	5.2	4.1	4.9	3.7	5.5
Tail height, base of sting	3.9	3.2	4.2	3.2	3.7	3.2	4.2	3.4	4.2
Cloaca length	5.4	4.8	8.9	4.8	8.9	5.9	7.0	5.5	6.6
Clasper, postcloaca length	-	18.4	20.0	18.4	20.0	0.0	0.0	17.6	19.5
Clasper, length from pelvic axil	-	7.9	10.1	7.9	10.1	0.0	0.0	8.6	9.8
Pect. insertion to sting origin	26.3	25.4	29.5	25.4	28.7	25.9	29.5	22.9	26.0
Cloaca origin to sting	28.8	29.2	36.1	29.6	36.1	29.2	35.7	29.1	32.4
Caudal sting 1 length	-	17.4	31.9	17.4	25.8	21.0	31.9	21.2	22.0
Caudal sting 2 length	-	22.9	34.5	24.6	30.4	22.9	34.5	31.7	32.7

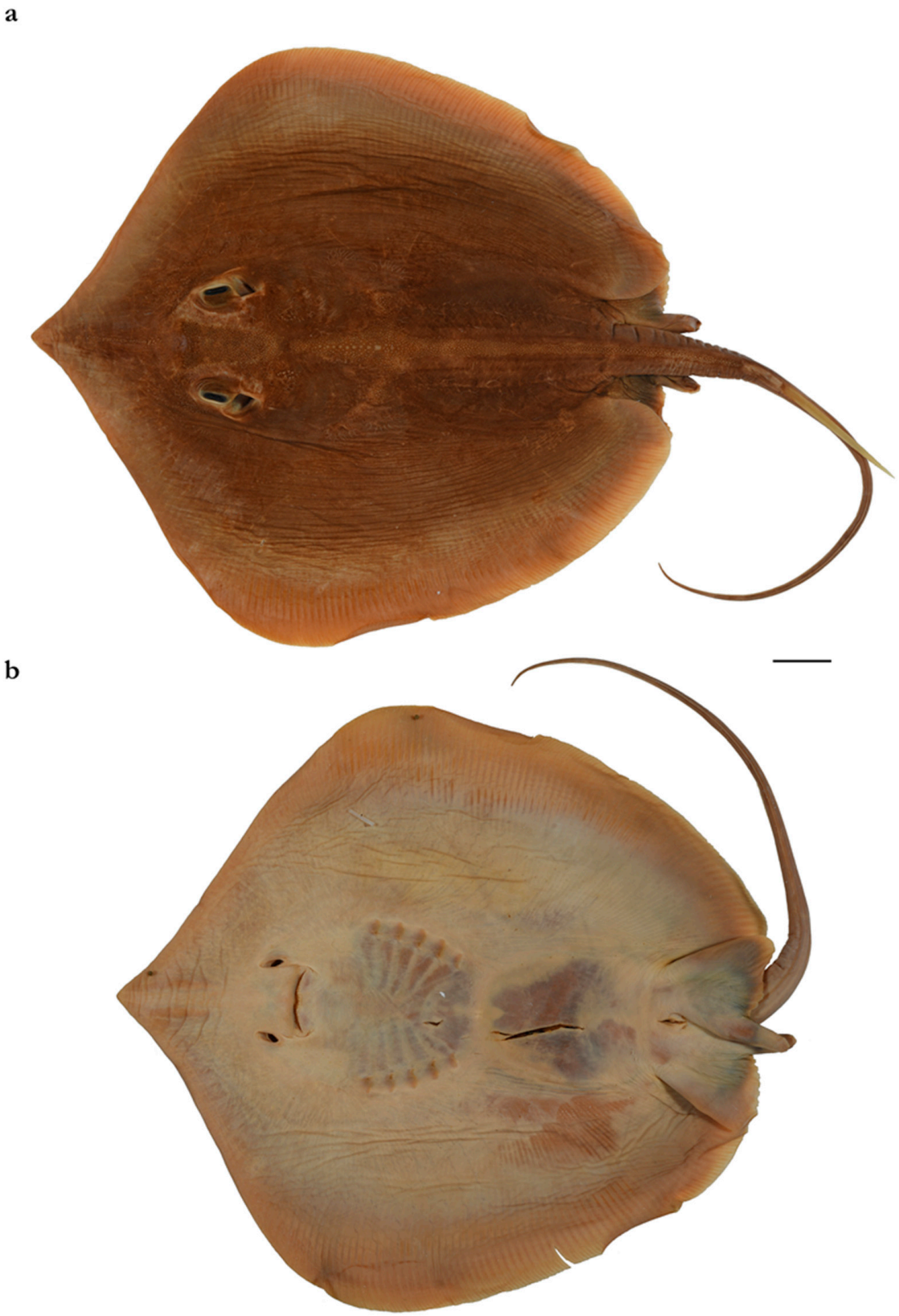

Figure 10. *Brevitrygon imbricata*, non-type BPBM 27597 (2 of 2), adult male 205 mm DW, Kerala, India (preserved): (**a**) dorsal surface; (**b**) ventral surface. Scale bar: 2 cm.

Figure 11. *Brevitrygon imbricata*, non-type BPBM 27597 (1 of 2), female 202 mm DW, Kerala, India (preserved): (**a**) dorsal surface; (**b**) ventral surface. Scale bar: 2 cm.

Juveniles. Two specimens, immature male (121 mm DW) and a smaller female (88 mm DW, Figure 12a) differ from adults in having a shorter (direct preorbital snout length 27.8–28.7% DW), less angular snout and less concave snout margin; small primary

denticle forming in scapular region of male but absent in smaller female; no secondary denticle band formed at this stage; dorsal surface pale yellowish, uniformly white ventrally. As in adults, the disc is slightly longer than wide (1.01–1.03 times longer) and the tail is short relative to the disc size (total length 1.95–1.98 times DW) compared to other *Brevitrygon* species.

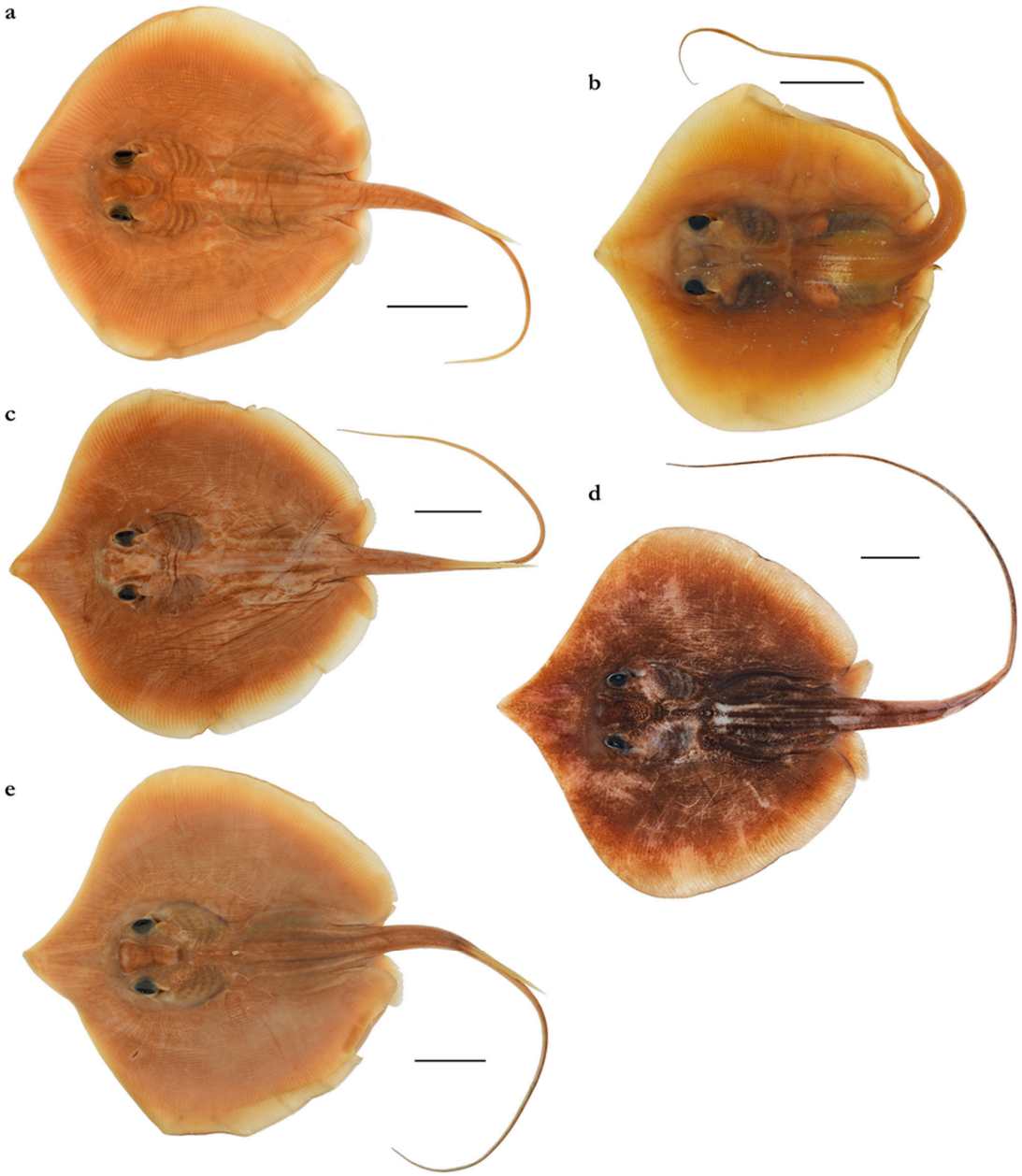

Figure 12. Dorsal disc and tail of early juveniles of (**a**) *B. imbricata* (USNM 222564, juvenile female 88 mm DW, Sri Lanka); (**b**) *B. walga* (CSIRO H 8666-02, late embryo male 82 mm DW, Myanmar); (**c**) *B. heterura* (BPBM 26574, juvenile female 104 mm DW, Indonesia); (**d**) *B. javaensis* (AMS I 46280-001, juvenile male 120 mm DW, Indonesia); (**e**) *B. manjajiae* **sp. nov.** (BPBM 33199 (1 of 2), juvenile male 103 mm DW, Kuwait). Scale bars: 2 cm.

Meristics. Total pectoral-fin radials 98–108, n = 5 for all radial counts; propterygials 44–48, mesopterygials 11–17, and metapterygials 41–49. Total pelvic-fin radials 23–25 in females; 16–18 plus clasper in males. Total vertebral segments (excluding first synarcual centra) 89–97, n = 5 for all vertebral counts; monospondylous centra (excluding first synarcuals) 32–39; diplospondylous centra 53–58.

Coloration. *When fresh:* dorsal surface of disc and pelvic fins uniformly brownish or yellowish (Figure 10); outer margin of disc slightly paler; main denticle band slightly paler brown and well defined from disc; eye blackish, darker than rest of orbit. Ventral surface uniformly white or with broad, well-defined, dusky band along outer margins of pectoral and pelvic fins. Tail including cutaneous folds like disc coloration dorsally; ventrally, whitish anteriorly and becoming greyish posteriorly; sides whitish and contrasted with darker areas of tail above and below. *In preservative*: similar to above, sometimes more greyish brown dorsally, paler near disc margin; ventral surface whitish with some dark areas.

Size. Adult males examined ranged from 171 mm DW (320 mm TL) to 205 mm DW (398 mm TL); females 138 mm DW (256 mm TL) to 204 mm DW (396 mm TL). Mature male holotype dry mounted, fragile, and possibly shrunken; ~310 mm total length, width difficult to determine given serious damage to disc margins but probably ~150 mm DW. Early juveniles (USNM 222564, immature male 120 mm DW, female 88 mm DW) have lost umbilical scars. Maximum disc width of 300 mm [10] is excessive.

Distribution. Historical information has been confused by misidentifications across the Indo-West Pacific. Material examined herein confirms the distribution of *B. imbricata* from the eastern Arabian Sea (Kerala, off eastern India), the Laccadive Sea (Chilaw, Jaffna, Lunawa, Negombo, Talaimannar, Sri Lanka), and into the southern Bay of Bengal (Coromandel coast, eastern India) (Figure 13). The northern most confirmed record off western India based on specimen data was Kollam (Kerala); the most northerly record off eastern India was Puducherry (Tamil Nadu). Haroon & Kibria [34] report *B. imbricata* from Myanmar, which is likely to be correct based on their description of the tail folds. The holotype of *Trygon dadong* Bleeker (RMNH.PISC.7446, Figures 8b and 14c) from Bintan Island (northwestern Indonesia, off Singapore) shares the morphometry and unique squamation of *B. imbricata*, suggesting this species may occur more widely. Three specimens (see Figure 15) collected by Leonard Compagno (LJVC 517–19), reported from Taiwan, also support the possible occurrence of this species in the western North Pacific. However, major regional fishing ports, such as those of Taiwan, source fishes from across Asia so the origin of these specimens cannot be confirmed. Despite this observation, Taiwanese fishing ports are routinely visited by local ichthyologists, and no rays of the genus *Brevitrygon* have reappeared in their collections (Hans Ho, pers. comm.).

Molecular data from Barcode of Life Data Systems (BOLD, unpublished data) indicates the presence of *B. imbricata* off Maharashtra, northwestern India (MUMDL–02). Also, tissues made available for the Tree of Life project from southern Indian stingrays identified as *B.* sp. B from Kollam and Trivandrum (Kerala), and specimens from Muttom, Thoothukudi and Tuticorin (Tamil Nadu), are confirmed to be this species.

Depth distribution not well documented but primarily in shallow water from near the shore to at least 45 m depth.

Etymology. Derived from *imbricata* (Latin), meaning overlapping each other, in allusion to the secondary denticle band, which is very narrow over the branchial region and abdomen in this species. The original description indicates "*serie unica squamarum ossearum imbricatarum in medio dorsi*": "a single series of overlapping [imbricatarum] bony scales on the midback". The original description ends with "Schn.", which apparently means that Schneider wrote this part, as also indicated by Karrer et al. [35]. Following Karrer et al. [35], it is generally difficult to determine if Schneider wrote the whole description so that authorship would be Schneider in Bloch and Schneider, 1801, or if Schneider just added part of it. Given this uncertainty, the authorship for *Trygon imbricata* is retained as Bloch & Schneider, 1801.

Vernacular name: Coromandel Whipray (newly proposed). Also referred to as the Bengal Whipray (i.e., *B. walga*), for which it has been confused with its close relative occurring off eastern India.

Remarks. *Raja imbricata* was described by Bloch & Schneider [21], based on a formally undesignated, single adult male specimen presumably collected at Tharangambadi

(formerly Tranquebar) in the Indian state of Tamil Nadu on the Coromandel Coast [3]. A dry-mounted, adult male ZMB 7585 specimen with 'Coromandel' written on its base board was assumed to be the type [9]. Earlier, Karrer et al. [35] noted that the species was described without any type specimen being designated albeit indicating that the description referred to a male specimen slightly exceeding 1 foot long (~305 mm) from Coromandel, India. This specimen, which has suffered significant damage probably from insect attack (Figure 7), has been examined on several occasions by one of us (PL); the disc width was estimated to be ~125 mm and the length closer to 250 mm than 300 mm. Hence, while some uncertainties exist, ZMB 7585 fits Bloch and Schneider's description of *Raja imbricata* in having a short tail and the presence of obvious dorsal and ventral fins (folds), which is a unique combination within the genus *Brevitrygon*. *Brevitrygon imbricata* has low elongate folds on both the dorsal and ventral surfaces that are evident without magnification; in other species these folds are rudimentary or absent. The absence of cutaneous folds on the tail was once considered a diagnostic feature of the genus *Himantura*; in addition to *Brevitrygon*, the group also included the currently recognized genera *Fluvitrygon*, *Maculabatis*, and *Pateobatis*. The pattern of squamation in *B. imbricata* is unique within the genus, and, despite damage to the proposed type, the comparatively poorly developed, secondary denticle band typical of new material collected near the type locality is also evident in ZMB 7585 (see Figure 7b). Hence, we support the formal assignment of Bloch and Schneider's specimen by colleagues to the status of holotype.

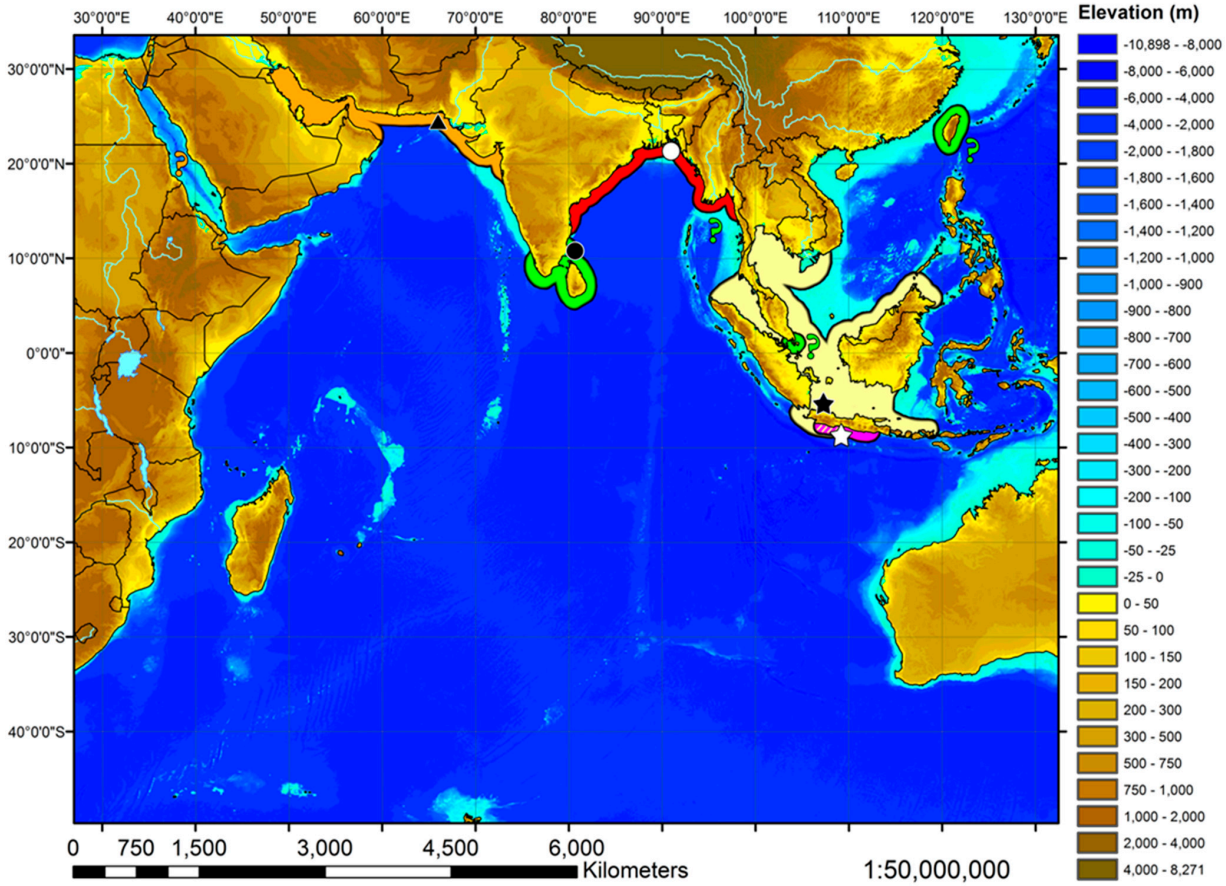

Figure 13. Map of the Indo-West Pacific showing the localities of the primary types (symbols) and confirmed ranges (polygons) of *Brevitrygon imbricata* (black circle, green polygons; occurrences off Myanmar, Singapore, and Taiwan questionable, indicated by green question marks), *B. walga* (white circle, red polygon), *B. heterura* (black star, yellow polygon), *B. javaensis* (white star, pink polygon; yellow stripes indicate overlapping range with *B. heterura*), and *B. manjajiae* **sp. nov.** (black triangle, orange polygon; occurrence in the Red Sea questionable, indicated by orange question mark).

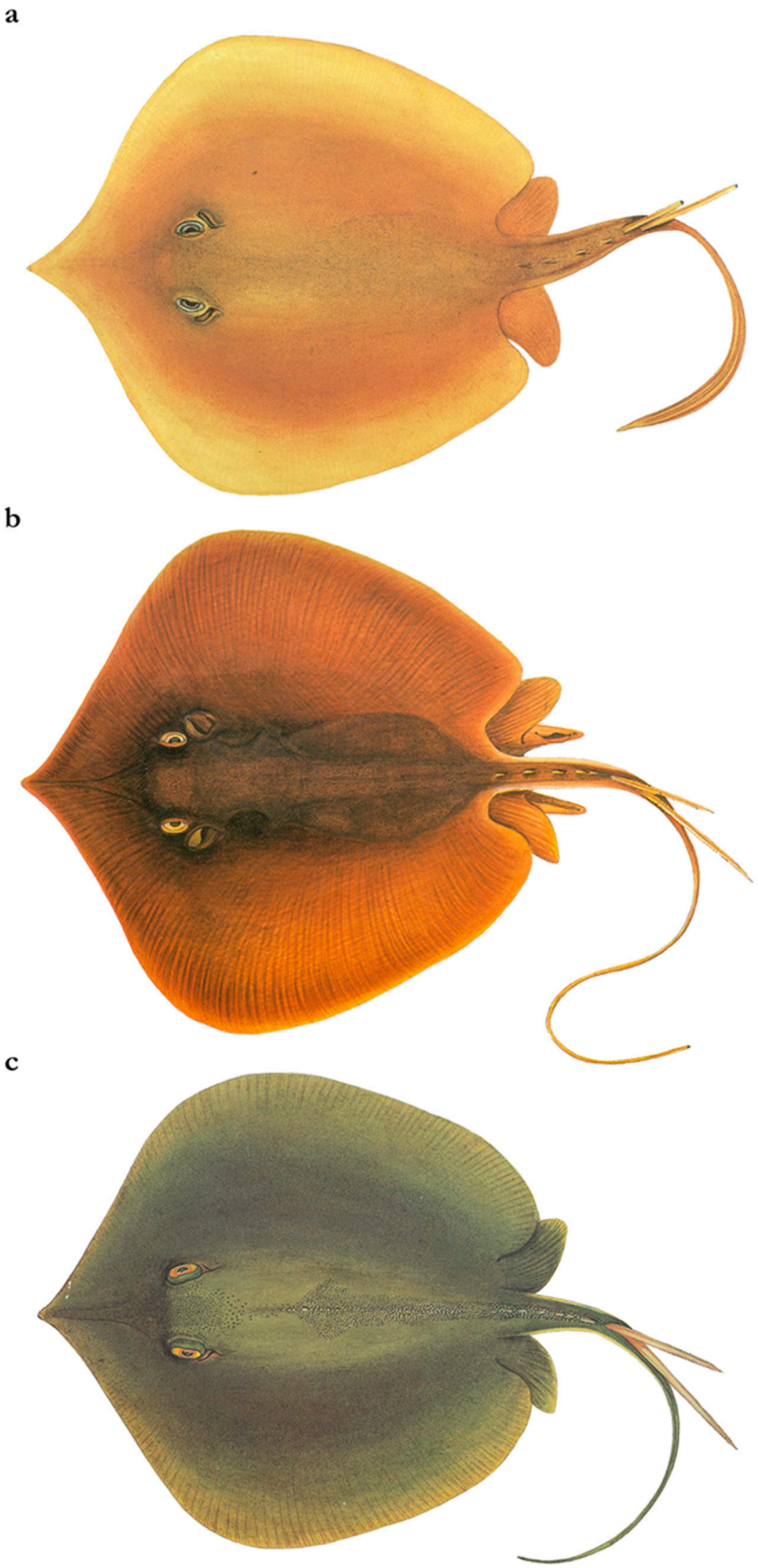

Figure 14. Illustrations of *Brevitrygon* from Bleeker's (1874) ichthyological atlas: (**a**) *Leiobatis* (*Himantura*) *heterurus* (=*B. heterura*, female, Pl. 35, 1a,b); (**b**) *Leiobatis* (*Himantura*) *walga* (=*B. heterura*, male, Pl. 41, 1a,b); (**c**) *Leiobatis* (*Himantura*) *dadong* (=*B. imbricata*, Pl. 36, 1a).

