A new species of box jellyfish, *Carybdea wayamba* sp. nov. (Cnidaria: Scyphozoa: Cubomedusae: Carybdeidae) from Sri Lanka

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**Abstract:** A new species of box jellyfish, *Carybdea wayamba* sp. nov. is described here based on forty specimens collected from the south and northeast coasts of Sri Lanka, with the type location being Bonavista Reef, Galle Bay. This species is classified in the genus *Carybdea* due to the possession of a typical heart-shaped rhopalia ostia with only one upper scale and epaulette-shaped gastric phacellae in the four corners of the stomach. This new species can be distinguished from other valid members of the genus *Carybdea* by the combination of the structure of the two velarial canal roots per octant with one broadly bi-forked velarial canal with narrow, lateral lobations on each root, and other morphological characters such as having typical knee-shaped pedalial canal bends without any appendages, and epaulette-shaped gastric phacellae with single-rooted, brush-shaped, multiple (three to five) short-stemmed, dendritically branched (both short and long branches) gastric filaments. This is the first novel cubomedusa described from Sri Lankan waters; and the first *Carybdea* species described with material from the North Indian Ocean.

**Key words:** Indian Ocean, morphology, nematocysts, taxonomy

**Introduction**

The cubomedusae included many doubtful taxa until the beginning of the 21st century. In several studies over the last two decades, biologists have revised the taxonomy of this group (Gershwin 2005a, b, 2006a, Bentlage et al. 2010, Bentlage & Lewis 2012, Lewis et al. 2013, Straehler-Pohl 2014, 2019a, b, 2020, Straehler-Pohl & Gul 2017, Acevedo et al. 2019), but there are still some uncertainties to be clarified. In the classification of box jellyfish, Carybdeidae is a monotypic family containing the genus *Carybdea*, which represents the oldest genus of box jellyfish established by Péron & Lesueur (1810), which was subsequently misspelled (e.g. *Charybdea*), by several authors between Milne-Edwards (1833) and Mayer (1910), before the original name, *Carybdea* was re-established by Kramp (1961).

The genus *Carybdea* previously contained a number of species that are now contained in other carybdeid families; for example, *Carybdea sivickisi* Stiasny, 1926 has been moved to the family Tripedaliidae while changing its genus name to *Copula* (Bentlage et al. 2010). Gershwin (2005a) recognized that *Carybdea alata* Reynaud, 1830 was in fact a whole species complex and transferred them to a separate family, Alatinidae, while changing the genus name to *Alatina* (Gershwin 2005b) based on morphological and phylogenetic differences. Likewise, *Carybdea stiasnyi* Bigelow, 1938 was also transferred to the family Alatidae, while changing the genus name to *Manokia* (Gershwin 2005b). Some species, such as *Carybdea periphylla* Péron & Lesueur, 1810, *Carybdea pisifera* Oken, 1815, and *Carybdea bitentaculata* Quoy & Gaimard, 1833 were not even box jellies and had to be transferred into other taxonomic groups.

Thereafter, only a few valid species remained in the genus *Carybdea*, with *Carybdea marsupialis* (Linnaeus, 1758) being the type species (Acevedo et al. 2019, Straehler-Pohl 2019b). Maas (1903, 1910), Bigelow (1909, 1938), Mayer (1910), and Kramp (1961) considered most of these *Carybdea* species as varieties of *C. marsupialis*, and
A systematic, year-round jellyfish survey was carried out in the pelagic zone of the continental shelf of Sri Lanka from March 2017 to April 2018. Forty (38 mature + 2 immature) specimens belonging to the new box jellyfish species were collected by a towed net (diameter 1 m, mesh size 1 mm) and a scoop net (mesh size 5 mm) from four locations along the south and northeast coasts of the country (Fig. 1). Water quality parameters (temperature, dissolved oxygen, pH, salinity, total dissolved solids, and turbidity) of each sampling locality were measured by using a digital multiparameter instrument (HACH HQ 40 D), and a portable turbidity meter (HACH 2100P). Coordinates of the sampling locations were recorded with a GPS unit (GARMIN 72H).

Seven different morphometric features of all medusae were measured while fresh according to Gershwin (2005a, b) and Straehler-Pohl (2014). Here, the distance between the apex and the turnover of the bell below the rhopalium was measured as the bell height (BH). The diagonal bell width (DBW) was measured as the distance between outer keels of pedalial base by laying specimens flat with two pedalia spread out to the left and right sides, and the other two facing up and down in the centre. The inter-rhopalial width (IRW) (from the rhopalium to another adjacent rhopalium) was measured after laying the specimens flat. Across the widest area of the pedalia, the ‘pedalial width’ (PW) was measured, while the distance between the base and the distal end of the pedalium was measured as the

**Materials and Methods**

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pedalial length (PL).

Two additional features were defined and measured; the distance from the apex to the rhopalium (DAR) and the distance between the rhopalium and the turnover of the bell (DRT). If there was more than one measurement on a single morphometric character per individual medusa, i.e., two DBW, four IRW, four DAR, four DRT, four PW (if the pedalia were unbroken), and four PL (if the pedalia were unbroken), average values of them were calculated. All measurements were performed using a digital caliper to the nearest 0.1 mm.

After recording the morphometric characteristics, samples were preserved in 5% formalin-seawater solution for taxonomic examinations. Minute structures of specimens were observed under a microscope (OLYMPUS CX22), and a stereo zoom microscope (OLYMPUS SZ 61). Nematocysts were identified following Gershwin (2006b) and were measured (under 400× magnification) with an inverted phase-contrast microscope with an imaging system (CARL ZEISS 415510-1101-000 Primovert). All the specimens inspected were deposited in the Museum of the Department of Aquaculture and Fisheries, Wayamba University of Sri Lanka (MDAFWU) by giving accession numbers.

Results

Systematics (based on Straehler-Pohl 2017, Jarms & Morandini 2019)
Phylum Cnidaria Verrill, 1865
Subphylum Medusozoa Petersen, 1979
Class Scyphozoa Götte, 1887
Order Cubomedusae Haeckel, 1880
Suborder Carybdeida Lesson, 1843
Family Carybdeidae Lesson, 1843
Genus Carybdea Péron & Lesueur, 1810
Carybdea wayamba sp. nov. (Figs. 2–3 and Supplementary fig. 1)

Type specimens. Of the 40 type specimens recognized in the study, the holotype (MDAFWU 2018/3, Male, 26 January 2018, Bonavista Reef, Galle Bay, Sri Lanka [6.0264°N, 80.2367°E], coll. by K.D. Karunarathne, with scoop net from surface; 21.1 mm BH, 24.2 mm DBW, 13.9 mm IRW, 17.4 mm DAR, 3.1 mm DRT, 10.9 mm PL, 4.0 mm PW) and 37 paratypes are mature (Table 1). The remaining two paratype specimens (MDAFWU 2018/15, Galle Bay, Sri Lanka [6.0278°N, 80.2289°E], 22 March 2018; 8.3 mm BH, 10.1 mm DBW, 5.1 mm IRW, 5.1 mm DAR, 3.2 mm DRT, 6.1 mm PL, 2.0 mm PW, MDAFWU 2018/28, Irakkandi, Sri Lanka [8.7238°N, 81.8150°E], 23 April 2018; 9.0 mm BH, 14.4 mm DBW, 7.5 mm IRW, 7.3 mm DAR, 2.1 mm DRT, 5.0 mm PL, 1.5 mm PW) are immature.