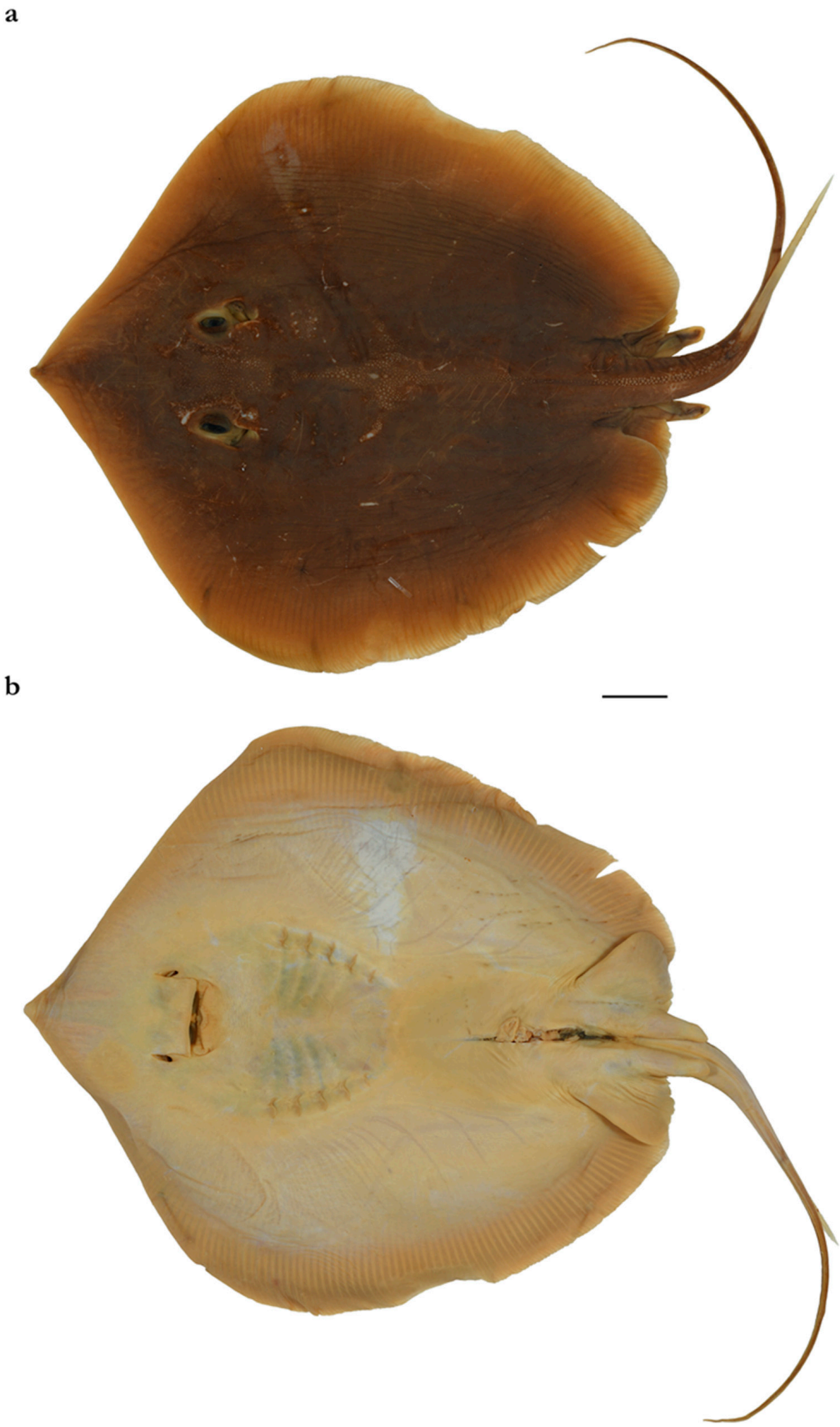

Figure 15. *Brevitrygon* cf. *imbricata*, non-type SAM—LJVC 517, adult male 185 mm DW, Taiwan: (**a**) dorsal surface, fresh; (**b**) ventral surface, preserved. Scale bar: 2 cm.

3.2.2. *Brevitrygon walga* (Müller & Henle, 1841)

[Bengal whipray]

(Figures 2–6, 12, 13, 16–22, and 39; Table 2)

Trygon walga (Müller & Henle, 1841 [36]): MNHN 2431 (lectotype, 1 of 10 syntypes), female 170 mm DW, Bay of Bengal (Ganges Delta), India (new type designation).

Trygon walga (non Müller & Henle): MNHN 2439 (2 former syntypes), female 138 mm DW, female 171 mm DW, Coromandel, India; MNHN 2438 (former syntype), adult male 155 mm DW, Pondicherry, India (misidentifications of *Brevitrygon imbricata* based on newly designated lectotype).

Trygon walga (non Müller & Henle): RMNH.PISC.2453 (former syntype), female 167 mm DW, Java, Indonesia; RMNH.PISC.2454? (former syntype), adult male 164 mm DW, Java, Indonesia; RMNH.PISC.2455 (former syntype), adult male 156 mm DW, Java, Indonesia (misidentifications of *Brevitrygon heterura* based on newly designated lectotype).

Trygon walga (non Müller & Henle): MNHN 2337 (former syntype), mature male 198 mm DW, Red Sea, western Indian Ocean (likely misidentification of *Brevitrygon manjajiae* sp. nov. based on newly designated lectotype).

Trygon walga (non Müller & Henle): Bleeker 1852, 67 (description). Localities: Batavia (=Java), Samarang (=Semarang), Indonesia (likely misidentification) [37].

Trygon (Himantura) walga (non Müller & Henle): Günther 1870, 475 (brief description). Locality: East Indies (likely misidentification of *B. heterura*) [24].

Leiobatis (*Himantura*) *walga*: Boeseman 1983, pl. 563 Figure 1a,b (Plagiostom. Pl. 41) (illustration of male syntype of *B. heterura*) [25].

Himantura imbricata (Bloch & Schneider): Séret & McEachran 1987, 20 (misidentification) [38].

Dasyatis walga (Müller & Henle, 1841): Krishnan & Mishra 1993, 211 (new combination) [39].

Himantura walga (non Müller & Henle): Last & Compagno 1999, 1492 (new combination, misidentification in part) [2].

Brevitrygon walga (Müller & Henle 1841): Last et al. 2016, 360 (new combination, misidentification in part) [1].

Brevitrygon imbricata (Bloch & Schneider): Golzarianpour et al. 2020, 332, Figure 1 (misidentification) [1].

We herein designate syntype MNHN 2431 (1 of 10 syntypes), female 170 mm DW, Bay of Bengal (Ganges Delta), India, housed in the collection of the Muséum National d'Histoire naturelle, Paris, France, as the lectotype of *Brevitrygon walga* (Müller & Henle, 1841) (Figure 16). The other nine putative syntypes represent 4 species of the genus *Brevitrygon*, including the questionable syntype BMHN 1889.2.1.4196, and as such are not designated as paralectotypes of *B. walga* (Müller & Henle, 1841). The providences of each of these specimens are discussed in the 'Remarks' section below.

Lectotype. MNHN 2431 (1 of 10 syntypes), female 170 mm DW, Bay of Bengal (Ganges Delta), India (new type designation) (Figure 16).

Material examined. BMNH 1852.8.30.16, female ~154 mm DW, Bay of Bengal (presumably off India); BMNH 1889.2.1.4196, female 223 mm DW, Madras, India (possible syntype, Fricke et al., 2023) (Figure 17); CAS 141045, immature male 141 mm DW, Dabia Is, mouth of Ganges River, Bay of Bengal, India; CSIRO H 8668-01 (GN17062), juvenile male 168 mm DW, W of Nabule, Myanmar, Andaman Sea, 14°17.04′ N, 97°33.95′ E, collected by Peter Psomadakis (as UNREG 116), 20 May 2015; CSIRO H 8666-01, female 233 mm DW, W of Nabule, Myanmar, Andaman Sea, collected by Peter Psomadakis (as UNREG 17), 3 May 2015; CSIRO H 8666-02, neonatal male 82 mm DW, female 79 mm DW, same locality as above, collected by Peter Psomadakis, 3 May 2015; CSIRO H 8667-01, mature male 193 mm DW, S of Thitpon Manuang, Myanmar, Andaman Sea, 18°14.25′N, 93°37.68′E, collected by Peter Psomadakis (as UNREG 18), 3 May 2015; CSIRO H 8669-01, female 197 mm DW with female embryo 47 mm DW, E of Bok Ye-gan (Moscos Is.), Myanmar, Andaman Sea, 14°17.04′ N, 97°33.95′ E, collected by Peter Psomadakis (as UNREG 115), 6 May 2015;

MTUF 29999, female 184 mm DW, Diamond Harbour, Hooghly River, India. Global Cestode Database (elasmobranchs.tapewormdb.uconn.edu; Caira et al., 2018): GN13957 (IN-11), female 180 mm DW, GN13963 (IN-17), male 170 mm DW, GN13970 (IN-24), male 203 mm DW, GN13972 (IN-26), female 170 mm DW, GN14009 (IN-63), female 190 mm DW, Digha, India, 21°37′49.4 N, 87°32′38.9 E; GN13957, IN_11, Digha, India; GN13961, IN_15, Digha, India; GN13962, IN_16, Digha, India; GN13964, IN_18, Talasari, India; GN13971, IN_25, Digha, India; GN17061, Myanmar; GN21954, Myanmar; GN21960, Myanmar; GN21961, Myanmar; GN22008, Myanmar; GN22011, Myanmar.

Figure 16. *Trygon walga* Müller & Henle, lectotype MNHN 0000-2431, female 170 mm DW, Ganges Delta, India, preserved: (**a**) dorsal surface, (**b**) ventral surface.

Figure 17. *Trygon walga* Müller & Henle, putative syntype BMNH 1889.2.1.4196, female 223 mm DW, Chennai, India, preserved: dorsal surface.

Diagnosis. A species of *Brevitrygon* (to at least 23 cm DW) distinguished by the following combination of features: snout length 31–34% DW, angle 103–108°; disc longer than wide; orbit small, diameter 5–6% DW; nostril length 4–5% DW and internasal width 11–12% DW; tail long, filamentous in males (length 1.6–1.8 times DW), not bulbous but thickened slightly beyond sting in adult females (length 1.2–1.6 times DW); post-sting tail with well-developed lateral ridges in females, a very shallow medial dorsal furrow without a fold, and a low rudimentary ventral fold present or absent (Figure 18); pelvic fin length 18–22% DW; short claspers, postcloacal length to 17% DW; 0–1 slightly enlarged, spear-shaped scapular denticles, no other enlarged denticles or thorns on disc; secondary denticle band very well formed in adults, subtriangular anteriorly and often extending well forward of orbits on snout, margins indented slightly over branchial region (narrower than interorbital width), very broad over abdomen, then margins converging abruptly before pectoral-fin insertions; tail with narrow band of small denticles and usually 5–6 enlarged denticles and scute-like thorns in adults preceding sting; dorsal disc brownish; ventral disc white; tail forward of sting brownish dorsally and white ventrally; in adult females, lateral fleshy ridges of distal tail whitish, and strongly contrasted with darker brownish dorsal and ventral surfaces; in males, posterior tail more uniformly dusky; pectoral-fin radials 101–106; total vertebral count (excluding first synarcual centra) 87–97.

Description. Based on recent material, and images and measurements of lectotype, with values for non-type specimens in parentheses (including adults and adolescents, see Table 2): Disc suboval and pointed anteriorly (Figures 19 and 20), width 0.90 times length in female lectotype (0.90–0.99 in other material); maximum thickness 11% (8–11%) of DW. Snout angle 106° (103–108°); disc width 1.92 (2.07–2.26) and distance from snout tip to pectoral-fin insertion 1.94 (1.99–2.18) times distance from snout tip to point of maximum width, respectively. Pelvic fins moderately elongate, length 21.7% (17.9–21.9%) DW; width across base 17.6% (16.3% in adult male, 15.4–17.4% DW in adult females), 1.23 (1.28 in adult

males, 1.02–1.16 in adult females) in pelvic-fin length. Mature clasper relatively short, stout basally, tapering distally, depressed slightly, its postcloacal length 16.8% DW in adult males. Tail of both sexes slender, semi-rigid, moderately elongate, weakly sexually dimorphic; in females length 1.37 (1.18–1.25, 1.60 in CSIRO H 8669-01) times DW, 1.46 (1.26–1.33, 1.61) times precloacal length, tapering gradually and evenly toward sting then semi-rigid, barely tapering, thickened slightly before its tip with smooth dorsal and ventral surfaces and lateral edge weakly convex; tail of males similar anteriorly to sting but more elongate, very weakly tapered and flexible distally, length 1.37–1.81 times DW, 1.44–2.03 times precloacal length, tail tip finely pointed; tail base relatively broad, moderately depressed, its width 1.43 (1.42–1.67, 1.01 in MTUF 29999 from the Hooghly River) times its height; slightly less depressed below sting base; sting positioned well forward on tail, distance from cloaca origin to sting 2.61 (2.43–2.85) in precloacal length, 32% (30–35%, 39% in MTUF 29999) of DL; dorsal groove housing caudal sting(s) tapering gradually and persistent less than snout length behind sting base. Preoral snout length 3.20–3.59 (3.08 in MTUF 29999) times mouth width, 2.60–2.89 (highest in females) times internarial distance, 1.35–1.51 times distance between first gill slits; direct preorbital snout length 2.95 (2.21–2.80) times interorbital length; distance from snout tip to maximum disc width 52% (44–49%) DW; eye length 1.70 (1.50–1.79) in spiracle length; orbit diameter 1.18 (0.96–1.15) in spiracle length, interorbital distance 1.89 (1.97–2.46) times orbit, intereye distance 2.73 (2.67–2.98) times eye length. Spiracle length 7.2% (5.5–6.5%) DW. Nostril length 2.35–2.90 in internasal distance; internasal distance 2.13–2.39 in prenasal length. Nasal curtain rectangular, width 1.79–1.93 times length. Mouth width 9.3–11.0% DW, 1.11–1.26 in internasal width; profile moderately arched, not obviously more so in males than females; upper jaw strongly double concave, dorsal to lower jaw; lower jaw notched near symphysis, largely concealing and slotting into symphysial knob of upper jaw; oronasal groove prominent, deep; skin along margin of lower jaw weakly papillose along its margin, otherwise smooth. Teeth of adult male (CSIRO H 8667-01) slightly larger in upper jaw than in lower jaw, those near symphysis of upper jaw noticeably so; upper jaw teeth broadly suboval, largest near symphysis and on lateral knobs, more strongly cuspid near jaw angle, cusps blunt near symphysis; lower jaw teeth in strong quincunx, suboval with long cusps, those at symphysis visible when mouth closed. In large adult female (CSIRO H 8666-01) teeth more broadly oval, in stronger quincunx, largely acuspid, slightly larger in upper jaw than in lower jaw. Tooth rows (in CSIRO H 8667-01 and H 8666-01) in ~45 in upper jaw, 55–58 in lower jaw. Floor or mouth with 2 well-developed, simple, widely spaced oral papillae (in CSIRO H 8667-01 and CSIRO H 8666-01), apices of papillae more truncate distally in female. Length of first gill slit 1.89 (1.06–1.49) times length of fifth, 2.87–3.85 in mouth width; distance between first gill slits 1.93–2.04 times internasal distance, 0.42 (0.38–0.42) of ventral head length; distance between fifth gill slits 1.08–1.33 times internasal distance, 0.24 (0.23–0.27) in ventral head length.

Table 2. Morphometric data for *Brevitrygon walga*: newly designated lectotype (MNHN 2431), putative syntype of *Trygon walga* Müller & Henle (BMNH 1889.2.1.4196), and other material from the Bay of Bengal. Measurements expressed as a percentage of disc width (mm).

	MNHN 2431	**BMNH 1889.2.1.4196**	**Other Material (n = 6)**	
	Lectotype	**Syntype *T. walga*?**	**Bay of Bengal**	
	Female	**Female**	**Min**	**Max**
Disc, width (mm)	170	223	141	233
Total length	231.2	215.8	211.4	270.8
Disc, length (direct)	111.5	106.0	100.6	111.7
Disc, thickness	8.9	11.2	9.4	13.3
Snout to origin of cloaca	94.2	90.5	89.5	99.7
Cloaca origin to tail tip	137.1	125.3	118.1	181.3
Snout to pectoral insertion	101.0	97.2	95.1	103.1
Snout to maximum width	52.0	45.9	44.2	48.8

Table 2. *Cont.*

	MNHN 2431	BMNH 1889.2.1.4196	Other Material (n = 6)	
	Lectotype	Syntype *T. walga*?	Bay of Bengal	
	Female	Female	Min	Max
End of orbit to pectoral insertion	62.1	61.1	56.3	108.4
Snout, preorbital (direct)	33.7	31.1	31.0	33.5
Snout, preorbital (horizontal)	33.2	27.3	30.3	32.9
Orbit diameter	6.1	5.3	5.3	5.9
Eye diameter	4.2	3.5	3.5	3.9
Spiracle length	7.2	6.4	5.5	6.5
Orbit and spiracle length	10.9	9.8	9.2	10.4
Interorbital width	11.4	12.6	11.4	14.0
Intereye width	16.5	15.5	15.6	16.4
Distance between spiracles	16.6	16.9	15.8	17.7
Head length (direct)	61.0	57.2	57.1	59.2
Snout, prenasal (direct)	30.2	25.8	26.0	28.6
Nostril length	3.9	3.7	4.1	5.1
Nasal curtain, length	6.6	5.3	5.8	7.5
Nasal curtain, width	-	11.1	11.7	13.1
Distance between nostrils	-	11.1	11.4	12.3
Snout, preoral (direct)	-	31.4	31.9	34.5
Mouth width	-	9.4	9.3	11.0
Width, 1st gill slit	2.5	3.3	2.5	3.2
Width, 3rd gill slit	2.4	3.5	2.4	3.3
Width, 5th gill slit	1.3	2.5	2.0	2.6
Distance between 1st gill slits	25.4	24.9	22.4	24.4
Distance between 5th gill slits	14.5	15.6	13.0	15.9
Length pelvic fin	21.7	20.3	17.9	21.9
Width across pelvic fin base	17.6	17.0	14.4	21.5
Greatest width across pelvic fins	39.1	13.2	32.3	40.8
Tail width, axil of pelvics	10.0	8.6	6.1	10.4
Tail height, axil of pelvics	7.0	5.9	5.6	7.2
Tail width, base of sting	5.3	4.1	4.2	6.1
Tail height, base of sting	3.9	3.2	3.4	4.0
Cloaca length	5.1	6.0	4.8	7.7
Clasper, postcloaca length	-	-	12.1	16.8
Clasper, length from pelvic axil	-	-	4.3	8.0
Pect. insertion to sting origin	31.9	34.6	25.2	35.2
Cloaca origin to sting	36.1	37.6	32.9	39.1
Caudal sting 1 length	-	-	21.0	28.0
Caudal sting 2 length	-	8.2	16.0	37.9

Squamation. Ontogenetic stages (definitions following Manjaji [3] and Last et al. [12]) 0, 4 evident; stages 2, 3 unavailable, stages 5, 6 appear to be inapplicable; denticle development likely to be rapid, no obvious sexual dimorphism. Developmental *Stage 0*: neonatal female 79 mm DW, male 82 mm DW entirely smooth. *Stages 2* and *3*: no specimens available, presumably short and occurring ~80–140 mm DW. *Stage 4* (>141 mm DW): secondary denticle band very well developed (Figure 4); scapular denticles absent or with one enlarged (length 2.1–3.7 mm, width 1.1–1.5 mm), distance from edge of spiracle 18.1–19.3% DW, occasionally with up to 4 slightly enlarged denticles preceding main denticle; band margins well defined and regular; extending forward of orbit, distance of denticle band from snout tip 29% DW (12–29% DW); covering almost entire interorbital space in adults, width of band across interorbit 10.6% (10.3–12.4%) DW; barely constricted over branchial region, band subequal to width at interorbit, narrowest width of band preceding scapular region 10.2 (10.4–17.1)% DW; band broad at scapulocoracoid, width 26.0% (21.8–28.6)% DW; similar over abdomen, width of band 27.0% (21.6–28.8)% DW; width of band at pectoral-fin insertion 5.6% (4.9–6.7)% DW; band narrow on tail with sharply

defined margins, ~14–16 denticles wide on mid pre-sting tail in adult male, covering about 1/2 width of tail in dorsal view, almost 90% in MTUF 29999). Tail with 6 (5–6) weakly oblique lanceolate thorns, sometimes preceded by a few other enlarged denticles; thorns similar in size or becoming slightly larger distally, evenly spaced on tail in lectotype; length of first thorn of series 3.4–5.5 mm, 1.86–2.93% DW; length of last thorn 6.3–8.0 mm, 3.17–5.70% DW; tail thorns of smallest specimen (CAS 141045, 141 mm DW) proportionately larger (e.g., last thorn width 1.8% vs. 0.8–1.1% DW; last thorn length 5.7% vs. 3.2–3.9% DW) than largest juveniles and adults (i.e., 168–233 mm DW), indicating that tail thorns may not increase much in size with growth. Caudal stings 2 (1–2), well developed, narrowly elongate, pungent; second usually longer than first (both broken in lectotype), reaching 40% DW, undamaged stings subequal to exceeding snout length.

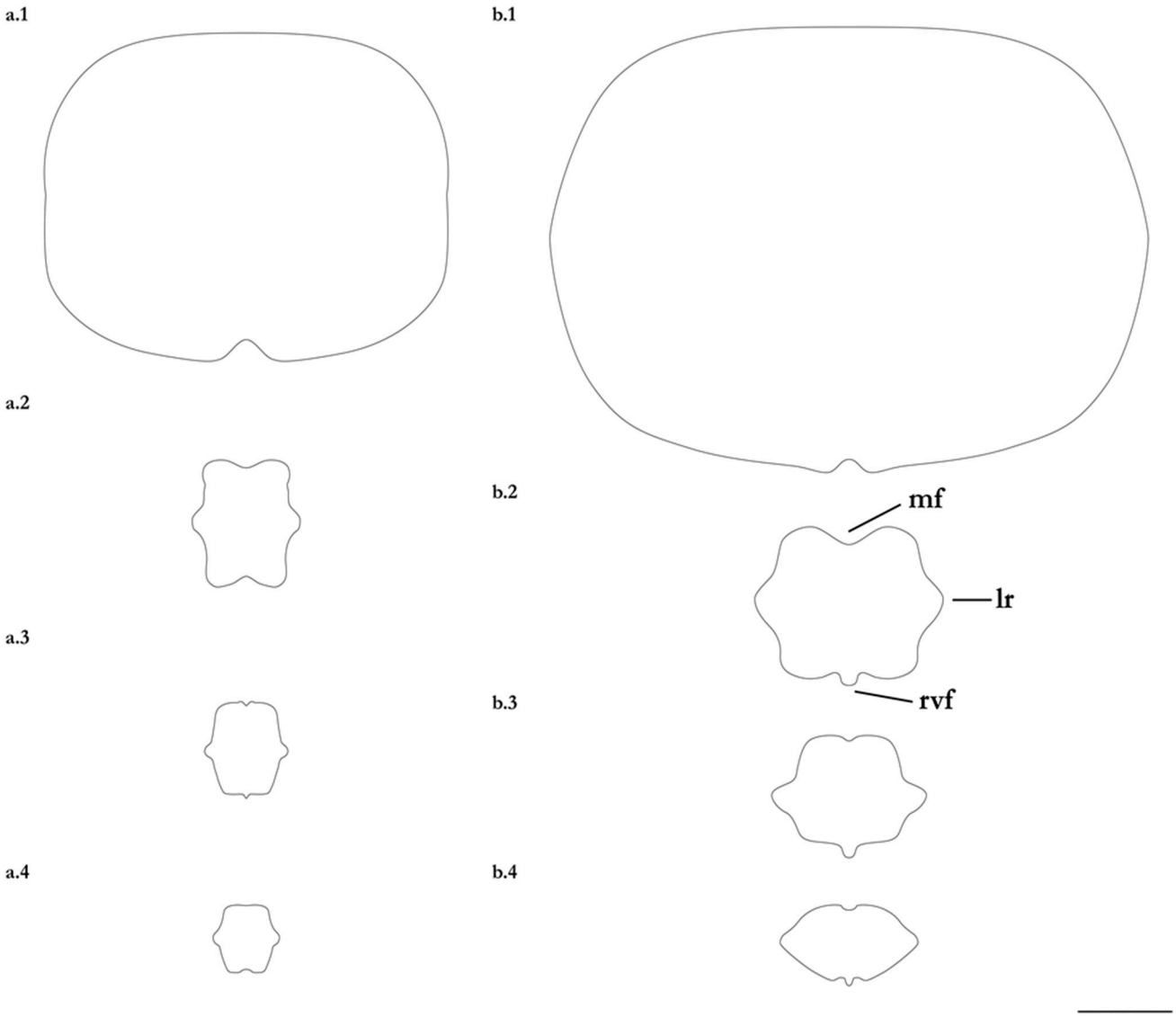

Figure 18. Schematic cross-sections of the post-sting tail of *Brevitrygon walga* for: (**a**) non-type CSIRO H 8667-01, adult male 193 mm DW, Myanmar; and (**b**) non-type CSIRO H 8669-01, female 197 mm DW, Myanmar. Sections taken at: 1. sting origin; 2. axis 25% distance from origin; 3. through midlength; and 4. axis 75% distance from origin. Abbreviations: mf = median furrow or groove, lr = lateral ridge, rvf = rudimentary ventral fold. Scale bar: 2 mm.