Diagnosis. Carybdea with a small, flimsy, slightly transparent body. Inner keel of scalpel-shaped pedalia without warts or freckles. Knee-shaped bend of pedalial canal without appendage. Velarial canal roots 2 per octant, with a broad, rounded, bident canal with narrow, lateral lobations on each root, all canals are equal in shape and complexity. Manubrium short, about one-third of the bell height. Gastric phacellae, epaulette-shaped with single-rooted, multiple (typically three to five) short-stemmed, dendritically branched (both short and long branches), brush-shaped gastric filaments.

Description (mature medusa). Bell: with thin, flimsy mesoglea; small to medium in size, up to 29.0 mm in life, nearly cuboidal, with dome-shaped apex, smooth appearance as both apex and bell lack prominent nematocyst warts in live specimens, however, there are microscopic gelatinous warts (Fig. 3E). Coronal indentation deep just below apex. Interradius thickened throughout BH, with moderately deep furrows reaching all the way to the pedarium. Adradial furrows pronounced, deeper in the lower half of bell.

Sensory niches: 4, perradial, heart-shaped, with single, shallowly convex covering scale and lack of lower scales (Fig. 2B); located approximately one-fifth of BH from velarial turnover; lacking rhopalial horns (Fig. 2B). Eyes 6 per rhopalium, 2 median lensed eyes plus 4 lateral pigmented eyespots (Fig. 2D). Rhopalial warts lacking. Stomalith shape unknown.

Pedalia: simple, unbranched, flattened, scalpel-shaped (Fig. 2F), moderate in size, about half of BH and three times higher than the width (Fig. 2A); lacking nematocyst clusters on the inner keel; outer keel rarely lined with a single row of white nematocyst clusters (Fig. 3A, B); distally inner keel quite rounder than outer, without tentacular overhang (Fig. 2F). Pedalial canal cross-section somewhat quadrate proximally, flat distally, straight at tentacle insertion; outer portion of knee-shaped bend without any appendix (Fig. 2E).

Tentacles: 4, with single tentacle per pedarium, round or flattened somewhat in cross-section, with segmented appearance in preserved specimens (Fig. 2F); base to about 1 mm thick.

Velarium: narrow, lacking nematocyst warts or freckles. Velarional canals, 2 roots per octant, 1 canal per root, widely biforked, typically U-shaped with narrow, lateral lobations bearing round or globular ends, non-anastomosing, both canals are equally complex (Fig. 2G). Perradial lappets absent. Frenulum well developed, about the root of a velarial canal in width, comprising a single hollow gelatinous structure, mostly reaching the velarial margin (Fig. 2H).

Manubrium: short, about one-third of the bell height; with four small, smooth-edged, broadly pointed lips about one-third of the manubrium length, without nematocyst warts (Fig. 2I). Poorly developed perradial mesenteries extending up to halfway to rhopalium (Fig. 2J) (only with some specimens in the collection). Stomach flat. Gastric saccules absent.

Phacellae: 4, epaulette-shaped (Fig. 2K), typically arising from the single root with three to five short stems giv-
**Fig. 2.** Morphological features of *Carybdea wayamba* sp. nov. (A–M): A. Lateral view of the holotype; B & C. Exumbrellar view and sub-umbrellar view of rhopaliar niche respectively (holotype), US—upper scale; D. Rhopalium dissected out from niche (MDAFWU 2017/358), note six eyes (*LPI*—lateral pit eye, *LSI*—lateral slit eye, *ULI*—upper lens eye, *LLI*—lower lens eye) and statolith (*S*); E. Pedial canal knee-shaped bend (arrow) without appendage (holotype); F. Pedalium (holotype), note the tentacle with segmented appearance; G. Biforked velarial canals with lateral lobations (holotype), *P*—pedalium, *VC*—velarial canals; H. Frenulum (MDAFWU 2017/358), *F*—frenulum, *VC*—velarial canals; I. Short manubrium with wide, pointed, four lips (MDAFWU 2017/358); J. Poorly-developed mesentery (MDAFWU 2017/359); K–M. Phacellum (MDAFWU 2017/359) as usual, distinguished four short stems with branches (arrows), and isolated short stem (arrow) respectively. Scales: D=0.5 mm; B, C, E, F, H, K–M=1 mm; G, I, J=2.5 mm; A=5 mm.
Carybdea wayamba n. sp. from the Indian Ocean

Fig. 3. Nematocyst features of Carybdea wayamba sp. nov. (A–E): A & B. Nematocyst clusters on the outer keel (arrows) of pedalia (MDAFWU 2018/11); C & D. Discharged tentacular nematocysts (Sml—small isorhiza, Spl—spherical isorhiza, ELE—elongate lemon-shaped eurytele); E. Microscopic warts on apex (holotype). Scales: D=10 µm; E=50 µm; B=2 mm; A=5 mm.

ing rise to several dendritical branches in different lengths that end in a brush-shaped cluster of filaments (Fig. 2L, M). Occasionally, one or two stems of phacellae can exist outside of the main root.

Gonads: attached along entire length of interradial septa; broadly leaf-shaped, typically overlapping along the interradius (Figs. 2A, 3A), pleated or simple. Interradial septa lacking perforations.

Nematocysts: tentacular nematocysts are of three types, namely small isorhizas, spherical isorhizas, and elongate lemon-shaped eurytele (Fig. 3C, D). The nematocysts of the exumbrella, phacellae and manubrium were not examined.

Colour in life: Bell and pedalia slightly transparent; gonads whitish; tentacles whitish.

Etymology. This is the first ever species which is originally described at the Wayamba University of Sri Lanka, due to it being a young institution; therefore, the species is named to honour the university. The Sri Lankan national reference-collection of jellyfish is maintained in the university.

Distribution. Currently known only from Sri Lanka, from Galle (6.0094°N, 80.2477°E) along the south coast to Hambantota (6.2800°N, 81.4267°E), and from Trincomalee (8.5679°N, 81.2391°E) along the northeast coast to Mulaitivu (9.3616°N, 80.7299°E).

Habitat. Frequently found in shallow waters (range 0–10 m in depth), around coral reefs and river or lagoon mouths. Physiochemical conditions measured: temperature 24.9–33.0°C, dissolved oxygen 5.9–9.0 ppm, pH 7.8–8.3, salinity 24.8–31.5, total dissolved solids 23.9–30.2 ppt, and turbidity 1.1–19.4 NTU.

Hazardousness. Mild stinger. However, when large numbers are in the water they can cause an uncomfortable prickly sensation.

Discussion

The genus Carybdea is differentiated from all other carybdeid families by the possession of a heart-shaped rhopaliar niche ostium with a single, upper covering scale and the lack of lower scales (Gershwin 2005a, Bentlage et al. 2010, Bentlage & Lewis 2012, Acevedo et al. 2019, Straehler-Pohl 2019b). Basically, due to the presence of lower covering scales at the rhopaliar niche opening and crescentic gastric phacellae, the species nominally considered to be Carybdea alata (C. alata, C. grandis, C. madraspatana, Carybdea moseri Mayer, 1906, Carybdea obeliscus Haeckel, 1880, Carybdea philippina Haeckel, 1880, Carybdea pyramis Haeckel, 1880, Procharybdis tetrapetra Haeckel, 1880, Procharybdis turricula Haeckel, 1880) were moved to a newly erected family, the Alatinidae, and into a new genus, Alatina, by Gershwin (2005b); likewise, Carybdea morandinii Straehler-Pohl & Jarms, 2011 was also transferred to the family Alatinidae and the genus Alatina by Straehler-Pohl & Toshino (2015). In this context, the new species described herein in the waters of Sri Lanka was classified under the genus Carybdea, particularly due to the possession of heart-shaped rhopaliar niche ostia with an upper scale and lack of lower scales (Fig. 2B), and the epaulette-shaped gastric phacellae (Fig. 2K).