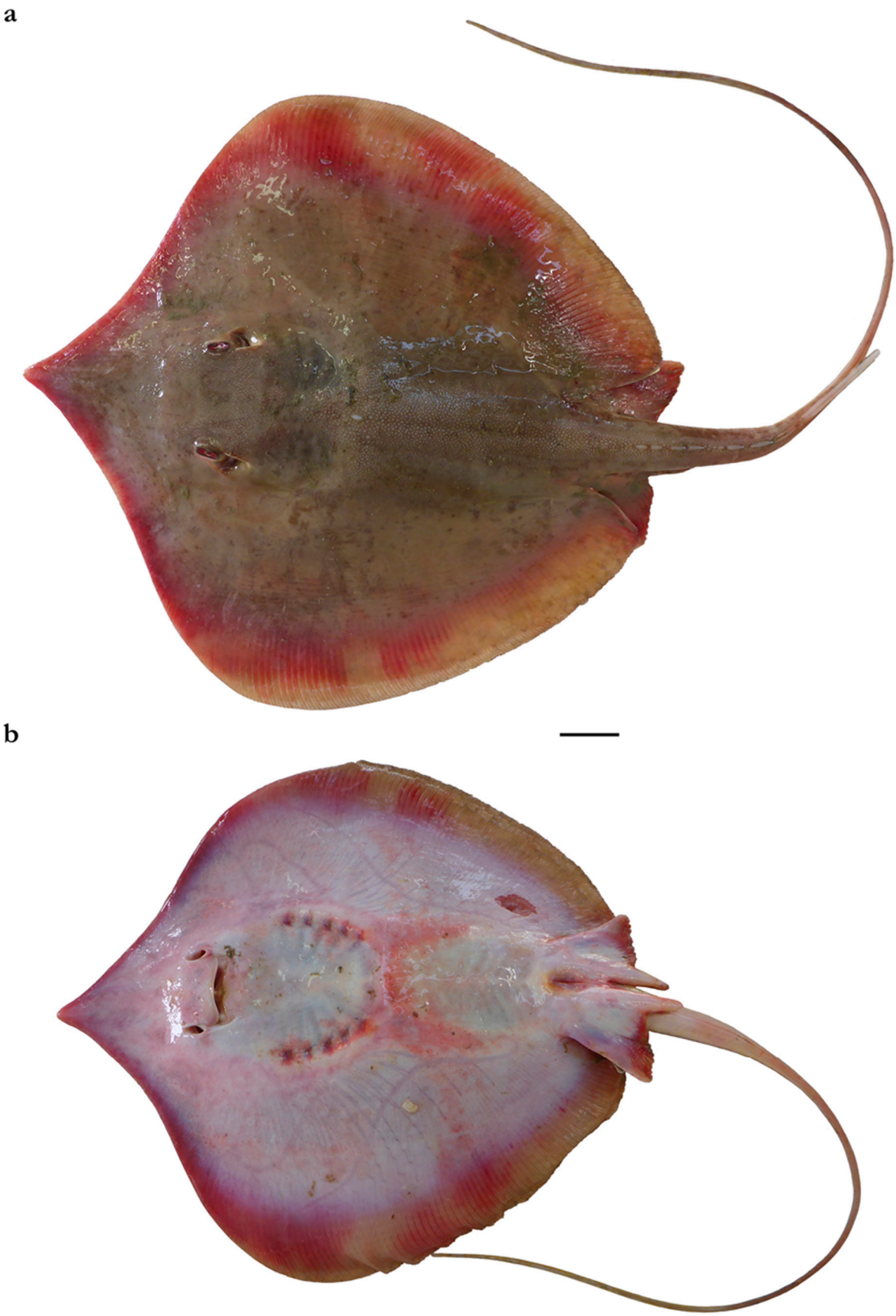

Figure 19. *Brevitrygon walga*, non-type CSIRO H 8667-01, adult male 193 mm DW, Myanmar, fresh: (**a**) dorsal surface, (**b**) ventral surface (photos P. Psomadakis). Scale bar: 2 cm.

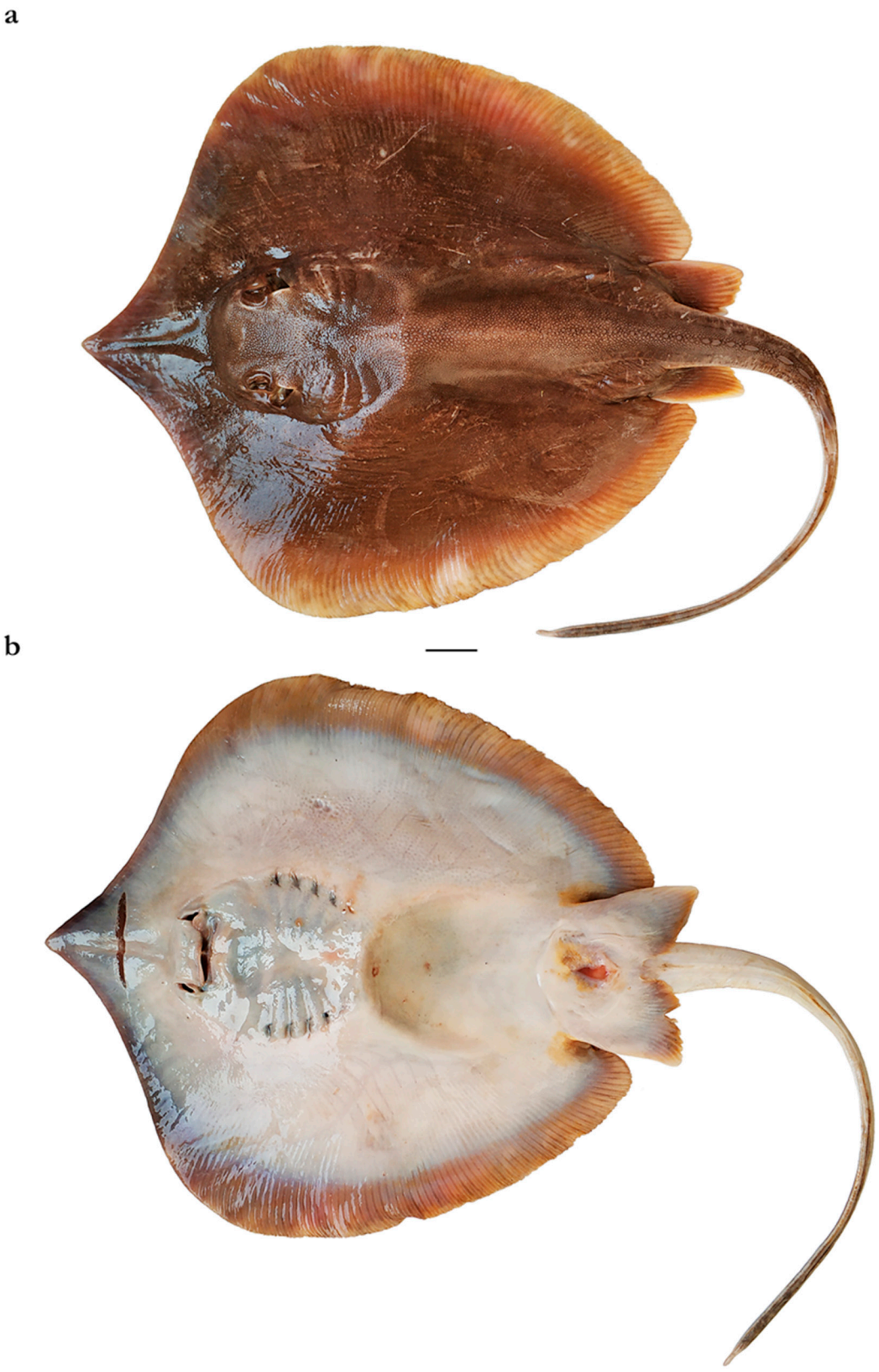

Figure 20. *Brevitrygon walga*, not retained, female 218 mm DW, Myanmar, fresh: (**a**) dorsal surface, (**b**) ventral surface (photos P. Psomadakis). Scale bar: 2 cm.

Meristics. Total pectoral-fin radials 101–102 (102–106, n = 4 for all radial counts); propterygials 48 (46–50), mesopterygials 13–14 (12–13), and metapterygials 40 (42–43). Total

pelvic-fin radials 18 (18–19) plus clasper in males. Total vertebral segments (excluding first synarcual centra) 87 (92–97, n = 5 or 6 for vertebral counts); monospondylous centra (excluding first synarcuals) 37 (34–38); diplospondylous centra 50 (56–60).

Coloration. *When fresh* (Figures 19 and 20): dorsal surface of disc and pelvic fins uniformly brownish or tan; outer fringe of disc marginally paler brown; tail similar to disc with distal half dusky. Main denticle band slightly paler brown and usually not well defined, thorns paler; eye black, slightly darker than rest of orbit. Ventral surface mainly white with broad, well-defined, continuous, brownish band along outer margins of pectoral and pelvic fins; gill slits dusky; tail uniformly white anteriorly with brownish ventral fold evident, posterior half dusky. Preserved *lectotype* (Figure 16) dark brown from long-term preservation with artifactual paler areas dorsally, slightly paler ventrally on disc and pelvic fins, with evidence of darker fin margins, tail darker brown.

Size. Largest available female (CSIRO H 8666-01, 233 mm DW, 494 mm TL) from off Myanmar; another smaller female (CSIRO H 8669-01, 197 mm DW) was in the process of pupping (embryo with umbilicus well developed, 47 mm DW). Two neonates, presumably from CSIRO H 8666-01 and lacking evidence of umbilical scars but with distended bellies, were 79 and 82 mm DW. Smallest confirmed adult male was 193 mm DW (482 mm TL); another specimen was immature at 168 mm DW.

Distribution. Available material from the Bay of Bengal, Madras (eastern India) to East of Bok Ye-gan (Myanmar) (Figure 13). Reported from Bangladesh where it is thought to venture into freshwater [34]. Depth distribution is not well documented but primarily in shallow water from near the shore in estuaries to nearby fishing grounds in bays.

Etymology. Presumably a variant spelling of *wolga*, from *Wolga Tenkée*, a local name for this or a related stingray from the Ganges Delta of India [40]. Vernacular name: Bengal Whipray. Confused in the literature with the Coromandel Whipray, which occurs further south and west off India.

Remarks. As stated earlier, resolution of nomenclatural issues within the genus *Brevitrygon* is dependent on the delineation of the two oldest nominal taxa, *B. imbricata* and *B. walga*. The existence of multiple species within the type series of *B. walga* has created a major source of nomenclatural confusion. The added complexities of unspecified syntypes were summarized in extracts of a doctoral dissertation by Manjaji [3] as follows (in quotation):

> "In the original species description, Müller and Henle (1841) mentioned a total of ten syntypes distributed in a number of museums across Europe. However, they did not provide any catalogue number, but some of which were later listed by Eschmeyer (On-Line, ver. 15 February 2002) (i.e., one BMNH; four MNHN, in addition to MNHN 2337 and MNHN 2431, and three RMNH). Some of these putative types were examined by P. Last (pers. comm. December 2000; June 2001). In addition, Last encountered several possible types in the museums where the syntypes were deposited and examined these as well. The number of specimens, including types and possible types of *H. walga*, examined by Last are seven from BMNH, six MNHN, and six RMNH. In the following, putative and possible types are discussed firstly, followed by non-types".

Séret & McEachran [38] searched the MNHN for the six specimens of *T. walga* but could only identify two syntypes (MNHN 2337 and MNHN 2431); these specimens have subsequently been listed by Fricke et al. [9] as the only confirmed syntypes of this species. Müller & Henle [36] clearly specified the type localities as India (MNHN 2431, Ganges region, collected by Dussumier), and the Red Sea (MNHN 2337, collected by Roux). However, these syntypes represent two separate species. Furthermore, the Red Sea specimen (presumably from Eritrea) is in poor condition, and we have been unable to source additional material from this region from the literature or collections (D. Golani, R. Fricke, S. Bogorodsky pers. com.) to determine its relationship with a common species of *Brevitrygon* occurring in the Arabian Sea and Persian/Arabian Gulf. However, molecular data provide

evidence of a distinct congener nearby off southern Oman in the Arabian Sea that may be conspecific with Roux's specimen.

> "For the BMNH specimens, only one is supposedly the syntype. Thus, minus the syntypes of three species, i.e., *H. heterurus*, *H. dadong* and *H. nuda*, the number is shortlisted to four. Of the four, one is of unknown locality, while each of the other three came from different localities, which is Muscat (Oman), Penang (Malaysia) and Madras (India). Based on the type locality given in the species description, the possible syntype is most likely the Madras specimen. This specimen BMNH 89.2.1.4196, is a female 222 mm DW, with denticle band well developed".

The identity of this BMNH specimen is clear; BMNH 89.2.1.4196 is conspecific with MNHN 2431, but there are questions over its validity as a syntype. The origin of Müller & Henle's [36] sketch of a long, slender-tailed specimen (Figure 21a), given as "Trygon Walga, nach dem Exemplar des Britischen Museums," indicated that the drawing might be based on the BMNH syntype and could be the juvenile specimen for which they provided morphometric data. The figured specimen is clearly not a 222 mm DW female based on tail length and development of the denticle band but apparently a juvenile of ~105 mm DW.

> "For the MNHN specimens, two are confirmed as syntypes (MNHN 2337 and MNHN 2431) in agreement with Eschmeyer. MNHN 2337 is a mature male, 198 mm DW from the Red Sea, and MNHN 2431 is a female (maturity stage undetermined), 170 mm DW from Delta Grange (Ganges, India). The other four specimens appear to conform to the characteristics of the description. However, their locality differs from that of the type locality, with one of them unknown and the rest from 'Gulf of Thailand.' The specimen with locality unknown is most likely the syntype referred to in the original description, i.e., 'the skin of the youngest one quite smooth.' This specimen, MNHN 2438, 155 mm DW, mature male, has a patch of denticle band above the fontanelle and a narrow band developing at the tail base to sting origin, but otherwise the dorsal surface is smooth. A smaller specimen, ca. 97.5 mm DW (sex not determined), BMNH 1904.5.25 is completely void of denticles on its dorsal surface. All other specimens including those from BMNH and RMNH have a well-developed denticle band, and none as smooth. Therefore, this specimen (MNHN 2438) is designated as one of the syntypes. Other unique characteristics of this specimen are the presence of a well-developed stinging spine, the tail not tapering to a point (although it appears as damaged during its lifetime), disc plain yellowish brown, and tail darkish in color. As for the three specimens from Gulf of Thailand, these remain unconfirmed syntypes of *H. walga*. It is worth mentioning the denticle bands in all three mature males, size between 144–150 mm DW, are well developed as opposed to the designated syntype (MNHN 2438).

Three of the other four putative syntypes referred to by Manjaji [3] from the MNHN were collected off India from the Bay of Bengal (incorrect above as Gulf of Thailand): MNHN 2438 (Pondicherry, India) and MNHN 2439 (two specimens from Coromandel, India) are consistent with Müller & Henle's [36] type locality. However, all of these specimens are conspecific with *B. imbricata*. The identity of the fourth syntype is unknown.

> "For the RMNH specimens, three specimens are listed as the syntypes. Based on type locality, two Batavia/ Singapore specimens are excluded as the possible types. One other specimen is anonymously labelled as *Trygon chindrakee* Cuvier, a name in synonymy thus not available (Eschmeyer). This specimen and the remaining two are all of unknown locality, however, it is likely that all three specimens are the syntypes of *H. walga*".

The validity of these putative syntypes is unclear. These specimens (RMNH.PISC.2453, 2454, 2455), which were apparently collected by Kuhl & van Hasselt from Java (Indonesia), are conspecific with *B. heterura* and well outside the documented collection localities of the

T. walga syntypes. Two Dutch specimens (RMNH.PISC.7932, RMNH.PISC.7963), collected from Pondicherry and Madras, respectively, are potential Indian syntypes but may have been collected after *T. walga* was described.

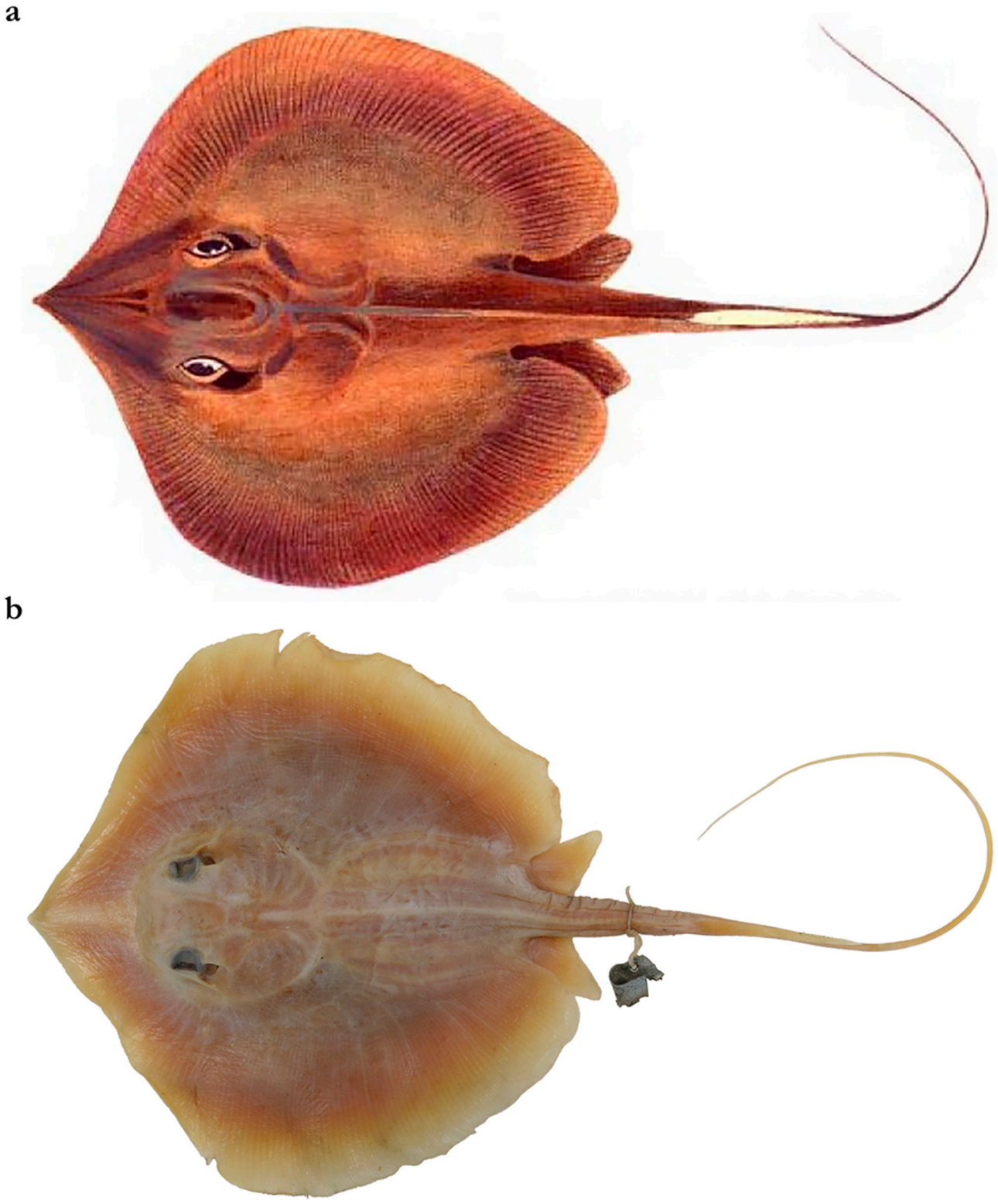

Figure 21. (**a**) *Trygon walga* Müller & Henle 1841, Systematische Beschreibung der Plagiostomen, Pl. 51 from manuscript, ~105 mm DW. (**b**) *Trygon nuda* Günther 1870, syntype BMNH 1845.3.7.19, 105 mm DW.

In summary, we have been able to confirm the putative syntypes of *T. walga* discussed by Manjaji [3] contain four of the five confirmed species of *Brevitrygon*, including three specimens unambiguously conspecific with the type of *T. imbricata* (i.e., MNHN 2439 (1 and 2), MNHN 2438). The remaining syntypes are represented by separate species-level taxa in the Arabian Sea, Persian/Arabian Gulf, Bay of Bengal, and possibly throughout the Indo-Malay Archipelago. Müller & Henle's [36] description of *T. walga* is clearly a composite of these specimens; however, the origin of their sketch of possibly the juvenile specimen measured is unclear. Interestingly, a syntype of *T. nuda* Günther (BMNH 1845.3.7.19-20, also 105 mm DW) collected from Singapore (outside the localities of the syntypes) fits the appearance of Müller & Henle's [36] image of *T. walga*, but its tail is notably longer.

Clearly, the application of the epithet 'walga' is not unique to any of the other three taxa and has been used inconsistently for each of them in the recent literature, mainly applied to the Indo-Malay species [2,3] and to the western Indian Ocean species [6,18] in recent faunal reviews and presented in trees based on molecular data (see Phylogeography section). In addition, *B. walga* has been listed from the Red Sea based on the syntype [41] and recently reported from the Arabian (Persian) Gulf [42–44], Arabian Sea [45,46], Bay of Bengal [47], and the Indo-Malay Archipelago [48]. To add to this confusion, McIvor [49] based on Golani & Fricke [41], listed *B. imbricata* from the Red Sea, and two species of *Brevitrygon* (i.e., *B. imbricata* and *B. walga*) have been reported from off Iraq in the Persian/Arabian Gulf [50], the Arabian Sea off Pakistan [51], and off Myanmar [52]. Hence, there are no unambiguous grounds for selecting the lectotype solely to conserve the name 'walga' based on consistent current usage in the literature.

However, a comment 'Apparently based on multiple species; lectotype designation needed to restrict species to current usage' in the current Catalogue of Fishes [9] underlines the urgency of the situation but also underscores the inconsistent application of the name 'walga.' The newly designated lectotype (MNHN 2431) and an earlier designated syntype (BMNH 1889.2.1.4196) of *T. walga* represent a common Indian species frequently collected in the 19th century from the Bay of Bengal and subsequently disseminated across European museums. Valid alternative younger names are available for the Indo-Malay species (i.e., *Trygon heterurus* Bleeker, 1852, *T. nuda* Günther, 1870, *Dasybatis uylenburgi* Giltay, 1933); a name applied to the western species (i.e., *Raja obtusa* Ehrenberg in Klunzinger 1871) does not belong to a species of the genus *Brevitrygon*. The validity of these names will be discussed further in the following treatments.

A female specimen collected at Diamond Harbour on the Hooghly River (MTUF 29999, 184 mm DW, Figure 22) differed slightly in morphometrics from other material of *B. walga*. Notably, its tail base is much less depressed (width 1.01 times height at axils of pelvic fins vs. 1.42–1.45 in 4 other females and 1.47–1.67 in 3 males), denticle band slightly less indented over its gills (width 17.1% vs. 11.2–16.3% in other material), interorbit slightly narrower (width 11.4% vs. 12.6–14.0% in other material), and pelvic fin shorter (17.9% vs. 19.4–21.9% in other material). Minor molecular differences also exist between material of *B. walga* from Myanmar and West Bengal (see Section 4 below). A comprehensive study of *Brevitrygon* populations is needed across the Bay of Bengal/Andaman Sea to evaluate variability and determine the precise ranges of these species.

3.2.3. *Brevitrygon heterura* (Bleeker, 1852)

[Dwarf whipray]

(Figures 2–6, 12–14, 23–29, and 39; Tables 3 and 4)

Trygon heterurus Bleeker 1852: 67, Batavia [=Java], Indonesia. Holotype: BMNH 1867.11.28.158 (1), female 162 mm DW (original description) [37].

Trygon walga Müller & Henle, 1841: RMNH.PISC.2453 (female 167 mm DW), 2454 (adult male 164 mm DW), 2455 (adult male 156 mm DW) (former syntypes), Java, Indonesia (misidentifications based on newly designated lectotype) [36].

Trygon walga (non Müller & Henle): Bleeker 1852, 67 (description), Batavia [=Java], Samarang [=Semarang], Indonesia (misidentification in part) [37].

Figure 22. *Brevitrygon walga*, non-type MTUF 29999, female 184 mm DW, Hooghly River, India: dorsal surface, preserved. Scale bar: 2 cm.

Trygon (*Himantura*) *walga* (non Müller and Henle): Günther 1870, 475 (brief description). Locality: East Indies (misidentification in part) [24].

Trygon nuda Günther 1870: 476, Singapore [24]. Syntypes (4): BMNH 1845.3.7.19–20 (2), immature male 105 mm DW; BMNH 1851.10.4.101 (1, dry) immature male 95 mm DW, Singapore (original description). Syntype BMNH 1953.8.10.16 non Müller & Henle, adolescent male 318 mm DW, India (not a *Brevitrygon*).

Trygon nudus: Martens 1876, 408 (listed). Locality: Singapore [53].

Leiobatis (*Himantura*) *heterurus*: Boeseman 1983, pl. 558 Figure 1a,b (Plagiostom. Pl. 36) (illustration of female holotype, new combination) [25].

Leiobatis (*Himantura*) *walga* (non Müller and Henle): Boeseman 1983, pl. 563 Figure 1a,b (Plagiostom. Pl. 41) (misidentification in part, illustration of male syntype of *B. heterura*) [25].

Dasybatus (*Himanturus*) *imbricatus* (non Bloch & Schneider): Garman 1913, 379. Locality: East Indies (description, misidentification in part) [26].

Dasyatis imbricatus (non Bloch & Schneider): Fowler 1930, 179. Localities: China, Indian Ocean, Malaysia, East Indies (brief description, misidentification in part) [54].

Dasybatis uylenburgi Giltay 1933: 13, Figures 3–6, East Indies. Holotype: IRSNB 38, adult male 180 mm DW (original description) [55].

Dasyatis nudus: Fowler 1938, 16 (listed). Locality: Singapore [56].

Himantura walga (non Müller and Henle): Last & Compagno 1999, 1493 (new combination, misidentification in part) [2]; Weigmann 2011, 265–272, 299–302 [20].

Brevitrygon heterura (Bleeker): Last et al. 2016, 533 (new combination) [1].

Holotype. BMNH 1867.11.28.158, female 162 mm DW, Batavia [=Java], Indonesia (Figure 23).

Figure 23. *Trygon heterurus* Bleeker, holotype BMNH 1867.11.28.158, female 162 mm DW, Jakarta, Indonesia, preserved): (**a**) dorsal surface; (**b**) ventral surface.