Species of the genus Carybdea are distinguishable based
on a combination of 3 characters (velarial canal system, pedalial knee structure and pattern of gastric phacellae—horizontal row or epaulette-shape) according to Straehler-Pohl et al. (2017), Acevedo et al. (2019) and Straehler-Pohl (2019a). Some other characters, such as the size of the bell, and more detailed characteristics like the formation and arrangement of gastric filaments in the phacellae are also important (Gershwin 2005a, Straehler-Pohl et al. 2017, 2019a,

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**Table 1.** Morphometric characteristics of the 38 mature specimens (BH: bell height; DBW: diagonal bell width; IRW: inter-rhopialial width; DAR: distance from apex to rhopalium; DRT: distance from rhopalium to turnover of bell; PL: pedalial length; PW: pedalial width), which were found in the coastal localities of Sri Lanka (L₁—Alampil [9.1877°N, 80.8609°E]; L₂—Ambalantota [6.0964°N, 80.9937°E]; L₃—Galle Bay [6.0278°N, 80.1850°E]; L₄—Irakkandi [8.7238°N, 81.1850°E]). Abbreviations used: n (number of specimens), SD (standard deviation).

| Locality | Sampling date | Accession no. (MDAFWU) | Morphometric characteristics (measurements in mm) |
|----------|---------------|-------------------------|--------------------------------------------------|
|          |               | BH  | DBW  | IRW  | DAR  | DRT  | PL   | PW   |
| L₁ (n=01) | 22 April 2018 | 2018/17 | 17.0 | 23.1 | 11.5 | 13.5 | 3.5  | 8.1  | 2.9  |
| L₂ (n=03) | 26 October 2017 | 2017/534 | 29.0 | 33.0 | 20.1 | 23.3 | 5.8  | 12.5 | 3.8  |
|          |               | 2017/535 | 26.7 | 30.3 | 17.5 | 21.4 | 5.3  | 10.4 | 3.5  |
|          |               | 2017/536 | 18.7 | 18.4 | 11.0 | 15.6 | 3.1  | 8.5  | 3.0  |
| L₃ (n=15) | 27 October 2017 | 2017/537 | 20.2 | 24.5 | 15.2 | 17.4 | 3.2  | 9.7  | 3.0  |
|          |               | 2017/538 | 21.0 | 26.6 | 15.1 | 16.5 | 4.5  | 10.8 | 2.8  |
|          |               | 2017/539 | 14.3 | 15.3 | 9.3  | 12.2 | 2.1  | 7.0  | 2.0  |
|          | 26 January 2018 | 2018/3* | 21.1 | 24.2 | 13.9 | 17.4 | 3.1  | 10.9 | 4.0  |
|          |               | 2018/4 | 13.0 | 18.1 | 8.5  | 10.5 | 2.5  | 7.4  | 2.3  |
|          |               | 2018/5 | 19.0 | 24.1 | 12.5 | 16.5 | 5.8  | 8.8  | 3.8  |
|          |               | 2018/6 | 17.1 | 23.2 | 10.1 | 14.0 | 3.1  | 9.4  | 3.1  |
|          |               | 2018/7 | 16.0 | 21.4 | 11.2 | 12.5 | 3.5  | 9.9  | 3.3  |
|          |               | 2018/8 | 13.4 | 17.2 | 8.3  | 10.2 | 3.2  | 7.9  | 2.4  |
|          |               | 2018/9 | 14.4 | 17.3 | 9.3  | 10.3 | 4.1  | 6.8  | 2.0  |
|          |               | 2018/10 | 13.4 | 18.1 | 9.4  | 11.4 | 2.0  | 7.8  | 2.0  |
|          | 22 March 2018  | 2018/11 | 19.0 | 23.1 | 13.1 | 13.5 | 5.5  | 8.9  | 2.6  |