Material examined. BMNH 1845.3.7.19, immature male 105 mm DW, Singapore (syntype of *Trygon nuda*); BMNH 1845.3.7.20, immature male 95 mm DW, Singapore (syntype of *Trygon nuda*); BMNH 1851.10.4.101, immature male 95 mm DW, India (dry mounted syntype of *Trygon nuda*, unidentifiable *Brevitrygon*); BMNH 1896.6.25.230, adult male 184 mm DW, Pinang [=Penang], Malaysia; 3 specimens, BPBM 26574, female 104 mm DW, immature male 91 mm DW, female 78 mm DW, Indonesia, Java, Jakarta fish market, 18 August 1978; 11 specimens, CSIRO H 4924-14, male embryo 65 mm DW, CSIRO H 4924-02, mature male 175 mm DW, CSIRO H 4924-03, female 175 mm DW, CSIRO H 4924-04, mature male 174 mm DW, CSIRO H 4924-05, mature male 187 mm DW, CSIRO H 4924-06, female 193 mm DW, CSIRO H 4924-07, female 197 mm DW, CSIRO H 4924-08, female 166 mm DW, CSIRO H 4924-10, mature male 172 mm DW, CSIRO H 4924-11, mature male 168 mm DW, CSIRO H 4924-13, female 185 mm DW, fisherman's wharf Prachuap Khiri Khan, Thailand (Gulf of Thailand), 5 December 1993; 2 specimens, CSIRO H 4927-04, female 210 mm DW, CSIRO H 4924-01, female 189 mm DW, market near Trang, Thailand (Andaman Sea), 8 December 1993; CSIRO H 6131-01, female 187 mm DW, Muara Angke market, Jakarta, Indonesia, 6 April 2001; CSIRO unreg. (IndoOZ, G43), female 244 mm DW, Cilacap, southern Java, Indonesia, 10 June 2002; CSIRO H 4426-11, adult male 200 mm DW, Muara Angke market, Jakarta, Indonesia, 17 October 1995; 4 specimens, CSIRO H 5471-04, immature male 102 mm DW, CSIRO H 5471-05, immature male 107 mm DW, CSIRO H 5471-06, immature male 138 mm DW, CSIRO H 5471-07, mature male 180 mm DW, Menggatal Bay, near Kota Kinabalu, Sabah, Malaysia, 6 March 1999; CSIRO H 5474-01, mature male 197 mm DW, CSIRO H 5474-18, female 208 mm DW, Kota Kinabalu, Sabah, Malaysia, 15 February 1999; CSIRO H 5584-08, female 205 mm DW, Kota Kinabalu, Sabah, Malaysia, 24 February 1999; 2 specimens, CSIRO H 5473-01, female 179 mm DW, CSIRO H 5473-02, mature male 176 mm DW, Kudat, Sabah, Malaysia, 15 February; 7 specimens, CSIRO H 5474-02, mature male 200 mm DW, CSIRO H 5474-14, female 135 mm DW, CSIRO H 5474-15, female 140 mm DW, CSIRO H 5474-16, female 197 mm DW, CSIRO H 5474-17, female 205 mm DW, CSIRO H 5474-19, mature male 180 mm DW, CSIRO H 5474-20, mature male 191 mm DW, Kota Kinabalu fish market, Sabah, Malaysia, 15 February 1999; 2 specimens, CSIRO H 5584-07, female 200 mm DW, CSIRO H 5584-09, mature male 191 mm DW, Kota Kinabalu fish market, Sabah, Malaysia, 24 February 1999; 2 specimens, CSIRO H 4924-09, female 169 mm DW, CSIRO H 4924-12, female 160 mm DW, Thailand, fisherman's wharf Prachuap Khiri Khan, Thailand (Gulf of Thailand), 5 December 1993; IRSNB 38, adult male 180 mm DW, Poeloe Endoe [=East Indies] (holotype of *Dasybatis uylenburgi*); MNHN 7922, immature male 111 mm DW, Java, Indonesia; MNHN 7923, immature male 126 mm DW, Java, Indonesia; 3 specimens, MNHN 1985-277, adult male 152 mm DW, adult male 150 mm DW, adult male 155 mm DW, Gulf of Siam, Thailand; MNHN 1988-460, female 124 mm DW, Cambodia; MTUF 29998, adult male 175 mm DW, Vung Tau, Vietnam; NSMT P55350, adult male 182 mm DW, Phuket, Thailand; NSMT P55353, immature male 141 mm DW, Phuket, Thailand; NSMT P55355(1 of 2), adult male 158 mm DW, immature male 132 mm DW, Phuket, Thailand; NSMT P65995, immature male 132 mm DW, Phuket, Thailand; ; NSMT P71060(1 of 5), female 143 mm DW, Gulf of Thailand, Thailand; 4 specimens, PMBC unreg., mature male 206 mm DW, PMBC unreg.(1 of 3) female 197 mm DW, PMBC unreg.(2 of 3), immature male 91 mm DW, PMBC unreg.(3 of 3), female 77 mm DW, Phuket fish landing, Thailand, 16 May 2002; RMNH.PISC.2453, female 167 mm DW, Java, Indonesia (dry, probable syntype of *Trygon walga*) (Figure 24); RMNH.PISC.2454, adult male 164 mm DW, Java, Indonesia (dry, probable syntype of *Trygon walga*); RMNH.PISC.2455, adult male 156 mm DW, Java, Indonesia (dry, probable syntype of *Trygon walga*); RMNH.PISC.2457, adult male 153 mm DW, unknown location, possibly Indonesia (dry); RMNH.PISC.2459, adult male 171 mm DW, Java, Indonesia (dry); 2 specimens, RMNH.PISC.4262, female 135 mm DW, female 137 mm DW, Indonesia; RMNH.PISC.8009, adult male 185 mm DW, East Indies [=Indonesia]; ZMH 10357, female 130 mm DW, Shanghai, China; ZMH 10359, female 147 mm DW, Singapore, Malaysia; 4 specimens; ZMH 25690, adolescent female, 167 mm DW, adult female, 181 mm DW, adult female 185 mm DW, adult male, 172 mm DW,

adult male 174 mm DW, adult male 187 mm DW, off Prachuap Khiri Khan, Gulf of Thailand, about 50 m depth, 5 December 1993; ZMH 121965, immature male 112 mm DW, immature male 110 mm DW, immature female 93 mm DW, immature female 79 mm DW, Straits of Malacca, Malaysia. GN3415, BO_146, Sematan, Malaysia; GN3419, BO_150, Sematan, Malaysia; GN3420, BO_151, Sematan, Malaysia; GN3421, BO_152, Sematan, Malaysia; GN3454, BO_237, Mukah, Malaysia; GN3456, BO_239, Mukah, Malaysia.

Figure 24. *Trygon walga* not Müller & Henle (=*B. heterura*), syntype RMNH.PISC.2453, female 167 mm DW, Java, Indonesia: dorsal surface, dry mounted.

Diagnosis. A *Brevitrygon* (to at least 21 cm DW) distinguished by the following combination of features: snout length 28–32% DW, angle variable 103–118° (mainly 107–113°); disc longer than wide; orbit large, diameter mainly 6–8% DW; nostril length 4–5% DW and internasal width 10–14% DW; tail relatively short, longer in males (1.3–1.7 times DW) than females (0.6–1.3 times DW), no dorsal fold, ventral fold rudimentary or absent; distal portion of tail in adult females expanded distally, typically bulbous and often terminating as a slender filament; pelvic-fin large, length 19–27% (mainly 19–24%) DW; elongate claspers, postcloacal length to 23% DW; dorsal surface of disc typically lacking thorns, or with 1–7 slightly enlarged scapular denticles (usually 1–3 mm long when present); secondary denticle band well developed and sharply demarcated in adults, strongly constricted over

branchial region, width across scapulocoracoid and mid-abdomen subequal, then converging posteriorly toward pectoral-fin insertions; tail with well-developed denticle band forward of sting, midline with 0–7 (usually 3–6) lanceolate thorns (largest typically 5–7 mm long) and up to 5 additional enlarged denticles; dorsal surface uniformly greyish, brownish, or yellowish; undersurface white, margins of pectoral and pelvic fins darker; pectoral-fin radials 100–107; total vertebral count (excluding first synarcual centra) 84–94.

Description. Disc broadly suboval and pointed anteriorly (Figures 25 and 26), width 0.91 times length in female holotype (0.90–0.97 in recent material exceeding 100 mm DW); maximum thickness 10% (11–14)% DW. Snout angle 105–118°; disc width 1.99 (1.87–2.52) and distance from snout tip to pectoral-fin insertion 1.97 (1.76–2.38) times distance from snout tip to point of maximum width, respectively. Pelvic-fin length 26.8% (18.6–24.5)% DW; width across base 17.1% (15.4–18.7 in adult females, 12.9–15.2 in adult males)% DW, 1.56 (1.20–1.94) in pelvic-fin length. Tail slender, length 1.22 (0.64–1.28 in adult females, 1.28–1.71 in adult males) times DW, 1.34 (0.70–1.94) times precloacal length; tapering very gradually and evenly toward sting, flexible, almost filamentous beyond sting in males and juveniles, firmer in adult females; base narrow, depressed slightly, weakly convex dorsally with midline not elevated, more convex ventrally, its width 1.19 (1.23–2.06) times its height at pelvic-fin insertions; suboval, dorsal, and ventral surfaces convex at sting base; sting positioned well forward on tail, distance from cloaca origin to sting 2.69 (2.26–3.22) in precloacal length, 31% (26–39)% DL. Post-sting tail in males slender with prominent, dorsal median furrow extending for anterior half its length with corresponding low ridge (rudimentary fold) on ventral surface; fleshy lateral ridge weak but evident (Figure 27); in females, tail much more robust, typically bulbous distally (often terminating as a slender filament), median furrow broader, ventral fold weak (barely detectable), fleshy lateral ridges obscure (Figure 27). Preoral snout length 3.35 (2.76–4.04) times mouth width, 2.81 (2.20–3.08) times internarial distance, 1.39 (1.13–1.56) times distance between first gill slits; direct preorbital snout length 2.55 (2.34–2.96) times interorbital length; distance from snout tip to maximum disc width 50% (40–53)% DW; eye length 1.26 (1.11–1.99) in spiracle length; orbit diameter 0.83 (0.68–1.20) in spiracle length, interorbital distance 1.88 (1.21–2.14) times orbit, intereye distance 3.50 (3.55–5.05) times eye length. Spiracle length 5.5% (4.9–6.9)% DW. Nostril length 2.45 (2.10–3.48) in internasal distance; internasal distance 2.25 (1.72–2.51) in prenasal length. Nasal curtain width 2.09 (1.61–2.88) times length. Mouth width 9.8% (7.9–10.6)% DW, 1.19 (1.09–1.40) in internasal width; profile similarly arched in males and females; upper jaw double concave, dorsal to lower jaw; lower jaw notched near symphysis, largely concealing and slotting into symphysial knob of upper jaw, 1–2 outer tooth rows visible when mouth closed; oronasal groove prominent, deep; skin along margin of lower jaw weakly papillose or smooth along its margin. Teeth of adult male (CSIRO 5473-02) slightly larger in upper jaw than in lower jaw; upper jaw teeth in weak quincunx, suboval to rhomboidal, largest near symphysis and on mid-lateral knobs, cusps short and pungent across jaw; lower jaw teeth in strong quincunx, similar in size and shape across jaw, suboval, cusps similar to those of upper jaw. In large female (CSIRO H 5474-17) teeth more broadly oval, slightly larger in upper jaw, in stronger quincunx than male, acuspid. Tooth rows (CSIRO 5473-02 and CSIRO H 5474-17) ~37–44 in upper jaw; ~43–45 in lower jaw. Floor or mouth with 0, or 2–3 simple, short to elongate oral papillae (absent in CSIRO 5474-19), 2 widely space papillae in CSIRO 5471-06; CSIRO 5473-02 and CSIRO H 5474-17 with 2 short papillae situated well apart, and a shorter medial and more anteriorly positioned papilla. Length of first gill slit 1.64 (1.07–2.27) times length of fifth, 3.19 (2.42–3.81) in mouth width; distance between first gill slits 2.02 (1.81–2.19) times internasal distance, 0.41 (0.36–0.44) of ventral head length; distance between fifth gill slits 1.30 (1.16–1.46) times internasal distance, 0.27 (0.25–0.30) in ventral head length.

Figure 25. *Brevitrygon heterura*, non-type KA 351, adult male 162 mm DW, Kalimantan, Indonesia: (**a**) dorsal surface, fresh; (**b**) ventral surface, fresh (photos K. Jensen). Scale bar: 2 cm.

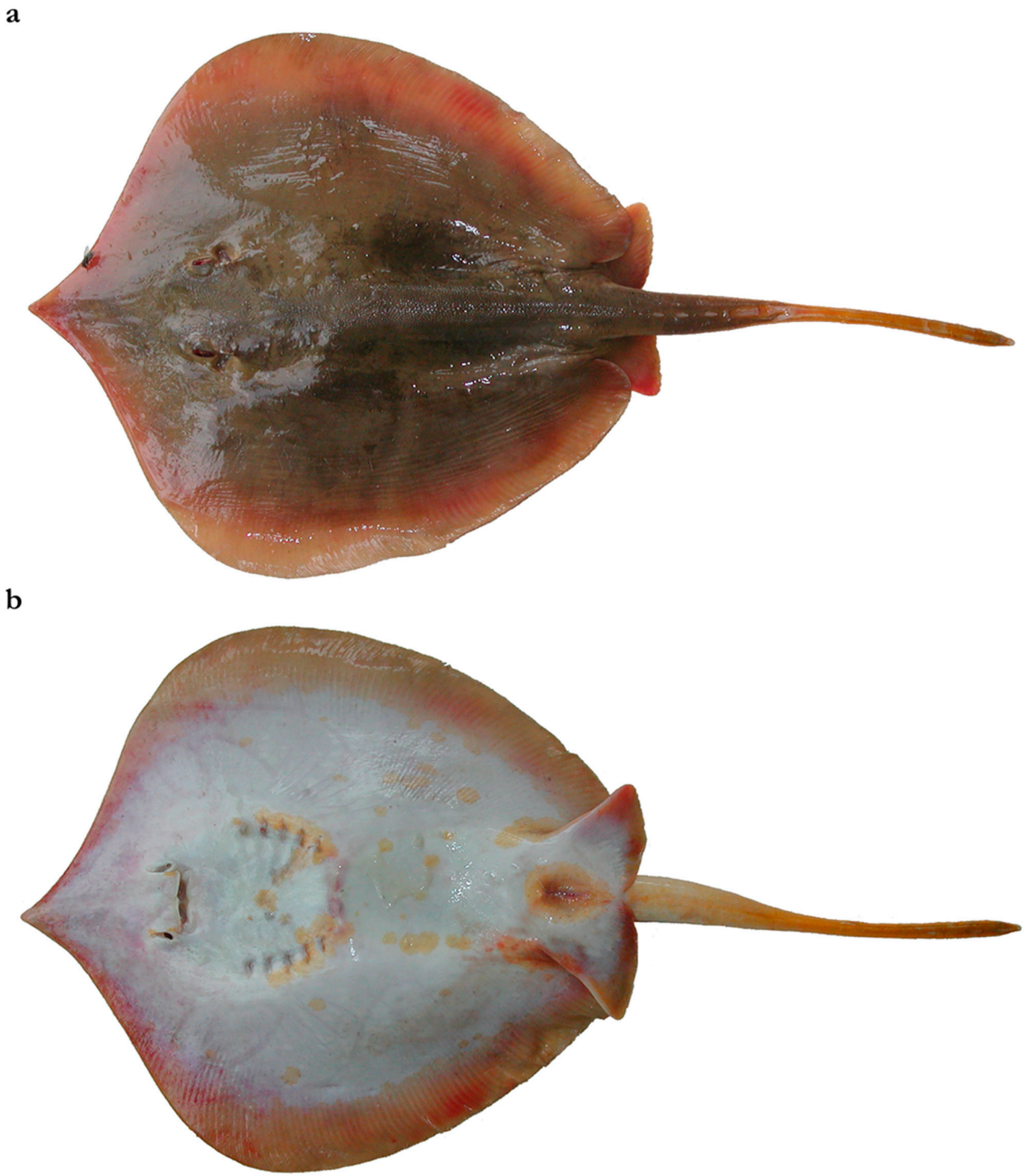

Figure 26. *Brevitrygon heterura*, non-type Phuket fishing port, female 162 mm DW, Phuket, Thailand: (**a**) dorsal surface, fresh; (**b**) ventral surface, fresh.

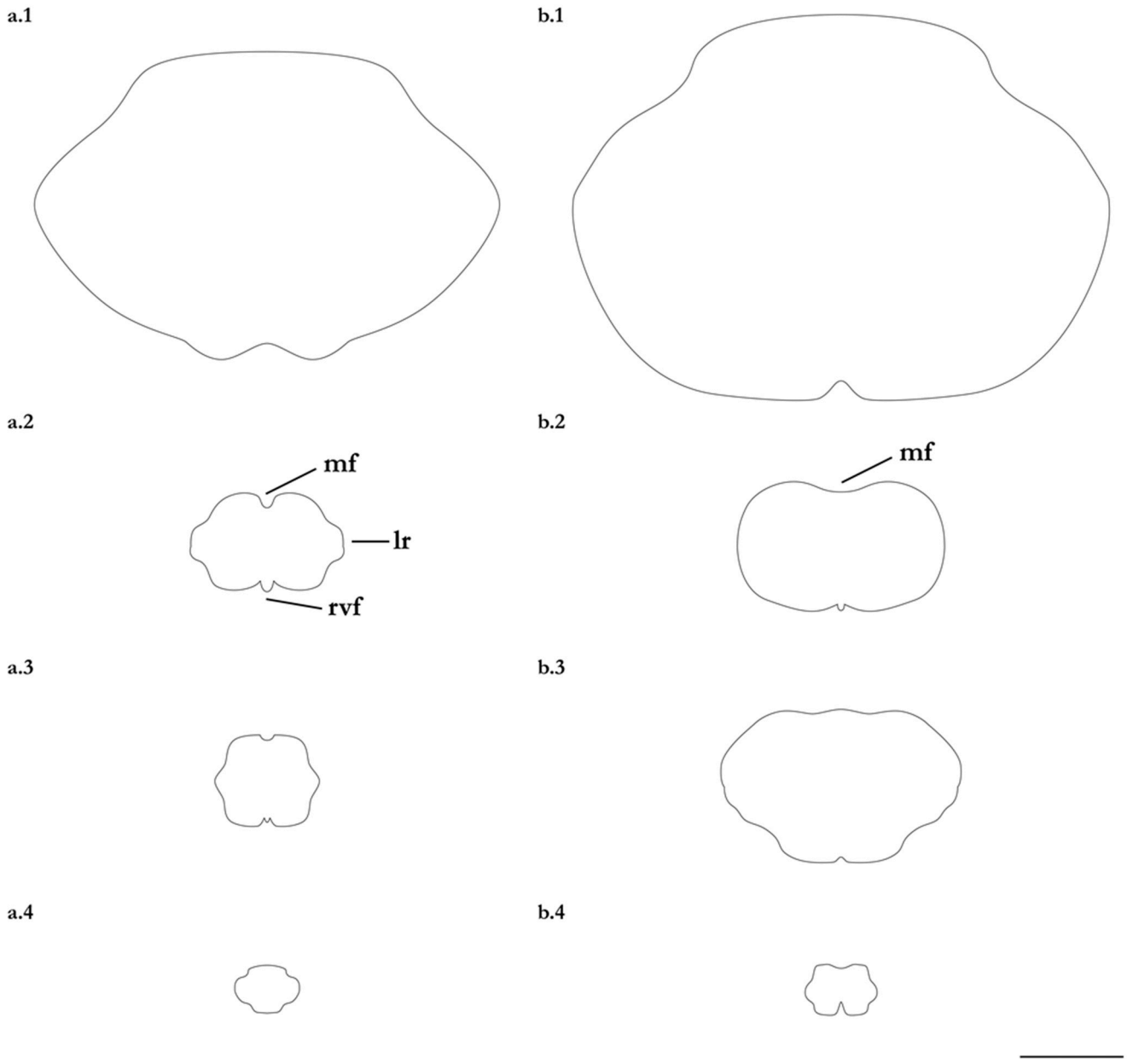

Figure 27. Schematic cross-sections of the post-sting tail of *Brevitrygon heterura* for (**a**) non-type CSIRO H 4924-02, adult male, 175 mm DW, Gulf of Thailand; and (**b**) non-type CSIRO H 4924-03, female 175 mm DW, Gulf of Thailand. Sections taken: 1. sting origin; 2. axis 25% distance from origin; 3. through midlength; and 4. axis 75% distance from origin. Abbreviations: mf = median furrow or groove, lr = lateral ridge, rvf = rudimentary ventral fold. Scale bar: 2 mm.

Squamation. Ontogenetic stages 0–4 evident from material (definitions following Manjaji [3] and Last et al. [12]); stages 5 and 6 appear to be inapplicable; denticle development relatively rapid, no obvious sexual dimorphism. Developmental *Stage 0* (77–107 mm DW): 6 early juveniles entirely smooth, apart from presence of embryological tail thorn in a young male and female. *Stages 1, 2, and 3* (90–138 mm DW): rapid and variable onset of denticles and thorns; female (ZMH 121965, 1 of 4, 90 mm DW) at Stage 3 with developed tail thorns but no other squamation on disc; immature male (ZMH 121965, 2 of 4, 109–111 mm DW) at Stages 2, 3 with secondary band in early development and embryological tail thorn obvious; female (CSIRO H 5474-14, 135 mm DW) largely naked but with evidence of denticles forming in scapular region and embryological thorns on tail; adolescent male (CSIRO H 5471-06, 138 mm DW) with scattered denticles in interorbital region, narrow

band forming a weak cruciate pattern over scapulocoracoid, then extending posteriorly as a slender band (narrower than eye width) to sting base, ~7 small thorns forming on tail. *Stage 4* (>147 mm DW): secondary denticle band well developed in adults (Figure 4); enlarged scapular denticles often absent or, when present small, seed- or heart shaped, irregular in shape and size (1–7 enlarged scapular denticles and/or thorns, length 0.5–3.0% DW and distance from edge of spiracle 9.6–20.2% DW; largest denticles typically 1–3 mm long, <1 mm wide; largest thorn 5.6 mm long); band margins well defined and slightly irregular; extending very slightly forward of orbit (distance of denticle band from snout tip 28% [23–28] DW; covering most of interorbital space in adults, width of band across interorbit 10.6% (5.5–12.6%) DW; noticeably constricted over branchial region (band much narrower than on interorbit), narrowest width of band preceding scapular region 8.7 (3.0–14.8)% DW; width of band at scapulocoracoid 21.9% (7.6–23.0)% DW; expanded over abdomen (broadest posterior to scapulocoracoid usually about distance equivalent to interorbital width), width of band variable 27.1% (2.9–29.7)% DW; width of band at pectoral-fin insertion 6.6% (1.7–5.9)% DW; band well developed on tail, broad (~6–12 denticles wide on mid pre-sting tail, covering about 1/2 width of tail in dorsal view) with sharply defined margins. Tail with 4 (0–7, usually 3–6) enlarged, weakly oblique, lanceolate thorns, and up to 5 noticeably smaller, enlarged denticles; denticles irregular in size, sometimes closely and regularly spaced, tips often overlapping; length of largest thorn of series 3.2–7.3 mm, 1.69–4.91% DW; denticles absent from post-sting tail. Caudal stings 1–2 (usually 2), well developed.

Meristics. Total pectoral-fin radials 100–107, n = 22 for all radial counts; propterygial 45–50, mesopterygial 9–15, and metapterygial 40–47. Total pelvic-fin radials 21–26 in females (n = 10), 15–19 plus clasper in males (n = 11). Total vertebral segments (excluding first synarcual centra) 84–94 (n = 20–21 for all vertebral counts); monospondylous centra (excluding first synarcuals) 35–40; diplospondylous centra 46–57.

Coloration. *When fresh*: Dorsal disc and pelvic fins greyish brown (based on KA 351, Figure 25), slightly paler distally, clasper tips dark; denticle band paler, sharply demarcated; lower eyelid and spiracle white; thorn like denticles and sting white; dorsal tail beyond sting pale, whitish on margins, dusky dorsally; ventral disc, pelvic fins white, margins semitranslucent; ventral tail white. Populations in Indian Ocean, off western Thailand (Figure 28) yellowish brown dorsally, distinctly paler around margin of disc and pelvic fins; denticle band less distinct and white areas on orbito-spiracular region often absent; tail beyond sting, ventral margin of disc and pelvic fins, spots around central disc and around cloaca orange or yellow. Upper surfaces of Pacific populations sometimes greyish, yellowish, or greyish green. *Holotype* (after preservation for more than 150 years, Figure 23): Disc and pelvic fins yellowish dorsally, paler around its margin; white (possible artifactual) areas on mid-snout, around interorbit and laterally on parts of disc; branchial region, most of denticle band and tail darker, brownish; eyes black. Ventral disc pale yellow, darker around its margin.

Size. Males reaching at least 206 mm DW (483 mm TL), females to 243 mm DW (439 mm TL); females shorter than males. Smallest adult male 168 mm DW; 4 smallest males (91–138 mm DW) were immature. Smallest juvenile, female 77 mm DW (188 mm TL). Males mature at ~16–18 cm DW and females mature at ~17 cm DW; size at birth 8–10 cm DW [6].

Distribution. Indo-Malay Archipelago, from western Nusa Tenggara, Indonesia north to Vung Tau (Vietnam) in the western Pacific Ocean, and north to Raya Island, off Phuket (western Thailand) in the eastern Indian Ocean; inshore off the coasts of Indonesia (Java, western and southern Kalimantan, and Sumatra), Brunei Darussalam, Singapore, Malaysia (Sabah, Sarawak, and both eastern and western Peninsula coasts), Thailand (both eastern and western coasts), Vietnam, and possibly Cambodia (Figure 13). Not known from eastern Kalimantan or east of the Wallace Line. May be sympatric with *B. imbricata* in parts of the Pacific and sympatric with *B. javaensis* off southern Java (Indonesia). Female holotype collected from Java in the mid-19th century, presumably from a local fish market. Depth

information not precise but likely to occur on the inner continental shelf at depths of 25 m or more.

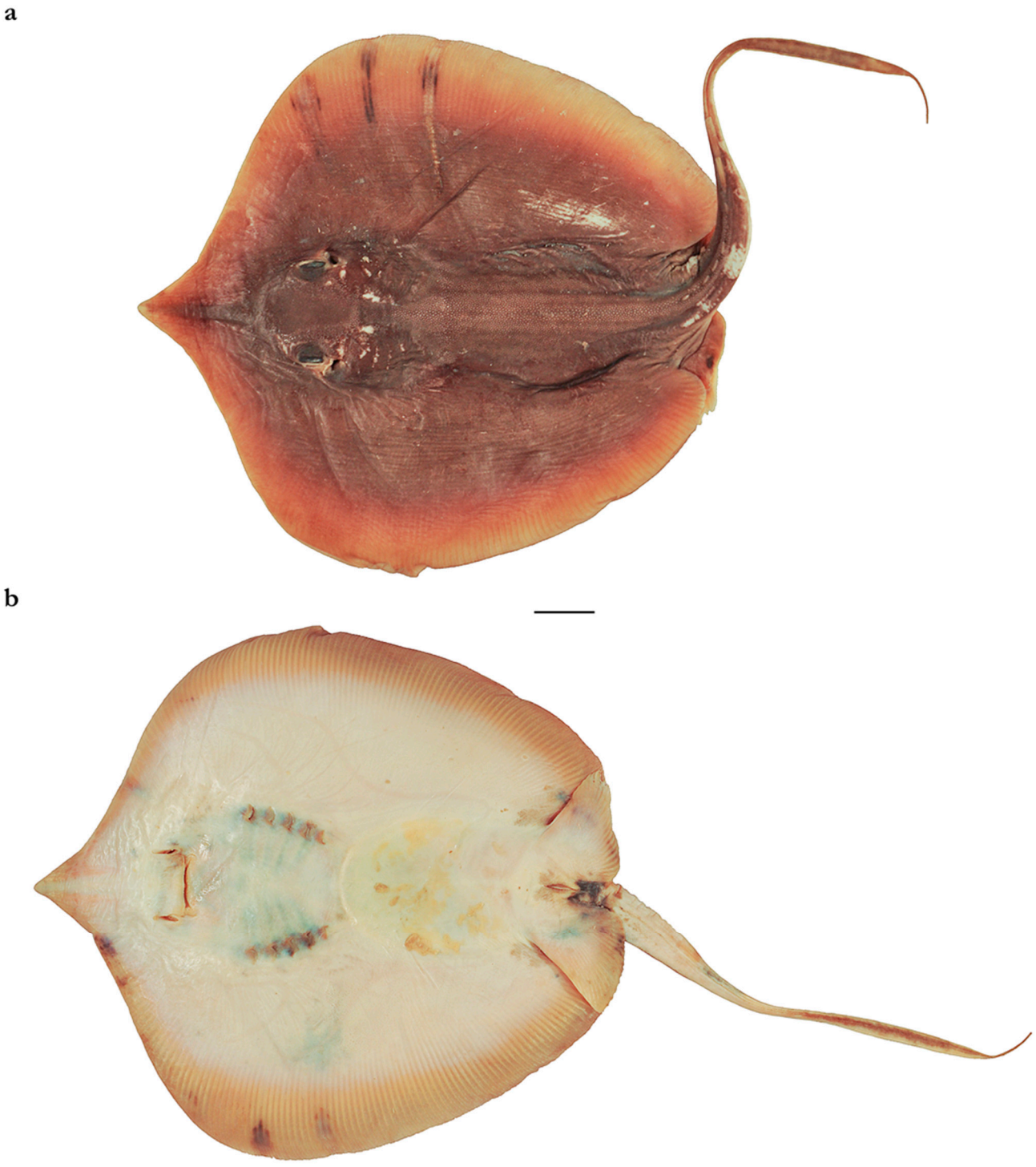

Figure 28. *Brevitrygon heterura*, non-type ZMH, adult female 185 mm DW, Prachuap Khiri Khan, Thailand: (**a**) dorsal surface, preserved; (**b**) ventral surface, preserved. Scale bar: 2 cm.

Etymology. Derived from *héteros* (Greek ἕτερος), meaning different and *ourá* (Greek οὐρά), meaning tail, but treated as an adjective (tailed), referring to the posterior half of tail being considerably thicker in the middle compared to *B. walga* [40]. According to Bleeker's key to treated species (Bleeker [37], p. 64), *Brevitrygon heterura* differs from *B. walga* in the following two characters: (1) *Cauda postice medio crassior, parte postspinali disco corporis multo*

brevior, meaning posterior part of tail thicker in the middle, postspinal part much shorter than (body) disc (vs. *Cauda a basi usque ad apicem gracilescens,* meaning tail tapering from base to tip); (2) *Rictus latitudine 3 in longitudine rostri praeorali,* meaning mouth width 3 times in preoral snout length (vs. *Rictus latitudine 2 circiter in longitudine rostri praeorali*, meaning mouth width about 2 times in preoral snout length). In a comment written in Dutch, Bleeker [37] describes the tail differences: "Deze soort heeft de meeste verwantschap met *Trygon walga* MH. doch laat er zich gemakkelijk van onderkennen, evenals van alle andere soorten van *Trygon*, doordien de staart aan de achterste helft aanmerkelijk dikker is dan in het midden en in gedaante veel heeft van de vrucht van *Rhizophora mangle*". This translates to "This species is most closely related to *Trygon walg*a MH. but is easily distinguished from it, as from all other species of *Trygon*, by the way the tail at the posterior half is considerably thicker than in the middle and has a shape similar to the fruit of *Rhizophora mangle* (referring to a mangrove propagule)". Bleeker [37] was aware that the tail of adult females, which is typically more expanded distally than in males, is a diagnostic character of *Brevitrygon heterura*, albeit he apparently did not know that this does not apply to males. Vernacular name: Dwarf Whipray.

Remarks. As discussed in earlier treatments, the type series of *T. walga* Müller & Henle possibly contained material of the Indo-Malay *Brevitrygon* (i.e., RMNH.PISC.2453, RMNH.PISC.2454, RMNH.PISC.2455), as well as 3 other species; this name has been assigned now to a Bay of Bengal species by the lectotype designation. Other valid names were available for the Indo-Malay species: *Trygon heterurus* Bleeker, 1852 from Java (Indonesia) (Figure 23), *T. nuda* Günther, 1870 from Singapore (in part) (Figure 21b), and *Dasybatis uylenburgi* Giltay, 1933 from the Indo-Malay Archipelago (=East Indies) (Figure 29); of these taxa, Bleeker's species has priority.

Brevitrygon heterura is highly abundant in the fish markets of southeast Asia and was most likely equally or more prolific in the 19th century. Bleeker's acute taxonomic eye led to the recognition of multiple valid stingray species in the region that were subsequently dismissed as variations by others. The unique tail shape of adult female *B. heterura*, resembling a mangrove propagule or a green bean, immediately distinguishes this species from other dasyatids in regional fish markets, as well as other *Brevitrygon* species. Curiously, Bleeker did not associate the male of this species (identified and figured as *Leiobatis walga*, see Figure 14b) with his female (Figure 14a).

Brevitrygon heterura is somewhat variable in disc shape, the extent of development of the secondary denticle band and enlarged denticles/thorns, and the shape of the bulbous tail in adult females. Two weakly divergent groups referable to this species were detected a decade ago by molecular analysis (see [17], Figure 12). However, a comparison of material available from across the distributional range of the species failed to detect any consistent morphological differences between populations (Table 3). Like several other members of the genus, the tail morphology and its relative length are the most striking differences between adults of the sexes in *B. heterura*. A comparison of males and females from Kota Kinabalu (Malaysian Borneo) and Prachuap Khiri Khan (northern Gulf of Thailand) revealed consistent morphological differences between sexes (Table 4); the undamaged tail of males was typical longer (distance from cloaca to tail tip 1.4–1.7 times DW in Malaysian and 1.3–1.4 times DW in Thailand males vs. 0.9–1.3 times DW and 0.6–1.2 times DW in Malaysian and Thailand females, respectively). Males have a more flexible tail that tapers evenly, rather than being expanded distally; juvenile females resemble males indicating that the enlarged and shorter tail is due to ontogenetic change with the onset of maturity.

Some members of the genus *Brevitrygon*, and in particular *B. heterura*, exhibit overt sexually dimorphic traits compared to most other members of the family Dasyatidae. Combine this with their intraspecific variability and significant ontogenetic changes, and subtilities between populations are difficult to detect without undertaking a more comprehensive, cross-regional study of the species using both morphological and molecular analyses of new material.

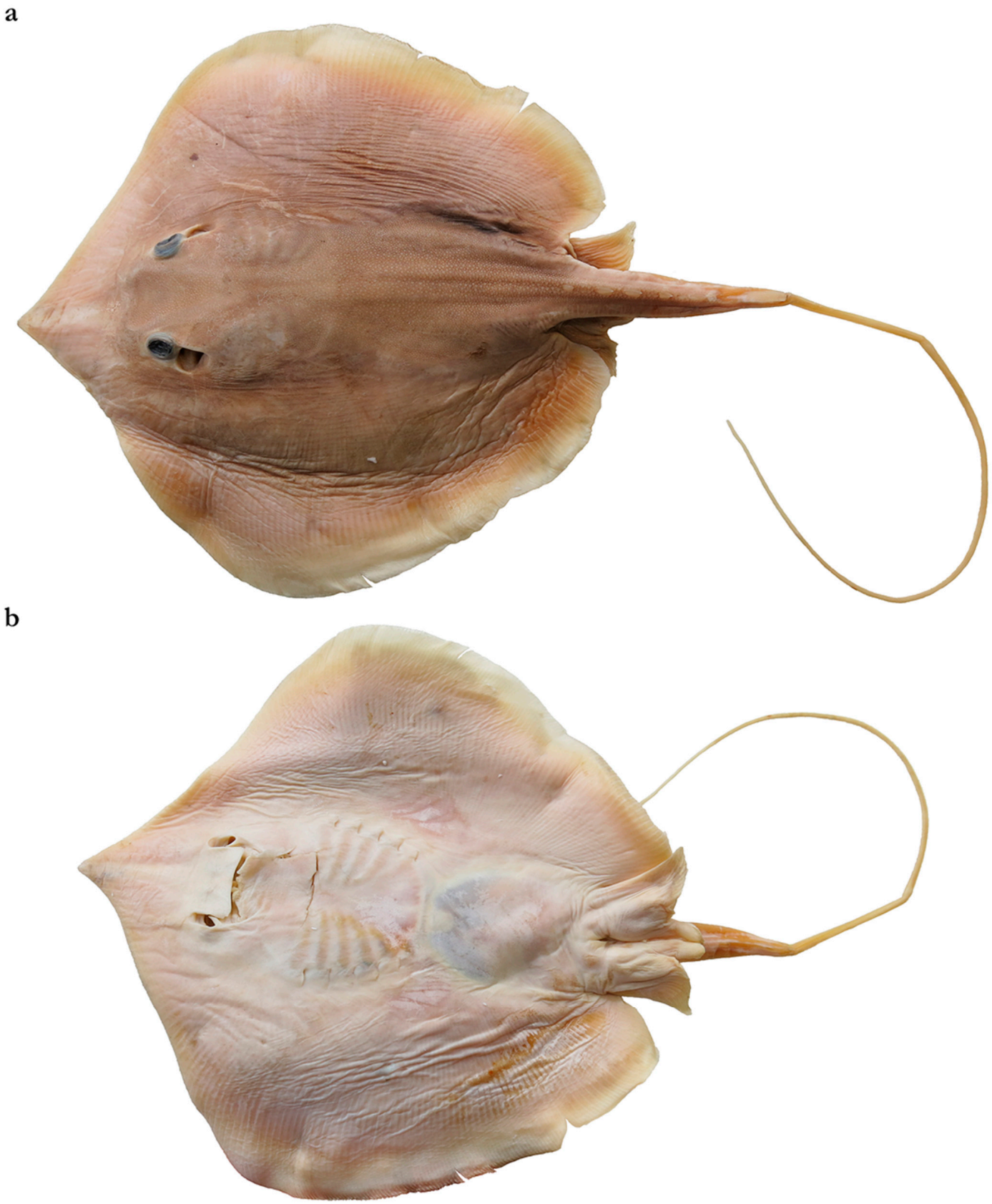

Figure 29. *Dasybatis uylenburgi* Giltay (=*Brevitrygon heterura*), holotype IRSNB 38, adult male 180 mm DW, East Indies (Indonesia): (**a**) dorsal surface, preserved; (**b**) ventral surface, preserved.

Table 3. Morphometric data for *Brevitrygon heterura*: holotype (BMNH 1867.11.28.158), and non-types from Indonesia, Malaysia, Thailand, and Vietnam. Measurements expressed as percentages of disc width (mm). Data for non-types based on new and selective remeasurements of material from Manjaji [3].

	Holotype	**Non-Types**						
	BMNH 1867.11.28.158	**Indonesia (n = 4)**		**Malaysia (n = 21)**		**Thailand (n = 16)**		**Vietnam (n = 1)**
	Female, Java, Indonesia	**Min**	**Max**	**Min**	**Max**	**Min**	**Max**	
Disc, width (mm)	199	163	244	101	210	161	210	176
Total length	213.6	195.6	237.6	184.9	255.1	156.3	231.6	-
Disc, length (direct)	110.1	105.5	112.7	103.3	109.8	103.4	110.6	107.4
Disc, thickness	10.2	11.0	13.6	10.6	13.4	10.6	13.5	12.3
Snout to origin of cloaca	91.5	88.7	97.9	85.0	92.9	85.6	95.6	91.4
Cloaca origin to tail tip	122.1	100.4	142.3	93.1	168.3	64.3	142.7	-
Snout to pectoral insertion	98.9	95.2	104.7	92.7	100.8	93.5	102.1	97.4
Snout to maximum width	50.3	47.1	52.0	39.8	53.4	43.5	49.3	46.5
End of orbit to pectoral insertion	63.2	61.7	67.2	56.9	65.7	59.5	65.0	62.9
Snout, preorbital (direct)	31.7	29.6	32.4	28.3	32.1	27.6	31.1	30.0
Snout, preorbital (horizontal)	30.6	28.6	31.5	27.0	30.7	25.6	29.5	27.0
Orbit diameter	6.6	5.3	6.7	5.8	7.7	5.8	7.9	6.5
Eye diameter	4.4	3.3	4.8	3.7	5.2	3.8	4.6	4.1
Spiracle length	5.5	5.2	7.0	5.2	6.9	4.9	6.2	5.7
Orbit and spiracle length	10.1	9.7	10.6	9.4	11.8	9.2	11.0	10.7
Interorbital width	12.4	10.5	13.4	10.3	13.0	10.0	12.3	12.5
Intereye width	15.3	15.8	16.9	16.1	18.6	15.7	17.2	16.9
Distance between spiracles	16.7	16.6	18.0	15.4	18.0	15.5	17.4	18.8
Head length (direct)	57.6	55.9	59.3	52.3	59.3	54.6	58.8	58.2
Snout, prenasal (direct)	26.4	23.9	27.2	23.5	26.7	22.7	26.6	22.7
Nostril length	4.8	4.2	5.3	3.6	5.2	3.8	5.2	3.6
Nasal curtain, length	5.5	5.6	7.6	5.1	7.1	6.3	7.8	6.9
Nasal curtain, width	11.6	11.7	13.8	10.3	17.9	11.0	14.5	13.4
Distance between nostrils	11.7	11.1	13.2	10.4	12.9	10.8	13.7	12.6
Snout, preoral (direct)	33.0	29.5	33.4	28.5	33.1	28.2	32.8	29.7
Mouth width	9.8	9.3	10.4	7.9	9.9	8.3	10.2	10.6
Width, 1st gill slit	3.1	2.7	3.7	2.6	3.4	2.6	3.7	3.0
Width, 3rd gill slit	3.5	2.7	4.1	2.9	3.8	3.1	3.9	3.5
Width, 5th gill slit	1.9	2.0	2.6	1.4	2.5	1.9	2.5	2.0
Distance between 1st gill slits	23.7	22.7	25.1	21.0	25.1	22.3	24.4	25.2
Distance between 5th gill slits	15.3	14.9	15.7	14.1	16.5	14.6	16.6	16.4
Length pelvic fin	26.8	21.2	25.1	20.0	24.1	18.6	24.5	23.7

Table 3. *Cont.*

	Holotype	Non-Types						
	BMNH 1867.11.28.158	**Indonesia (n = 4)**		**Malaysia (n = 21)**		**Thailand (n = 16)**		**Vietnam (n= 1)**
	Female, Java, Indonesia	**Min**	**Max**	**Min**	**Max**	**Min**	**Max**	
Width across pelvic fin base	17.1	16.1	16.7	12.9	18.7	13.8	17.8	15.2
Greatest width across pelvic fins	-	35.6	40.4	32.1	45.8	33.5	42.5	40.3
Tail width, axil of pelvics	7.8	8.4	10.0	8.1	11.2	7.4	11.2	9.7
Tail height, axil of pelvics	6.6	5.4	5.9	5.0	6.9	5.3	6.6	6.0
Tail width, base of sting	5.0	5.7	6.2	3.7	6.4	4.2	5.9	-
Tail height, base of sting	4.1	4.0	4.1	2.9	4.0	3.3	4.2	-
Cloaca length	5.7	5.0	8.3	4.0	7.3	4.5	7.2	5.9
Clasper, postcloaca length	-	18.7	20.4	12.0	22.6	20.6	22.8	19.2
Clasper, length from pelvic axil	-	9.2	13.3	7.5	20.3	9.3	17.1	13.6
Pect. insertion to sting origin	28.7	29.1	29.6	23.7	32.1	20.2	27.0	-
Cloaca origin to sting	34.0	32.5	33.6	29.4	37.1	26.8	31.3	-
Caudal sting 1 length	-	-	-	-	-	-	-	-
Caudal sting 2 length	-	-	-	-	-	-	-	-

Table 4. Morphometric data for *Brevitrygon heterura*: males and females from Malaysia and Thailand, respectively. Measurements expressed as percentages of disc width (mm) and given as ranges with means.

	Malaysia (n = 11)			**Malaysia (n = 10)**			**Thailand (n = 7)**			**Thailand (n = 10)**		
	Adult Males			**Females**			**Adult Males**			**Females**		
	Min	**Max**	**Mean**	**Min**	**Max**	**Mean**	**Min**	**Max**	**Mean**	**Min**	**Max**	**Mean**
Disc, width (mm)	107	200	173	136	210	184	170	207	183	161	199	180
Total length	227.9	255.1	239.0	185.5	215.6	202.6	215.3	231.6	224.1	156.3	205.3	182.7
Disc, length (direct)	103.7	108.0	105.3	104.3	109.8	107.0	103.4	107.6	105.0	105.3	110.6	108.3
Disc, thickness	11.2	13.4	12.6	10.6	13.2	12.1	11.8	13.5	12.7	10.9	13.1	12.4
Snout to origin of cloaca	86.8	92.3	88.8	87.8	92.9	90.2	85.6	93.2	88.8	88.9	95.6	92.2
Cloaca origin to tail tip	139.5	168.3	150.6	93.1	127.8	112.7	122.4	142.7	134.2	64.3	116.1	90.4
Snout to pectoral insertion	92.9	98.3	94.8	93.4	100.8	97.0	93.5	98.2	95.4	95.0	102.1	98.8
Snout to maximum width	45.4	53.4	48.7	43.0	50.6	46.5	43.5	49.1	46.3	46.5	49.3	48.0
End of orbit to pectoral insertion	57.0	62.0	59.4	57.3	65.7	61.6	59.5	61.4	60.7	60.0	65.0	62.8
Snout, preorbital (direct)	29.5	32.0	30.8	28.3	32.1	30.5	27.6	30.1	29.0	28.8	31.1	29.7
Snout, preorbital (horizontal)	28.2	30.6	29.4	27.0	30.7	29.4	26.9	29.5	28.1	25.6	29.0	27.8

Table 4. *Cont.*

	Malaysia (n = 11)			Malaysia (n = 10)			Thailand (n = 7)			Thailand (n = 10)		
	Adult Males			Females			Adult Males			Females		
	Min	**Max**	**Mean**	**Min**	**Max**	**Mean**	**Min**	**Max**	**Mean**	**Min**	**Max**	**Mean**
Orbit diameter	5.9	7.7	6.4	5.8	6.6	6.1	6.2	7.3	6.7	6.3	7.9	7.1
Eye diameter	3.9	5.2	4.2	3.8	4.5	4.2	4.1	4.5	4.1	3.8	4.6	4.3
Spiracle length	5.5	6.9	6.3	5.2	5.8	5.5	4.9	6.1	5.6	5.5	6.2	5.9
Orbit and spiracle length	10.0	11.8	10.5	9.4	10.2	9.8	10.0	11.0	10.5	9.2	10.9	10.3
Interorbital width	11.9	13.0	12.5	10.9	11.6	11.3	10.3	12.3	11.1	10.0	11.6	10.9
Intereye width	16.3	18.6	17.5	16.1	17.5	16.6	16.2	17.2	16.7	15.7	16.8	16.4
Distance between spiracles	16.7	18.0	17.1	15.4	16.8	16.1	16.7	17.4	17.0	15.5	16.4	16.0
Head length (direct)	56.4	59.3	57.6	52.3	57.6	56.0	54.6	58.8	56.6	55.1	57.5	56.3
Snout, prenasal (direct)	23.5	26.6	25.0	24.2	26.6	25.4	22.7	25.0	23.5	23.4	26.6	24.9
Nostril length	3.6	5.2	4.3	4.2	4.9	4.5	3.8	4.9	4.5	4.4	5.1	4.7
Nasal curtain, length	6.4	7.1	6.8	5.4	6.9	6.2	6.7	7.8	7.4	6.3	7.1	6.8
Nasal curtain, width	11.2	14.1	12.7	10.9	11.7	11.3	12.9	14.5	13.2	11.0	12.6	11.7
Distance between nostrils	11.3	12.9	12.0	10.5	11.1	10.8	12.2	13.7	12.6	10.8	11.4	11.0
Snout, preoral (direct)	29.4	32.4	31.1	29.1	33.0	31.5	28.2	31.6	29.7	29.8	32.8	31.0
Mouth width	8.8	9.9	9.5	8.3	8.8	8.5	9.0	10.2	9.7	8.3	10.2	9.0
Width, 1st gill slit	2.7	3.3	2.9	2.6	3.4	3.0	2.7	3.7	3.0	2.6	3.2	2.9
Width, 3rd gill slit	2.9	3.7	3.4	2.9	3.6	3.2	3.1	3.9	3.4	3.1	3.7	3.3
Width, 5th gill slit	1.7	2.3	1.9	1.6	2.5	2.1	1.9	2.2	2.1	1.9	2.5	2.1
Distance between 1st gill slits	22.3	25.1	23.2	21.3	22.4	21.9	23.0	24.4	23.8	22.3	24.4	23.3
Distance between 5th gill slits	15.1	16.5	15.7	14.1	15.3	14.8	14.6	16.5	15.6	14.6	16.6	15.4
Length pelvic fin	20.7	23.4	22.3	20.0	23.3	21.2	22.0	24.5	23.3	18.6	24.0	22.4
Width across pelvic fin base	12.9	15.2	13.8	13.7	18.7	16.6	13.8	15.5	14.8	15.4	17.8	16.9
Greatest width across pelvic fins	-	-	-	-	-	-	40.4	42.5	41.6	34.3	42.1	37.8
Tail width, axil of pelvics	8.1	10.4	9.6	10.0	11.2	10.7	7.4	9.1	8.8	9.2	11.2	10.0
Tail height, axil of pelvics	5.4	6.5	5.8	5.2	6.5	5.9	5.3	6.1	5.6	5.4	6.6	5.9
Tail width, base of sting	3.7	6.4	5.2	4.1	5.4	4.8	4.2	5.6	5.3	5.1	5.9	5.5
Tail height, base of sting	3.0	4.0	3.5	2.9	3.6	3.3	3.3	3.9	3.8	3.5	4.2	3.8
Cloaca length	4.0	5.6	4.9	4.5	7.3	5.8	4.5	5.3	4.9	4.9	7.2	5.9
Clasper, postcloaca length	13.0	22.6	20.2	-	-	-	20.6	22.8	21.3	-	-	-
Clasper, length from pelvic axil	7.5	20.3	15.1	-	-	-	9.3	17.1	15.7	-	-	-
Pect. insertion to sting origin	25.1	32.1	28.1	24.8	30.9	27.8	20.2	26.7	23.4	20.7	27.0	23.7
Cloaca origin to sting	29.4	37.1	32.2	29.7	35.6	33.4	26.8	31.3	28.7	28.8	31.3	30.1
Caudal sting 1 length	-	-	-	-	-	-	-	-	-	-	-	-
Caudal sting 2 length	-	-	-	-	-	-	-	-	-	-	-	-

3.2.4. *Brevitrygon javaensis* (Last & White, 2013)

[Javan whipray]

(Figures 2–6, 12, 13, 30–32, and 39; Table 5)

Himantura javaensis Last & White 2013: 11–19, figs, tab., Cilacap landing site, Central Java, Indonesia, 10 June 2002. Holotype: MZB 21461, female 164 mm DW (original description) [17].

Himantura cf. *walga*: White et al. 2006, 260, figs (images are of holotype) [57].

Himantura sp. 1: Ward et al. 2008, accessory publication 1 (page 1 of tree; 4 of the *H. javaensis* paratypes) [58].

Holotype. MZB 21461, female 164 mm DW, Cilacap landing site, Central Java, Indonesia, 10 June 2002.

Material examined. Paratypes. (10 specimens) CSIRO H 5859-01, female 190 mm DW, CSIRO H 5859-03, adult male 212 mm DW, Cilacap landing site, Central Java, Indonesia, 17 April 2001; CSIRO H 5860-08 (Genbank accession EU398861), female 197 mm DW, CSIRO H 5860-11 (Genbank accession EU398860), female 234 mm DW, CSIRO H 5860-12, female 198 mm DW, CSIRO H 5860-14, female 170 mm DW, Cilacap landing site, Central Java, Indonesia, 22 March 2002; CSIRO H 6129-01, adolescent male 173 mm DW, Cilacap landing site, Central Java, Indonesia, 23 March 2002; AMS I 46280-001, juvenile male 120 mm DW, NMV A 30997-001, adult male 210 mm DW, MZB 15053 (Genbank accession EU398859), female 171 mm DW, MZB 15060 (Genbank accession EU398858), male 169 mm DW, Cilacap landing site, Central Java, Indonesia, 10 January 2002. Other material. (3 specimens) MZB 15055, male 144 mm DW, Cilacap landing site, Central Java, Indonesia, 23 March 2002; MZB 15057, female 231 mm DW, MZB 15061, female 173 mm DW, Cilacap landing site, Central Java, Indonesia, 10 January 2002; GN11216, Cilacap, Indonesia; GN11219, Cilacap, Indonesia; GN11220, Cilacap, Indonesia; GN6954, Cilacap, Indonesia.

Diagnosis. A species of the genus *Brevitrygon* (to at least 23 cm DW) distinguished by the following combination of features: snout length 28–30% DW, angle 104–111°; disc length equal to or slightly longer than its width; orbit small, diameter 5–6% DW; nostrils short, length 3–4% DW, and internasal space narrow, 9–10% DW; tail very slender, 2.1–2.2 times DW, prominent median groove on ventral surface, skin folds absent on both dorsal and ventral surfaces (Figure 30); tail with paired dorsolateral rows of short oblique denticles, each partly concealed in a depression highlighted by dense cluster of melanophores (Figure 3f); pelvic fins relatively small, length 17–20% DW; postcloacal length to 19% DW; 1–3 (usually 1) small, seed- or heart-shaped scapular denticles (length <2 mm), no scute-like thorns on dorsal surface of disc or tail; secondary denticle band well developed and sharply demarcated in adults, very narrow over branchial region, broadest over abdomen, then converging posteriorly near pectoral-fin insertions; dorsal disc mainly uniformly brownish, tail appearing speckled due to rows of melanophore clusters; ventral disc and tail white with dark margins on pectoral and pelvic fins, and dark blotches over first 4 gill slits; oral papillae 4; pectoral-fin radials 103–108; total vertebral count (excluding first synarcual centra) 96–100.

Description. Following Last & White [17] with no additional material available; morphometric data provided in Table 5. Disc variably suboval and pointed anteriorly (Figures 31 and 32), width 0.95–1.00; maximum thickness 7–9% DW. Snout angle 104–111°; disc width 2.04–2.14 and distance from snout tip to pectoral-fin insertion 1.88–1.98 times distance from snout tip to point of maximum width, respectively. Pelvic fin length 17.3–19.7% DW; width across base 15.1–17.9% DW, 1.06–1.19 in pelvic-fin length. Tail very slender in both sexes, semi-rigid, long, length 2.09–2.21 times DW, 2.35–2.49 times precloacal length; tapering gradually and evenly toward sting, then with very weak taper beyond sting to finely pointed tail tip; base relatively narrow, moderately depressed, its width 1.41–1.84 times its height at pelvic-fin insertions; slightly less depressed below sting base, its width 1.32–1.46 times its height at base of sting; sting not positioned well forward on tail, distance from cloaca origin to sting 2.09–2.33 in precloacal length, 37–40% DL; dorsal groove

housing caudal sting(s) tapering gradually and persistent for about snout length behind sting base; in adults posterior tail subrectangular, its dorsal surface almost flat, ventral surface with shallow median furrow, lateral edge weakly convex. Preoral snout length 3.23–3.80 times mouth width, 2.85–3.26 times internarial distance, 1.32–1.43 times distance between first gill slits; direct preorbital snout length 2.28–2.62 times interorbital length; eye length 1.54–1.94 in spiracle length; orbit diameter 0.95–1.22 in spiracle length, interorbital distance 1.91–2.45 times orbit, intereye distance 4.07–4.92 times eye length. Spiracles large, length 5.6–6.6% DW. Nostril length 2.43–2.80 in internasal distance; internasal distance 2.35–2.77 in prenasal length. Nasal curtain width 1.85–2.16 times length. Mouth width 7.5–9.1% DW, 1.07–1.23 in internasal width; profile moderately arched but variably, not obviously more so in adult male than in large females; upper jaw strongly double concave, dorsal to lower jaw; lower jaw concave near symphysis, largely concealing and slotting into expanded symphysial knob of upper jaw; oronasal groove prominent, deep; skin along margin of lower jaw barely corrugated, confined to narrow strip around lips. Teeth of adult male with larger cusps in upper jaw than in lower jaw; upper jaw teeth suboval to rhomboidal, largest near symphysis and on lateral knobs, more strongly cuspid near jaw angle; lower jaw teeth in strong quincunx, suboval near symphysis, more cuspid near jaw angle. Female teeth more broadly oval, in strong quincunx, largely acuspid. Tooth rows ~38–42 in upper jaw. Floor or mouth with 4 well-developed, simple, slender, elongate oral papillae; a pair situated close together centrally and one on either side of mouth near its corners; medial papillae slightly longer than those near corner. Length of first gill slit 1.15–1.65 times length of fifth, 2.28–3.06 in mouth width; distance between first gill slits 2.09–2.43 times internasal distance, 0.39–0.42 of ventral head length; distance between fifth gill slits 1.30–1.55 times internasal distance, 0.24–0.26 in ventral head length.

Squamation. Ontogenetic stages (definitions following Manjaji [3] and Last et al. [12]) 2 and 4, evident from type series; Stages 3, 5, and 6 appear to be inapplicable; denticle development relatively rapid, no obvious sexual dimorphism.

Developmental *Stages 0–1*: no specimens available. *Stage 2* (based on juvenile male 120 mm DW): squamation consisting of 2 slightly enlarged, seed-shaped, scapular denticles surrounded by narrow band of primary denticles; primary denticles small, flattened, heart-shaped; a smaller patch of denticles either side of scapular denticles. Small median patch of interspiracular denticles anteriorly, forming loose connection with scapular band. Posterior-most denticles of scapular band about an orbit diameter behind scapular denticles. Remainder of body naked, apart from small, widely spaced, upright denticles on dorsal surface of tail behind sting. *Stage 4* (164–234 mm DW): secondary denticle band well developed (Figure 4), relatively consistent in shape in adults; semi-truncate just forward of orbit, covering most of interorbit, usually narrowing slightly at interspiracular space, constricted over branchial region; usually broadest over abdominal region with its lateral margins converging posteriorly to merge at about level of pectoral-fin insertion or extending onto tail in very narrow medial band a few denticles wide; remainder of disc and pre-sting tail naked; scapular denticles small but distinctly larger than those adjacent. Denticles on post-sting tail in paired dorsolateral and lateral rows, absent from dorsal mid-line of tail; small, partly embedded anteriorly in shallow pockets in dorsolateral rows. No enlarged thorns on tail or disc; scapular denticles 1–3 (mostly 1), seed- or heart-shaped, 2–4 mm long, 1.5–3 mm wide (1.1–2.1% DW), distance from edge of spiracle 18.9–19.9% DW; distance of denticle band from snout tip 24.8–27.5% DW; width of band across interorbit 10.2–11.1% DW; narrowest width of band preceding scapular region 6.8–9.3% DW; width of band at scapulocoracoid 20.3–25.0% DW; width of band over abdomen 25.1–30.6% DW; width of band at pectoral-fin insertion 0.9–5.8% DW. Caudal stings 2 in one paratype but broken off near their bases; missing from all other types.

Meristics. Total pectoral-fin radials 103–108, n = 9 for all radial counts; propterygials 46–49, mesopterygials 11–13, and metapterygials 43–47. Total pelvic-fin radials 17–19 + clasper in males, 23–27 in females. Total vertebral segments (excluding first synarcual

centra) 96–100, n = 5–8 for all vertebral counts; monospondylous centra (excluding first synarcuals) 35–37; n = 9; diplospondylous centra 60–64, n = 4.

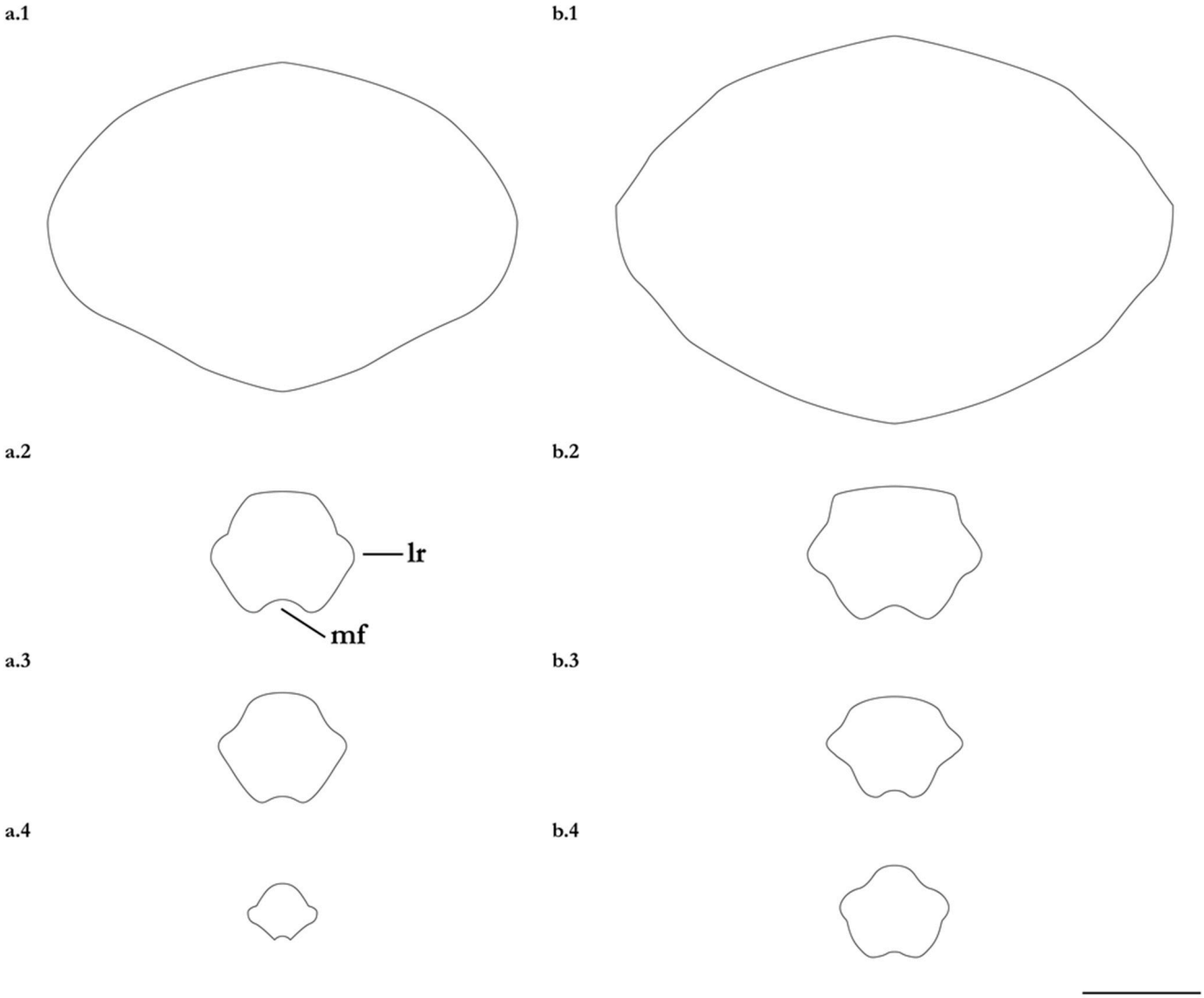

Figure 30. Schematic cross-sections of the post-sting tail of *Brevitrygon javaensis* for (**a**) paratype CSIRO H 6129-01, adolescent male 173 mm DW, Cilacap, Indonesia; and (**b**) paratype CSIRO H 5860-08, female 197 mm DW, Cilacap, Indonesia. Sections taken at: 1. sting origin; 2. axis 25% distance from origin; 3. through midlength; and 4. axis 75% distance from origin. Abbreviations: mf = median furrow or groove, lr = lateral ridge. Scale bar: 2 mm.

Coloration. *When fresh* (Figure 31): dorsal surface of disc, pelvic fins, and tail uniformly brownish or tan, outer margin of disc slightly paler brown; secondary denticle band slightly paler brown and well defined; eye blackish, darker than rest of orbit. Ventral surface whitish with a broad, well-defined, continuous, dusky band along outer margins of pectoral and pelvic fins; dusky area commencing at about level of mouth then extending to hind part of pectoral fin, its greatest width (slightly exceeding width of internasal flap) near pectoral-fin apex; prominent dusky blotches over anterior 4 gill slits; tail uniformly white. *In preservative* (Figure 32): similar to above, dusky areas on ventral surface becoming more greyish brown and dark branchial region becoming more contrasted with pale ventral surface.

Size. Reaches at least 243 mm DW; males mature at 17–18 cm DW and females mature at 18 cm DW [6]. White & Dharmadi [59] observed 654 specimens from the Cilacap fish landing site between 92 and 243 mm DW. Size at birth 5–9 cm DW.

Table 5. Morphometric data for all types of *Brevitrygon javaensis* based on Last & White [17]. Measurements expressed as percentages of disc width (mm).

	Min	Max
Disc, width (mm)	164	234
Total length	296.3	309.2
Disc, length (direct)	99.8	105.5
Disc, thickness	11.0	13.5
Snout to origin of cloaca	83.8	89.5
Cloaca origin to tail tip	209.8	220.7
Snout to pectoral insertion	90.9	96.6
Snout to maximum width	46.8	49.0
End of orbit to pectoral insertion	57.2	61.5
Snout, preorbital (direct)	28.3	30.2
Snout, preorbital (horizontal)	26.2	29.1
Orbit diameter	5.1	6.0
Eye diameter	3.2	3.8
Spiracle length	5.6	6.6
Orbit and spiracle length	9.3	9.9
Interorbital width	11.4	12.9
Intereye width	15.1	16.7
Distance between spiracles	17.0	18.4
Head length (direct)	52.1	55.5
Snout, prenasal (direct)	24.1	26.0
Nostril length	3.3	3.9
Nasal curtain, length	10.0	11.9
Nasal curtain, width	4.8	5.7
Distance between nostrils	9.0	10.3
Snout, preoral (direct)	28.6	30.7
Mouth width	7.5	9.1
Width, 1st gill slit	2.8	3.4
Width, 3rd gill slit	2.8	3.3
Width, 5th gill slit	2.0	2.8
Distance between 1st gill slits	20.5	22.3
Distance between 5th gill slits	13.2	14.3
Length pelvic fin	17.3	19.7
Width across pelvic fin base	15.1	17.9
Greatest width across pelvic fins	33.7	42.2
Tail width, axil of pelvics	8.3	10.0
Tail height, axil of pelvics	5.2	6.7
Tail width, base of sting	3.8	4.6
Tail height, base of sting	2.9	3.2
Cloaca length	5.5	7.3
Clasper, postcloaca length	18.4	18.9
Clasper, length from pelvic axil	8.1	8.7
Pect. insertion to sting origin	33.9	39.1
Cloaca origin to sting	38.1	42.1
Caudal sting 1 length	-	-
Caudal sting 2 length	-	-

Distribution. Caught only by trammel net fishers in the prawn fishery of coastal central southern Java (Indonesia); considered Endangered on the IUCN Red List [60], very restricted with its range extending from Tjikaret to Pacitan. It occurs in inshore coastal habitats adjacent to mangroves, close to heavily human populated areas, making it accessible to fishers (Fahmi unpubl. data 2020). In recent years, these habitats have declined across Indonesia by more than 30% [61,62]. Initially collected at the Cilacap fish landing site (Figure 13), its range has not been significantly extended from fish landing surveys in western and eastern Java, Bali, and Lombok (Fahmi, pers. comm.). Exact fishing grounds remain unknown.

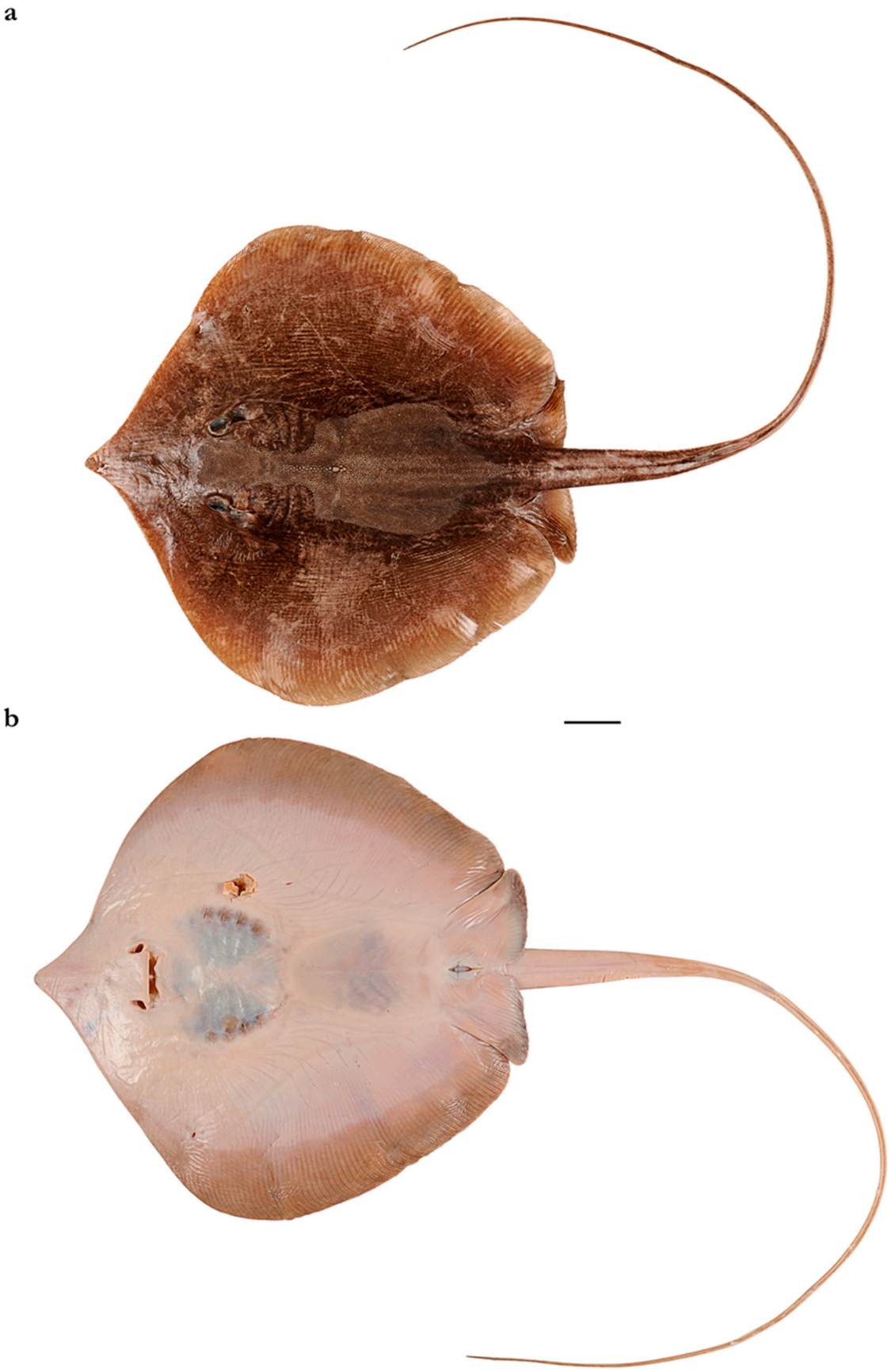

Figure 31. *Brevitrygon javaensis*, holotype MZB 21461, female 164 mm DW, Cilacap, Indonesia: (**a**) dorsal surface (fresh); (**b**) ventral surface (preserved). Scale bar: 2 cm.

Figure 32. *Brevitrygon javaensis*, paratype CSIRO H 6129-01, adult male 173 mm DW, Cilacap, Indonesia: dorsal surface (preserved).

Etymology. Named with references to the regional occurrence of this stingray, with the Latin suffix *-ensis* denoting the location: off Java (Indonesia). The species is presently considered to be locally abundant and endemic to the region.

3.2.5. *Brevitrygon manjajiae* sp. nov.

The species is registered in ZooBank under urn:lsid:zoobank.org:act:DA6B5F74-8CB6-4FDD-9688-7116E2FF5D87.

[Sandwich-tail Whipray]

(Figures 2–6, 12, 13 and 33–39; Table 6)

Trygon walga (Müller & Henle, 1841): MNHN 2337 (former syntype), adult male 198 mm DW, Red Sea (misidentification based on newly designated lectotype) [36].

Dasyatis imbricata (non Bloch & Schneider): Dor 1984: 17 (listed) [29].

Dasyatis walga (non Müller & Henle): Krishnan & Mishra 1993 (misidentification) [39].

Himantura imbricata (non Bloch & Schneider): Goren & Dor 1994 (misidentification) [63].

Himantura walga (non Müller & Henle): Last & Compagno 1999 (misidentification in part) [2].

Brevitrygon walga (non Müller & Henle): Last et al. 2016, 360 (misidentification in part) [1].

Holotype. USNM 222555, adult male 231 mm DW, off Miani Hor, Pakistan, Arabian Sea, 25°11′ N, 66°20′ E, collected RV *Anton Bruun*, 8 December 1963 (Figure 33).

Figure 33. *Brevitrygon manjajiae* **sp. nov.**, holotype USNM 222555, adult male 231 mm DW, Miani Hor, Pakistan, Arabian Sea (preserved): (**a**) dorsal surface; (**b**) ventral surface. Scale bar: 2 cm.

Paratypes. 24 specimens: CSIRO H 7627-02, adult male 174 mm DW, CSIRO H 7627-03, adult male 226 mm DW, Karachi fish market, Pakistan, August 2014; MNHN 7924, immature female 174 mm DW, Indian Ocean; USNM 470881(2), adult male 223 mm DW, adult male 217 mm DW, collected with holotype; LACM 38129-83(1), female 176 mm DW, LACM 38129-83(2), immature male 179 mm DW, LACM 38129-83(3), immature male 157 mm DW, WNW Korangi Creek, Sindh, Pakistan, 24–25 April 1978; USNM 222585, adult male 210 mm DW, off Gulf of Kutch, Gujarat, India, 22°21′ N, 68°42′ E, 14 fathoms (=26 m), 18 November 1963; USNM 222624(1), adult female with pup, 228 mm DW, USNM 222624(2), adult male 218 mm DW, USNM 222624(3), adult male 222 mm DW, USNM 222624(4), adult male 220 mm DW, off Bombay [=Mumbai], India; LACM 38130-60(1) adult male 213 mm DW, LACM 38130-60(2) adult male 227 mm DW, LACM 38130-60(3) adolescent male 203 mm DW, LACM 38130-60(4) female 176 mm DW, 20 km off Paitiani Creek, Sindh, Pakistan; LACM 38133-56(2 of 15), female 187 mm DW, adult male 236 mm DW, near Turshian Creek, Sindh, Pakistan, 26 April 1978; LACM 38314-24, adult male 246 mm DW, Sonmiani Bay, Baluchistan, Pakistan; LACM 38134-37, female 207 mm DW, off mouth of Hojambro Creek, Sindh, Pakistan; ZMH 1385, Arabian Sea, Alibag, India, 13 November 1955; ZMH 4465, Karachi, Pakistan, 1969.

Other material. 11 specimens: BPBM 33199(1), immature male 103 mm DW, BPBM 33199(2), female 187 mm DW, Kuwait, Persian/Arabian Gulf; CSIRO H 7625-04, adult male 200 mm DW, Karachi fish market, Pakistan, April 2014; CSIRO H 7627-01, female 207 mm DW, Karachi fish market, Pakistan, August 2014; MCZ 59269(1), adult male 167 mm DW, MCZ 59269(2), female 155 mm DW, MCZ 59269(3), female 136 mm DW, MCZ 59269(4), immature male 121 mm DW, MCZ 59269(5), female 90 mm DW, Khor Al-Subbiyah, Kuwait, Persian/Arabian Gulf, 29°30′ N, 49°15′ E, 9 August 1982; GN14196, Gulf of Oman, Iran; GN14355, Persian Gulf, Iran; GN1441, Genaveh, Iran; GN14417, Genaveh, Iran; GN14425, Genaveh, Iran; GN14436, Gulf of Oman, Iran; GN1693, Mumbai, India; GN18820, Mumbai, India; GN6580, Persian Gulf, Iran; GN6672, Gulf of Oman, Iran; GN7797, Kuwait City, Kuwait; GN9441, Mirbat, Oman.

Diagnosis (*based on Arabian Sea material*). A *Brevitrygon* (to at least 25 cm DW) distinguished by the following combination of features: snout length 28–30% DW, angle 108–113°; disc longer than wide; orbits small, diameter 5–6% DW; nostrils 4–5% DW and internasal width 11–13% DW; tail relatively short, longer in males (1.3–1.5 times DW) than females (0.9–1.3 times DW), with rudimentary, ridge-like ventral fold and fleshy lateral ridges (Figure 34); pelvic fins relatively small, length 17–19% DW; postcloacal length of clasper to 19% DW; 1–5 (usually 1) small, seed- or heart-shaped scapular denticles, no scute-like thorns on dorsal surface of disc; secondary denticle band well developed and sharply demarcated in adults, not strongly constricted over branchial region, width across scapulocoracoid and over abdomen subequal, then converging posteriorly near pectoral-fin insertions; tail with well-developed denticle band forward of sting, with 3–8 enlarged seed to weakly lanceolate denticles or small thorns (typically 2.5–5 mm long); dorsal surface mainly uniformly brownish when skin undamaged, disc margin slightly paler brown; ventral disc, pelvic fins, and tail white, margins of pectoral and pelvic fins dark; pectoral-fin radials 102–111; total vertebral count (excluding first synarcual centra) 87–101.

Description. Morphometric data provided in Table 6. Disc broadly suboval and pointed anteriorly (Figures 33 and 35), width 0.97 times length in adult male holotype (0.95–0.99 in 10 adult and adolescent paratypes); maximum thickness 13% (11–13)% DW. Snout angle 110° (108–113°); disc width 2.13 (2.02–2.33) and distance from snout tip to pectoral-fin insertion 2.00 (1.84–2.08) times distance from snout tip to point of maximum width, respectively. Pelvic-fin length 19.3% (17.1–19.3)% DW; width across base 16.3% (12.7–16.8 in adult males, 16.9–18.3 in females and juveniles)% DW, 1.19 (1.01–1.47) in pelvic-fin length. Tail very slender, flexible beyond sting, shorter in adult females than males, length 1.37 (1.34–1.53 in males, 0.94–1.30 in females) times DW, 1.56 (1.43–1.82) times precloacal length; tapering gradually and evenly toward sting, then slender, almost filamentous toward tip; base depressed, narrow, surface weakly convex dorsally with

midline not elevated, more convex ventrally, its width 1.48 (1.29–1.57) times its height at pelvic-fin insertions; suboval, both surfaces convex below sting base; sting positioned well forward on tail, distance from cloaca origin to sting 2.45 (2.41–2.84) in precloacal length, 35% (29–36)% DL. Dorsal and ventral surfaces of post-sting tail narrowly convex, separated by one or two fleshy lateral ridges; weak medial furrow housing posterior sting anteriorly on dorsal surface; indistinct rudimentary ridge-like ventral fold visible along mid-tail; dorsal fold and posterior medial grooves weak or absent. Preoral snout length 2.83 (2.98–3.17) times mouth width, 2.41 (2.19–2.72) times internarial distance, 1.17 (1.17–1.26) times distance between first gill slits; direct preorbital snout length 2.18 (2.16–2.41) times interorbital length; interorbital space almost flat, weakly concave across preorbit; eye length 1.23 (1.39–1.75) in spiracle length; orbit diameter 0.86 (0.99–1.33) in spiracle length, interorbital distance 2.09 (2.35–2.84) times orbit, intereye distance 3.89 (3.94–4.65) times eye length. Spiracles large, length 5.3% (5.0–6.7)% DW. Nostril length 2.52 (2.56–3.07) in internasal distance; internasal distance 1.92 (1.80–2.24) in prenasal length. Nasal curtain width 1.72 (1.82–2.04) times length. Mouth width 10.0% (8.8–10.4)% DW, 1.18 (1.16–1.41) in internasal width. Teeth of adult male (CSIRO H 7627-03) slightly larger in upper jaw than in lower jaw; upper jaw teeth in rows, broadly suboval with short cusps, largest near symphysis and on lateral knobs; lower jaw teeth in quincunx, suboval, more strongly cuspid near symphysis (Figure 36a–c); immature male (LACM 38314-24, 246 mm DW) with similar-sized, quincuncial teeth in both jaws, cusps weak. In slightly smaller female (LACM 38134-37, 207 mm DW), teeth more broadly oval, in strong quincunx, acuspid (Figure 36d–f). Tooth rows in CSIRO H 7627-03 and LACM 38129-83, 1 of 3, ~33–46 in upper jaw, ~42–56 in lower jaw, ontogenetic differences in counts likely. Floor or mouth with 2 well-developed, simple, slender oral papillae (LACM 38129-83, 2 specimens; CSIRO H 7627-03); papillae situated centrally, slightly apart. Length of first gill slit 1.18 (1.07–1.50) times length of fifth, 3.26 (2.68–3.70) in mouth width; distance between first gill slits 2.06 (1.78–2.17) times internasal distance, 0.43 (0.40–0.43) of ventral head length; distance between fifth gill slits 1.37 (1.18–1.34) times internasal distance, 0.29 (0.26–0.28) in ventral head length.

Squamation. Ontogenetic stages (definitions following Manjaji [3] and Last et al. [12]) 0, 2, and 4, evident from type series; Stages 3, 5, and 6 appear to be inapplicable or with short phases; denticle development relatively rapid, no obvious sexual dimorphism.

Developmental Stage 0: single female 90 mm DW from Kuwait entirely smooth. *Stage 2*: no specimens available. *Stage 4* (>160 mm DW): secondary denticle band very well developed (Figure 4); scapular denticles large (3–5 mm long, 1.5–2.5 mm wide), largest denticle 2.6 mm long, 2.3 mm wide in adult male holotype, smaller laterally; band margins well defined and slightly irregular; extending well forward of orbit in holotype (distance of denticle band from snout tip 8.8% DW, 16–26% DW in adult paratypes); covering almost entire interorbital space in adults, width of band across interorbit 12.1% (11.7–12.7%) DW; barely constricted over branchial region in holotype, often more so in paratypes (band narrower or broader than on interorbit), narrowest width of band preceding scapular region 21.3 (6.5–13.6)% DW; width of band at scapulocoracoid 29.9% (20.3–23.9)% DW; expanded over abdomen and broadest over posterior disc, width of band 25.5% (18.1–24.3)% DW; width of band at pectoral-fin insertion 5.7% (4.3–8.1)% DW; band well developed on tail, broad (~16–18 denticles wide on mid pre-sting tail in holotype, covering about 1/2 to 3/4 width of tail in dorsal view) with sharply defined margins. No thorns on disc but with 2 slightly enlarged, low, scapular denticles in holotype (usually 1 but up to 5 seed to weakly lanceolate denticles in paratypes), length 2.1% (1.4–2.5)% DW and distance from edge of spiracle 20.9% (18.6–22.4)% DW. Tail with 5 (3–8) slightly enlarged, weakly oblique thorns, and up to 2 additional noticeably smaller denticles in series before sting; thorns irregular in size and spacing on tail; length of first thorn of series 3.3 mm (2.7–3.5 mm), 1.42% (1.31–1.84)% DW; length of last thorn 3.4 mm (2.5–5.1 mm), 1.47% (1.13–2.27)% DW; thorns originating from above tail base to mid pre-sting tail; not progressively increasing in size posteriorly; denticles largely absent from post-sting tail. Caudal stings 2, well developed,

narrowly elongate, pungent; undamaged stings exceeding $^{2}/_{3}$ of snout length in holotype, similar in paratypes.

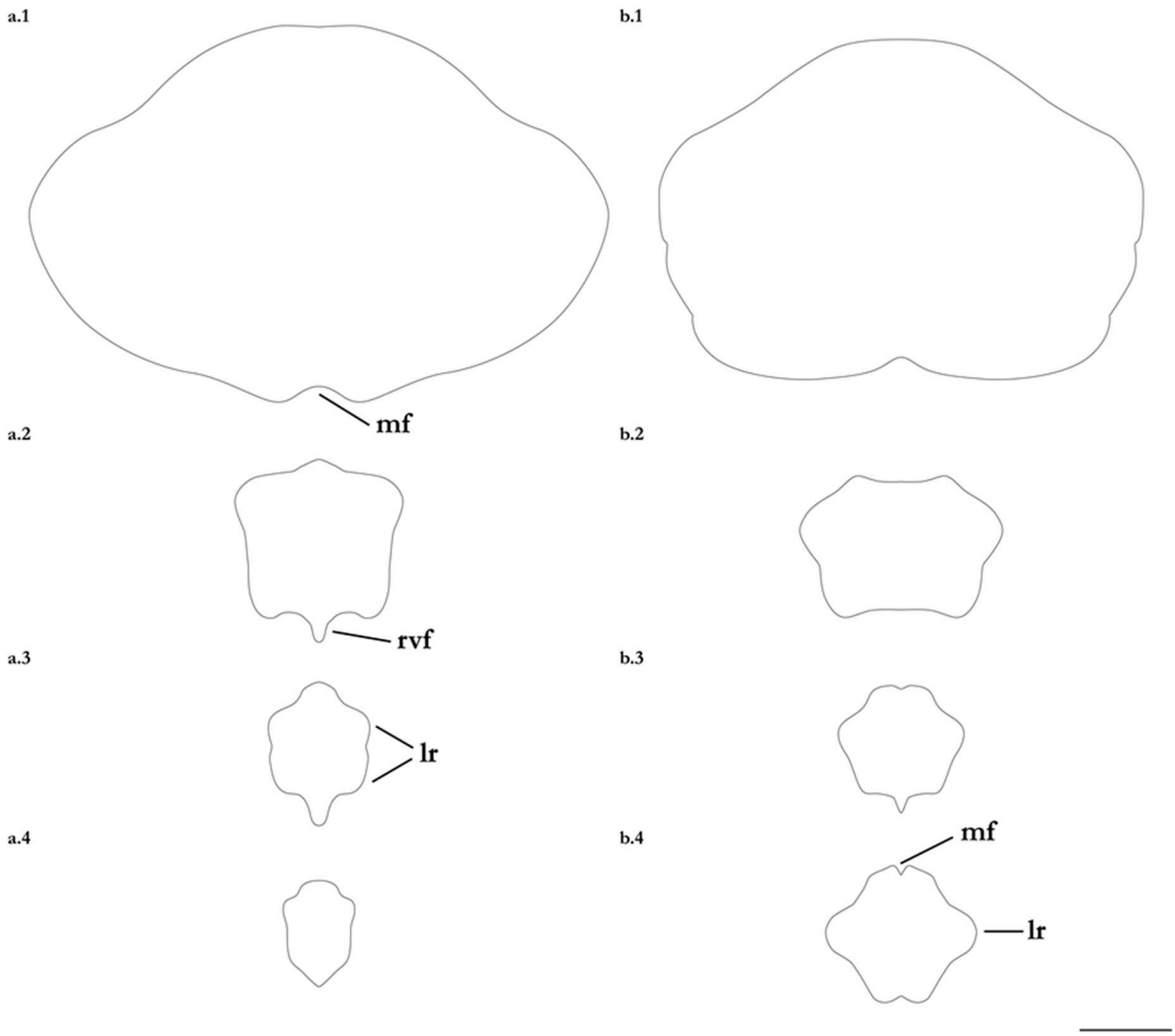

Figure 34. Schematic cross-sections of the post-sting tail of *Brevitrygon manjajiae* **sp. nov.** for (**a**) paratype LACM 38314-24, adult male 246 mm DW, Pakistan; and (**b**) paratype LACM 38134-37 (1 of 2), female 207 mm DW, Pakistan. Sections taken at: 1. sting origin; 2. axis 25% distance from origin; 3. through midlength; and 4. axis 75% distance from origin. Abbreviations: mf = median furrow or groove, lr = lateral ridge, rvf = rudimentary ventral fold. Scale bar: 2 mm.

Meristics. Total pectoral-fin radials 106–107 (102–111, n = 16 for all radial counts); propterygials 48–49 (44–52), mesopterygials 13–14 (10–15), and metapterygials 44–45 (41–47). Total pelvic-fin radials 19+ clasper (16–20 + 1) in males, 19–25 in females. Total vertebral segments 97 (87–101, excluding first synarcual centra; n = 15–16 for all vertebral counts); monospondylous centra (excluding first synarcuals) 39 (32–39); diplospondylous centra 58 (50–66).

Coloration. *When fresh* (based on image from Karachi, H. Osmany): dorsal surface of disc and pelvic fins uniformly brownish or tan, slightly paler toward disc margins and over denticle band. Tail thorns, caudal sting, and inner margins of clasper whitish. Most of ventral surface of disc and pelvic fins white, with sharply defined broad brownish margins; dusky areas on pre-sting tail. Tail beyond sting increasingly dark distally, blackish with evidence of pale lateral margins. *Preserved* holotype (Figure 33) pale brownish dorsally, more yellowish brown laterally; denticle band demarcated, enlarged denticles and thorns

pale; circum-orbital area whitish; post-sting tail dusky dorsally and ventrally with distinct pale lateral margins; ventral disc and anterior tail pale yellowish to whitish.

Table 6. Morphometric data for holotype and 5 paratypes of *Brevitrygon manjajiae* **sp. nov.**, and two other non-type specimens from Kuwait. Measurements expressed as percentages of disc width (mm).

	Pakistan			**Kuwait**	
	Holotype	**Paratypes**		**Non-Types**	
	USNM 222555	**Min**	**Max**	**BPBM 33199**	**MCZ 59269 (1 of 5)**
Disc, width (mm)	231	174	226	187	167
Total length	224.2	220.2	239.0	191.8	238.7
Disc, length (direct)	103.2	101.3	102.9	109.1	107.5
Disc, thickness	12.6	10.6	13.2	10.9	10.1
Snout to origin of cloaca	87.6	84.5	87.2	92.3	93.2
Cloaca origin to tail tip	136.6	134.1	152.2	98.6	145.4
Snout to pectoral insertion	94.0	88.7	93.7	100.2	100.1
Snout to maximum width	47.0	42.9	47.4	46.2	50.7
End of orbit to pectoral insertion	60.5	56.3	59.6	62.6	60.1
Snout, preorbital (direct)	28.5	28.0	30.0	31.1	34.2
Snout, preorbital (horizontal)	27.5	27.2	28.4	29.2	33.8
Orbit diameter	6.2	5.3	6.3	6.5	6.8
Eye diameter	4.4	3.8	4.5	4.4	4.4
Spiracle length	5.3	5.0	6.7	5.8	6.4
Orbit and spiracle length	10.0	9.1	10.5	11.4	11.6
Interorbital width	13.0	12.0	13.8	12.5	-
Intereye width	16.9	15.1	16.8	16.6	-
Distance between spiracles	16.4	16.2	17.7	16.6	-
Head length (direct)	55.8	53.9	56.1	57.0	59.7
Snout, prenasal (direct)	22.5	21.0	24.6	26.3	28.0
Nostril length	4.6	3.6	4.6	4.7	5.0
Nasal curtain, length	7.3	5.6	6.7	7.1	7.0
Nasal curtain, width	12.5	10.8	13.3	11.6	11.6
Distance between nostrils	11.7	11.1	12.4	10.6	11.5
Snout, preoral (direct)	28.2	26.5	30.0	32.1	34.2
Mouth width	10.0	8.8	10.4	9.8	-
Width, 1st gill slit	3.1	2.7	3.6	3.7	3.3
Width, 3rd gill slit	3.4	3.3	3.9	3.5	3.1
Width, 5th gill slit	2.6	2.1	2.8	2.6	2.5
Distance between 1st gill slits	24.1	21.5	23.1	21.9	22.1
Distance between 5th gill slits	16.0	13.6	15.6	14.9	15.0
Length pelvic fin	19.3	17.1	19.3	20.2	18.1
Width across pelvic fin base	16.3	15.9	18.3	18.0	14.9
Greatest width across pelvic fins	36.5	29.8	38.7	35.1	36.6
Tail width, axil of pelvics	8.3	8.1	10.4	9.4	9.8
Tail height, axil of pelvics	5.6	5.4	6.1	6.4	5.8
Tail width, base of sting	4.0	4.2	4.6	4.3	4.8
Tail height, base of sting	3.2	3.4	3.7	3.2	3.8
Cloaca length	5.7	4.6	7.0	7.2	5.9
Clasper, postcloaca length	18.5	11.7	17.1	-	17.9
Clasper, length from pelvic axil	7.2	5.5	7.4	-	8.2
Pect. insertion to sting origin	30.7	28.7	35.9	31.2	30.1
Cloaca origin to sting	35.8	31.5	40.2	37.4	36.0
Caudal sting 1 length	17.4	6.9	21.0	18.2	21.6
Caudal sting 2 length	24.6	23.0	23.5	-	29.6

Size. Males reach at least 246 mm DW (550 mm TL), females to 228 mm DW (439 mm TL). Smallest adult male 200 mm DW, one specimen (LACM 38130-60, 1 of 4) was adolescent at 203 mm DW; five smallest males (103–179 mm DW) were immature. Smallest juvenile, female 90 mm DW (206 mm TL). Westernmost populations (from the Persian/Arabian

Gulf) possibly smaller with a male (MCZ 59269 1 of 5) mature at 167 mm DW (396 mm TL); Moore et al. [64] (as *Himantura imbricata*) reported males mature at about 18 cm DW in Kuwait and Qatar and a female of 23.2 cm DW was gravid in Qatar.

Figure 35. *Brevitrygon manjajiae* **sp. nov.**, paratype LACM 38134-37 (1 of 2), female 207 mm DW, Pakistan (preserved): (**a**) dorsal surface; (**b**) ventral surface. Scale bar: 2 cm.

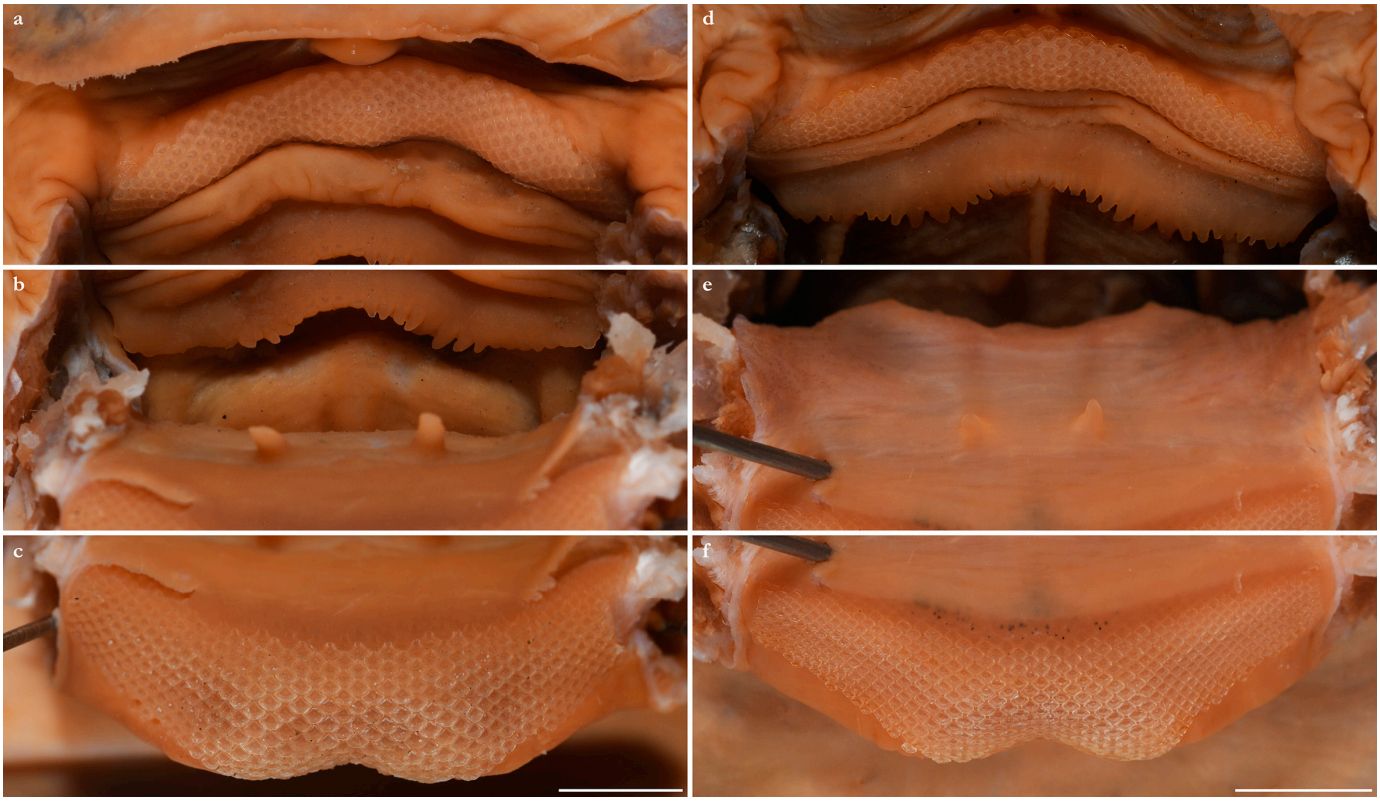

Figure 36. *Brevitrygon manjajiae* **sp. nov.**, upper jaws (**a**,**d**), oral papillae (**b**,**e**), and lower jaws (**c**,**f**) of (**a**–**c**) paratype LACM 38314-24, adult male 246 mm DW, Sonmiani Bay, Baluchistan, Pakistan and (**d**–**f**) paratype LACM 38134-37, female 207 mm DW, off mouth of Hojambro Creek, Sindh, Pakistan. Scale bars: 5 mm.

Distribution. Adult male holotype collected off Miani Hor, Pakistan, by the RV *Anton Bruun*, during a survey of the Arabian Sea in 1963 (Figure 13). Other type material collected from Miani Hor (Pakistan) to Mumbai (western India), but further range extensions east and west are likely with targeted collecting. Western populations from the Persian/Arabian Gulf are likely to be distinct from those to the east; specimens from the northern Gulf (previously reported as *Himantura imbricata*) appear to be different from those in the Arabian Sea (Moore, unpubl. data). Populations from the Red Sea and Gulf of Aden may be non-conspecific. Depth information imprecise but mostly soft substrates of the inner continental shelf at depths to 30 m but occasionally to 40 m (Akhilesh pers. observation, 2 May 2017).

Etymology. Named in honor of Dr. Mabel Manjaji-Matsumoto (University of Malaysia Sabah), for her contribution to the taxonomy of the whiprays (formerly all taxa within the genus *Himantura*). She was the first person to identify a unique feature of the tail coloration of this new species (as a morph of *Himantura imbricata*): dark brown on dorsal and ventral surfaces with white sides, which she called the 'sandwich-tail' (Manjaji [3], 5-254). Dr Manjaji-Matsumoto identified minor differences in the two populations of her '*Himantura imbricata*,' which she tentatively termed 'Kuwait sandwich-tail' and 'Pakistan sandwich-tail'; the tail is slightly darker on the dorsal surface than on the ventral surface in the 'Kuwait sandwich-tail.' The 'Pakistan sandwich-tail' is uniformly dark on both dorsal and ventral surfaces of the tail, although it can be slightly paler on the ridge-like ventral fold.

Vernacular name: Suggested 'Sandwich-tail Whipray' rather than 'Scaly Whipray,' which has been used interchangeably across the region for members of the genus.

Remarks. Stingrays of the genus *Brevitrygon* have been known from the western sector of the Indian Ocean since the early 1800s and subsequently identified as *B. imbricata* and

B. walga (see earlier discussion under *B. walga*). The adult male syntype (MNHN 2337) of Bloch and Schneider's [21] *Trygon walga* from the Red Sea, and now in poor condition (Figure 37), is undoubtedly a *Brevitrygon* but most likely close to, if not conspecific with, *B. manjajiae* sp. nov. Hence, the designation of a lectotype of *B. walga* for another taxon from the Bay of Bengal makes this name inapplicable for the western Indian Ocean species. Another taxon, *Raja obtusa* Ehrenberg in Klunzinger 1871, described from the Red Sea and listed in the synonymy of *B. walga* [18,41], does not belong within the genus *Brevitrygon*. Images of the 430 mm female type (ZMB 7849), much larger than any known *Brevitrygon*, were kindly made available by Edda Aßel and suggest it belongs to *Pateobatis*, possibly *P. fai* rather than *Urogymnus polylepis*. The tail is especially long and has a low, ridge-like fold along its mid-ventral surface.

Figure 37. *Trygon walga* non Müller & Henle, syntype MNHN 0000-2337, adult male 198 mm DW, Red Sea: dorsal surface. Scale bar: 2 cm.

Both *Brevitrygon imbricata* and *B. walga* have been reported from the Arabian Sea off Pakistan by numerous authors and as multiple genera (*Dasyatis*, *Amphotistius* and *Himantura*) [51]. Members of the genus are important to artisanal fisheries in the region and the pectoral fins of large specimens are exported to Thailand and Malaysia. In a study of the species composition, distribution, and conservation of Pakistan stingrays, Moazzam & Osmany [51] concluded that two species of *Brevitrygon* are being landed in regional fish markets; these species, identified as *B. imbricata* and *B. walga*, were differentiated by eight primary character traits, including proportions of the disc, interspiracular distance, nasal curtain shape, tail length, and squamation. Most of these characters are intraspecifically variable within the genus, with the most useful being the interspiracular distance (character 2) and tail length (character 6). It appears as if their Figure 8a,b have been transposed as the tail width, broad in Figure 8a and narrower in Figure 8b, and do not coincide with the character traits specified in their Table 1 (character 7).

Material examined for the present study, from their Table 1 (characters 2, 6), fits the description of their *B. walga* so is most likely conspecific with *B. manjajiae* sp. nov. However, the presence of a second species amongst the Pakistan landings cannot be

unequivocally dismissed as no individuals of any *Brevitrygon* we examined had an interspiracular distance greater than 18% DW (range of types 16.2–18.0% DW) or a tail length exceeding 1.52 (range of types 1.30–1.52) times the DW; Moazzam & Osmany's taxon (identified as *B. imbricata*) had an interspiracular distance exceeding 18% DW (18–19% DW, character 2) and tail length 1.5–1.7 times DW [51]. Only eastern species, *B. walga* (1.6–1.8 in males) and *B. javaensis* (2.1–2.2), have tail lengths well in excess of 1.5 times DW.

Golzarianpour et al. [43], in a morphological and molecular investigation of chondrichthyans of the Persian/Arabian Gulf and Gulf of Oman, concluded that only a single species of *Brevitrygon*, *B. walga* (presumed western variant of *B. manjajiae*) occurs in the region. However, the existence of geographic differentiation within western Indian Ocean populations is weakly supported in (see Section 4 below) and by unpublished molecular data (Naylor); material from the Persian/Arabian Gulf is mildly divergent from specimens of *B. manjajiae* sp. nov. from the Arabian Sea (Pakistan and India). Although the sample size is small, two specimens from Kuwait (BPBM 33199, Figure 38; MCZ 59269, 1 of 5), and possibly one from Pakistan (USNM 470881, 1 of 2), differed subtly in several morphometric characters from the types of *B. manjajiae* sp. nov.; noticeably in disc shape (i.e., snout angle 108–113° in *B. manjajiae* sp. nov. vs. 101–102° in the 'western material'; disc length 101–106% DW vs. 106–109% DW; snout to pectoral-fin insertions 88.7–97.6% DW vs. 99.0–100.2% DW), obvious head proportion differences (i.e., direct preorbital snout length 28.0–30.1% DW vs. 30.7–34.2% DW; orbit diameter 4.7–6.3% DW vs. 6.5–6.8% DW; head length 53.9–56.1% DW vs. 57.0–59.7% DW; preoral length 26.5–30.0% DW vs. 31.3–34.2% DW; prenasal length 21.0–24.6% DW vs. 25.6–28.0% DW; and nasal curtain length 5.6–6.7% DW vs. 7.0–7.2% DW), some other ratios (e.g., preoral length/distance between first gill slits 1.17–1.26 vs. 1.34–1.55; mouth width/length first gill slit 2.68–3.70 vs. 2.48–2.68), and the primary denticle band was closer to the snout tip (length of naked region on snout anterior of main denticle band 15.7–26.4% DW vs. 26.5–30.7% DW) and this band was slightly broader across the scapulocoracoid (width 20.3–23.9% DW vs. 19.5–20.3% DW). Moreover, the two Kuwait specimens appeared to have a more acute snout than all other *Brevitrygon* examined (snout angle 101–102° vs. 105–118°). However, the disc shapes of species of *Brevitrygon* are intraspecific. Potentially diagnostic ratios above were applied to images of two rays (from A. Moore, discarded) and a specimen from the Louisiana State University Museum of Natural Science (LSUMZ 18020, 1 of 3), all taken from the Persian/Arabian Gulf. These three individuals possessed features of both forms but conformed better with the typical eastern *B. manjajiae* populations rather than those from Kuwait. The examination of additional new material from India, Pakistan, and the Persian/Arabian Gulf is needed to clarify the issue of conspecificity within *B. manjajiae* and to ascertain the existence, or otherwise, of *Brevitrygon* in the Red Sea and nearby Gulf of Aden.

Figure 38. *Brevitrygon manjajiae* **sp. nov.**, non-type BPBM 33199 (2 of 2), female 187 mm DW, Kuwait: dorsal surface, preserved. Scale bar: 2 cm.

4. Discussion

4.1. Interspecific Comparisons

Members of the genus *Brevitrygon* are morphologically variable and superficially similar to each other, so despite subtle differences in squamation and characteristics of the tail, it is understandable their identities have been confused. Combine this taxonomic impediment with their longstanding nomenclatural complexities, and the task even for specialist identifiers is difficult. Like other members of the subfamily Urogymninae, the group has a median denticle band on the dorsal surface of adults and lacks a pronounced ventral fold on the tail [1], although small or rudimentary fold(s) are present in some species. The tail exhibits marked sexual dimorphism in length and shape in adults, with females of some species having a shorter, more distally expanded tail than males. *Brevitrygon* species (attaining ~25 cm DW as adults) are amongst the smallest members of the subfamily.

All species are confirmed to have a secondary denticle band, and most possess enlarged scapular denticles and/or small thorns along the dorsal midline of the tail in adults. Only in *B. javaensis* is the pre-sting tail partially naked and thorns or enlarged denticles always absent. *Brevitrygon javaensis* has the longest tail of any member of the genus (undamaged tail 2.4–2.5 times precloacal length and 3.0–3.1 times DW vs. 0.7–1.9 and 1.6–2.6, respectively, in all other species). The known geographic range of *B. javaensis,* which has been expanded little since it was described a decade ago, overlaps with *B. heterura* in southern Indonesia. Apart from tail and squamation, the species differ in the following: *B. javaensis* has a higher vertebral count (total segments excluding first synarcual centra 96–100 vs. 84–94 in *B. heterura*), a more posteriorly positioned sting (distance from pectoral-fin insertion to sting origin 34–39% vs. 20–32% DW), slightly shorter adult claspers (post-cloacal length 18–19% vs. 20–23% DW), shorter pelvic fin (length 17–20% vs. 19–25% DW, 27% DW in lectotype),

shorter distance between the 5th gill slits (length 13–14% vs. 14–17% DW), and typically shorter nostril (length 3.3–3.9% vs. 3.6–5.3% DW) and nasal curtain (length 4.8–5.7% vs. 5.1–8.2% DW). In *B. heterura*, the secondary denticle band is broad and continues along the dorsal surface of the pre-sting tail (either weakly represented or absent in *B. javaensis*) with 1–7 median thorns (absent in *B. javaensis*).

Arguably the most distinctive member of the genus is *B. imbricata*, easily distinguished from the four other *Brevitrygon* species by its short tail with small but well developed, low fleshy dorsal and ventral folds (vs. absent dorsally and rudimentary or absent ventrally), distinctive cruciate pattern of the secondary denticle band over the scapulocoracoid, and comparatively narrow band of these denticles posteriorly (width over mid-abdomen less that eye length wide, less than 5% DW vs. well-formed and usually exceeding 18% DW in adults). The range of *B. imbricata* may overlap with *B. walga* (off eastern India) and *B. heterura* (in the western North Pacific). More collecting in fish markets of the region is needed to define their contemporary ranges.

Brevitrygon heterura differs subtly from *B. walga* and *B. manjajiae* sp. nov. in morphometry, squamation, tail morphology, and distribution. The tail of the adult female of *B. heterura* is often very short (0.6–1.3 times DW vs. 1.2–1.6 times DW in *B. walga*) and expanded distally, becoming unusually bulbous and thickest towards its tip (often terminating as a slender filament); this bulbous structure was originally compared to the shape of a mangrove seed [37] and later to the shape of a green bean [20]. The post-sting tail of adult female *B. walga* is usually expanded slightly and extends over a greater length than *B. heterura*. The eyes of *B. heterura* are noticeably larger than the other species (orbit diameter typically 6–8% DW vs. 5–6% DW), and, like *B. manjajiae* sp. nov., the snout is shorter and broader than *B. walga* (length 28–30% DW vs. 31–34% DW; snout angle typically 107–113° vs. 103–108°); a long narrow snout, more similar to *B. walga*, is evident in some Persian/Arabian Gulf material of *B. manjajiae* sp. nov. (snout length 31–34% DW, angle 101–102°). The claspers of *B. heterura* appear to be larger than those of *B. walga* (postcloacal length to 23% DW vs. to 17% DW in material examined). The secondary denticle bands of the three species are well developed in adults, covering most of the interorbital space, becoming slightly constricted over the brachial region, then expanded laterally over the scapulocoracoid and abdomen before tapering to the mid-dorsal tail. Unlike some other ray genera, counts of pectoral-fin radials and vertebral centra are intraspecifically variable and not of significant use for distinguishing these taxa. Similarly, tooth row counts appear to increase with growth and are of limited value in discriminating species. *Brevitrygon heterura*, which seems to be confined to the Indo-Malay Archipelago (western North Pacific and eastern Indian Ocean), does not appear to overlap with the distributions of *B. walga* and *B. manjajiae* sp. nov.

In addition to characters discussed above, *Brevitrygon manjajiae* sp. nov. from the Arabian Sea differs from other members of the genus in the following: *B. walga* has a shorter tail in both adult males (length 1.3–1.5 times DW vs. 1.6–1.8 times DW) and females (length 1.0–1.3 times DW vs. 1.2–1.6 times DW), a noticeably more acute snout (angle 103–108° vs. 108–113° in *B. manjajiae* sp. nov.), a typically more elongate disc (direct length 104–112% DW vs. 101–106% DW, snout to pectoral insertion 95–103% DW vs. 89–98% DW, precloacal length 91–100% DW vs. 84–91% DW), possibly slightly longer stings (length of first reaching 28%, second to 31% vs. 21% and 28%, respectively), and longer measurements around the head (head length 57–61% DW vs. 54–56% DW; preoral length 31–35% DW vs. 27–30% DW; prenasal length 26–30% DW vs. 21–25% DW). While both species have well-developed fleshy lateral ridges on the post-sting tail, and both have a rudimentary ventral fold present or absent, a striking dark and pale 'sandwich-like' color pattern of the post-sting tail is much more evident in fresh material of *B. manjajiae* sp. nov. *Brevitrygon heterura* has larger orbits (diameter 6–8% DW vs. 5–6% DW), pelvic fins (length 19–24% DW vs. 17–19% DW), claspers (length to 23% DW vs. to 19% DW), and thorns on the tail (longest typically 4–7 mm vs. 2–5 mm in *B. manjajiae* sp. nov.). The denticle band is usually more deeply incised over the branchial region in *Brevitrygon heterura*. Both *B. imbricata*

and *B. javaensis* are distinguishable from *B. manjajiae* sp. nov. in aspects of morphology, squamation, and tail length and shape as outlined above.

Limited material of neonatal/early juveniles of each species were available for examination. General shape of the disc was similar between the species, with subtle differences in the snout extension, being noticeably less pronounced in *B. imbricata* and *B. manjajiae* sp. nov. juveniles examined (Figure 12). Disc lengths of similar-sized specimens were proportionally longer in *B. imbricata* and *B. walga* (precloacal lengths 90–92% DW) than *B. heterura* and *B. javaensis* (precloacal length 88–90% DW); juveniles of *B. manjajiae* sp. nov. from Kuwait had the shortest disc (precloacal length 84–87% DW). The dorsal surfaces of all species, apart from *B. javaensis* (the largest of these specimens, AMS I 4628-01, 117 mm DW), were naked; *B. javaensis* has an obvious heart-shaped scapular thorn, as well as some development of the secondary denticle band on the post-orbital disc.

Interspecific differences in the relative tail lengths between adults of these species is consistent in the juveniles. *Brevitrygon javaensis* have the longest tails in both juveniles and adults (i.e., TL 3.2 times DW in AMS I 4628-01 and 3.0–3.1 times DW in intact adults). The tails of juvenile *B. imbricata* were shorter (TL 2.0–2.1 times DW, n = 2) than the other species (i.e., *B. walga* TL 2.3–2.4 times DW, n = 2; *B. heterura* 2.3–2.6, n = 5; and *B. manjajiae* sp. nov. from Kuwait, 2.2, n = 2). The dorsal and ventral folds on the post-sting tail of *B. imbricata* were evident as low fleshy ridges in the two juveniles examined (85–116 mm DW); a long, much more slender ridge (presumably a rudimentary fold) is visible along the ventral midline of some juveniles of the other species.

4.2. Phylogenetic Relationships

In the maximum likelihood tree (Figure 39), derived from the alignment of NADH2 sequences of different species of *Brevitrygon* from the Indo-West Pacific, localities sampled showed that sequences of all five species fall into well-supported monophyletic, species-level groups (~0.015 to >0.05 substitutions/site). Freshwater stingrays of the genus *Fluvitrygon* (Indo-Malay Archipelago), which was used as an outgroup, is the sister group of *Brevitrygon* with its basal member being an endemic Javanese species, *B. javaensis*.

The remaining four taxa are fully resolved with *B. manjajiae* sp. nov. and *B. imbricata* apparent successive sister species to *B. heterura* + *B. walga*. Two of these species, *B. javaensis* and *B. heterura*, are confirmed to be sympatric off Java, Indonesia; *B. imbricata* is sympatric with *B. walga* in the Bay of Bengal *and* may be (or once may have been) sympatric with *B. heterura* in the western North Pacific. Derivation of these taxa likely arose from allopatric speciation, and the present distribution of the species, *B. manjajiae* sp. nov (Arabian Sea, Persian/Arabian Gulf), *B. imbricata* (southern India to Myanmar), *B. walga* (Bay of Bengal), and *B. heterura* (Indo-Malay Archipelago), reflects this evolutionary pattern (Figure 13).

A possible sixth species in the Arabia Sea off southern Oman (Mirbat, GN 9441, Figure 39) was identified (>0.01 substitutions/site) that could be conspecific with Müller & Henle's enigmatic 19th-century syntype of *Trygon walga* from the Red Sea. However, no other material of this form was available for study. There is also evidence of lineage substructure within species (i.e., *B. walga*), but there is also marked intra-population variability within lineages as exemplified in *B. heterura* (~0.01 substitutions/site), where all material was sourced from a single region (Sarawak, Malaysian Borneo). Weak divergence between subgroups was observed in *B. manjajiae* sp. nov., a lineage in the Persian/Arabian Gulf (Kuwait and Iran) and a lineage in the Arabian Sea (Gulf of Oman to India). A similar pattern exists in *B. walga* (between Myanmar and Bengal lineages) and had been identified earlier in *B. heterura* (between lineages from Sabah, Malaysia, and from Vietnam/Indonesia) by Last & White ([17]; their Figure 12). Clearly, a more focused investigation of the precise ranges of each species, and an evaluation of possible lineage substructure within them, is needed as unresolved cryptic speciation and marginal sympatry between nearest neighbors may exist.

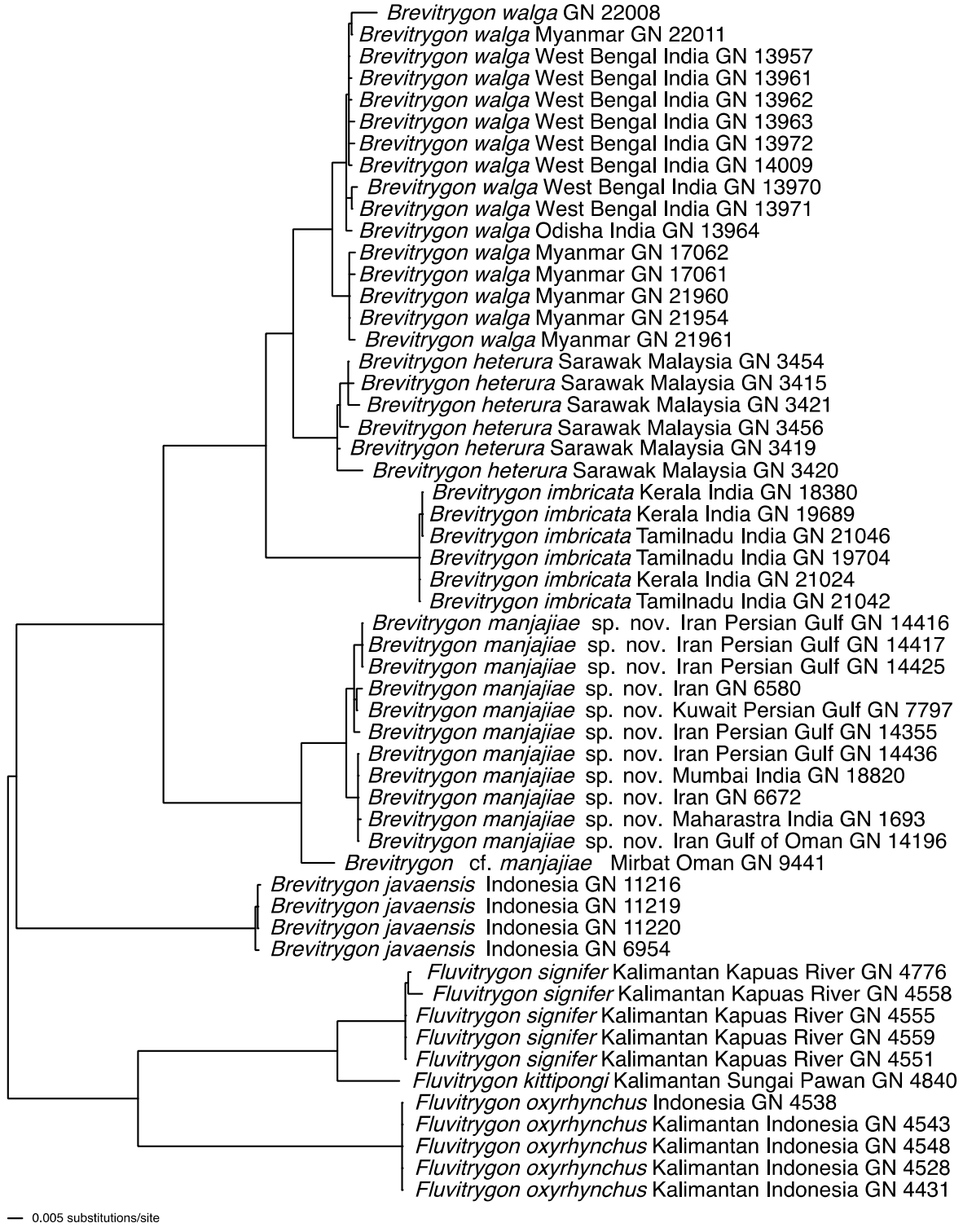

Figure 39. Maximum likelihood (ML) tree based on General Time Reversible (GTR) model accommodating observed proportion of Invariant sites (I) and Gamma distributed distribution of Variable sites Γ (i.e., the GTR + I + Γ model).

4.3. Key to Species of the Genus Brevitrygon (Morphometrics Based on Adolecents and Adults)

1. Tail relatively short, robust beyond sting in both sexes (length when undamaged 0.8–1.2 times DW); post-sting tail with obvious dorsal and ventral cutaneous folds (Figure 3a); secondary denticle band poorly developed in adults, expanded laterally to form

a cruciate pattern over scapulocoracoid, very narrow over branchial region and abdomen (narrower than eye diameter), margins not converging posteriorly on disc (see Figure 4a); Bay of Bengal and possibly Western North Pacific . . . . . *Brevitrygon imbricata*

- Tail more elongate, semi-rigid to filamentous, often sexually dimorphic (length when undamaged 1.3–2.2 times DW in males); post-sting tail with cutaneous folds absent or as rudimentary ridges (Figure 3b); secondary denticle band well developed in adults, not configured as above (Figure 4b–e) **2**

2. Tail relatively long, slender (length when undamaged 2.1–2.2 times DW); dorsal post-sting tail appearing speckled due to rows of melanophore clusters each bearing minute denticles (Figure 3f); enlarged denticles and thorns absent from tail (see Figure 5d); southern coast of Java, Indonesia . . . . . *Brevitrygon javaensis*

- Tail slender in males, more robust in females and often bulbous near its tip (length when undamaged 0.6–1.8 times DW); post-sting tail without melanophore clusters; enlarged denticles and/or thorns usually present on midline of pre-sting tail (Figure 5a–c,e) **3**

3. Tail beyond sting usually pale (Figure 3d); posterior part of tail in females noticeably bulbous, usually thicker just before tip than at its midlength (Figure 3e); secondary denticle band strongly constricted over branchial region (Figure 4c); relatively large eyes, orbit diameter typically 6–8% DW; large claspers in adult male, postcloacal length 18–23% DW; Indo-Malay Archipelago . . . . . *Brevitrygon heterura*

- Tail beyond sting usually dark dorsally and ventrally, fleshy lateral keels white and strongly contrasted with surfaces above and below (Figure 3b,h); posterior part of tail in females not greatly expanded distally, similar in thickness or becoming thinner distally (Figure 3c,i); secondary denticle band not or weakly constricted over branchial region (Figure 4b,e); eyes relatively small, orbit diameter typically 5–6% DW; smaller claspers in adult male, post cloacal length 15–19% DW **4**

4. Tail relatively short, length when undamaged 1.3–1.5 times DW in males, 1.0–1.3 times DW in females; preorbital snout short, length usually 28–30% DW; Persian/Arabian Gulf, Arabian Sea, possibly Red Sea . . . . . *Brevitrygon manjajiae* **sp. nov.**

- Tail longer, length when undamaged 1.6–1.8 times DW in males, 1.2–1.6 times DW in females; preorbital snout longer, length 31–34% DW; Bay of Bengal. . . . . *Brevitrygon walga*

Author Contributions: Conceptualization, P.R.L. and S.W.; methodology, P.R.L., S.W. and G.J.P.N.; software, P.R.L., S.W. and G.J.P.N.; validation, P.R.L., S.W. and G.J.P.N.; formal analysis, P.R.L., S.W. and G.J.P.N.; investigation, P.R.L., S.W. and G.J.P.N.; resources, P.R.L., S.W. and G.J.P.N.; data curation, P.R.L.; writing—original draft preparation, P.R.L.; writing—review and editing, P.R.L. and S.W.; visualization, P.R.L., S.W. and G.J.P.N.; supervision, P.R.L., S.W. and G.J.P.N.; project administration, P.R.L.; funding acquisition, G.J.P.N. All authors have read and agreed to the published version of the manuscript.

Funding: This research was co-funded by the Australian National Fish Collection (ANFC, CSIRO) and by a National Science Foundation (NSF) grant (Jaws and Backbone: Chondrichthyan Phylogeny and a Spine for the Vertebrate Tree of Life; DEB-01132229).

Data Availability Statement: The data presented in this study are available in this published article.

Acknowledgments: The authors especially acknowledge the contribution of Mabel Manjaji- Matsumoto who provided substantial new and unpublished information on members of this group, from a doctoral dissertation on the genus *Himantura*; John Pogonoski (ANFC) provided radiographs and assisted with the acquisition of meristic data; Helen O'Neal (ANFC) took images of type material and other specimens held at the ANFC; Travis Hutchins voluntarily prepared cross-sectional sketches of the tail of each species; Alastair Graham (ANFC) assembled and vetted collection data, as well as facilitating loans from other fish collections; Bruce Deagle (ANFC Director) approved the Honorary Research Fellowship awarded to P.L., enabling access to the collection and its resources. We acknowledge the efforts of Bob Ward and Bronwyn Holmes (CSIRO) and Dirk Steinke (University of Guelph) for their substantial efforts in molecular barcoding of fishes, including sharks and rays.

Jayne Last photographed critical material at international collections that proved invaluable in this study. Many fruitful discussions were held with William White (ANFC) on these rays. We thank the following former and present collection staff and research colleagues for providing access to their collections and assisting with material and loans, as well as translations: O. Crimmen, P. Campbell and J. Maclaine (BMNH, UK); G. Dally (NTM, Australia); B. Séret, R. Causse, G. Duhamel, P. Pruvost, Z. Gabsi (MNHN, France); R. Thiel, I. Eidus, and T. Weddehage (ZMH, Germany); P. Bartsch and E. Aßel (ZMB, Germany); R. Hadiaty and A. Arief (MZB, Indonesia); R. de Ruiter, M. Caspers, and M. van Oijen (RMNH, Netherlands); R. Vonk and H. Praagman (ZMA, Netherlands); G. Langlet (IRSNB, Belgium); H. Osmany (Pakistan); H.-C. Ho (NMMBP, Taiwan); K.E. Hartel and A. Williston (MCZ, USA); B. Brown, R. Arindell, J. Sparks, M. Stiassny, and S. Schaefer (AMNH, USA); J. Williams, K. Murphy, D. Pitassy, E. Wilbur, and S. Raredon (USNM, USA); R. Feeney and C. Thacker (LACM, USA); D. Catania (CAS, USA); A. Suzumoto and J. Randall (BPBM, USA); K. Bineesh (ANRC, India); K. Akhilesh (ICAR, India); B. Kimar; Fahmi and Dharmadi (BRIN, Indonesia), S. Bussarawit and C. Vidthayanon (PMBC, Thailand); A. Lo and G. Jonis (MUS, Malaysia); J. Caira (U. Connecticut); K. Jensen (U. Kansas); P. Psomadakis (FAO); M. Moazzam (WWF, Pakistan); H. Osmany (MFD, Pakistan); A. Henderson (UAE University, UAE); A. Moore (Bangor University, UK); C. Scharpf (The ETYFish Project, https://etyfish.org); H. Funk (Germany); and I. Isbrücker (retired from Zoological Museum of Amsterdam, Netherlands).

Conflicts of Interest: The authors declare no conflict of interest.

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