|          |               | 2018/12 | 22.0 | 25.4 | 13.2 | 16.5 | 5.5  | 10.0 | 3.0  |
|          |               | 2018/13 | 20.0 | 22.1 | 12.3 | 14.5 | 5.5  | 10.3 | 3.8  |
|          |               | 2018/14 | 23.2 | 30.2 | 15.5 | 18.1 | 5.1  | 10.0 | 3.6  |
| L₄ (n=19) | 21 November 2017 | 2017/540 | 25.0 | 29.2 | 17.5 | 20.5 | 4.5  | 10.0 | 4.0  |
|          |               | 2017/541 | 18.6 | 23.1 | 11.5 | 15.2 | 3.4  | 7.8  | 3.0  |
|          |               | 2017/542 | 20.0 | 24.3 | 12.2 | 17.5 | 2.5  | 9.0  | 3.0  |
|          |               | 2017/543 | 18.2 | 22.1 | 11.0 | 15.1 | 3.1  | 10.0 | 3.0  |
|          |               | 2017/544 | 21.1 | 26.1 | 13.2 | 16.5 | 4.5  | 10.6 | 3.8  |
|          |               | 2017/545 | 20.4 | 25.2 | 13.2 | 17.1 | 3.3  | 9.6  | 3.6  |
|          |               | 2017/546 | 20.4 | 26.0 | 13.1 | 16.2 | 4.2  | 9.2  | 3.7  |
|          |               | 2017/547 | 20.1 | 24.3 | 12.5 | 17.0 | 3.1  | 10.4 | 3.6  |
|          |               | 2017/548 | 12.5 | 16.2 | 9.1  | 10.0 | 2.5  | 5.9  | 2.0  |
|          | 23 April 2018  | 2018/18 | 18.2 | 22.5 | 12.1 | 14.2 | 4.1  | 8.3  | 2.3  |
|          |               | 2018/19 | 18.1 | 19.3 | 10.3 | 14.5 | 3.5  | 9.0  | 2.6  |
|          |               | 2018/20 | 17.3 | 21.2 | 10.4 | 14.1 | 3.3  | 8.0  | 2.5  |
|          |               | 2018/21 | 20.2 | 23.2 | 11.5 | 16.3 | 4.2  | 8.0  | 4.0  |
|          |               | 2018/22 | 15.5 | 21.3 | 10.5 | 12.5 | 3.2  | 8.0  | 2.0  |
|          |               | 2018/23 | 16.5 | 19.4 | 10.3 | 13.5 | 3.1  | 7.0  | 2.0  |
|          |               | 2018/24 | 15.1 | 20.1 | 9.5  | 12.5 | 2.5  | 7.1  | 2.0  |
|          |               | 2018/25 | 13.2 | 17.4 | 9.5  | 11.5 | 1.5  | 6.9  | 1.9  |
|          |               | 2018/26 | 10.2 | 13.3 | 9.1  | 8.2  | 2.1  | 5.0  | 1.8  |
|          |               | 2018/27 | 11.2 | 14.2 | 8.4  | 9.2  | 2.3  | 5.5  | 1.5  |

**Mean±SD (mm)**

| Range (mm) | 10.2–29.0 | 13.3–33.0 | 8.3–20.1 | 8.2–23.3 | 1.5–5.8 | 5.0–12.5 | 1.5–4.0 |

*The holotype. Others are paratypes.*
Table 2. Comparison of significant characters of species in the genus Carybdea Péron & Lesueur, 1810. Named species data from Kishinouye (1891), Maas (1897), Gershwin (2005a), Gershwin & Gibbons (2009), Chae et al. (2017), Acevedo et al. (2019), Straehler-Pohl (2020), and this study.

| Species                    | Distribution                  | Bell height; exumbrellar nematocyst warts in living specimens | Gastric phacellae; filament structure | Velarial canal roots; velarial canals | Pedalial outer keel in living specimens | Pedalial canal knee bend |
|----------------------------|-------------------------------|---------------------------------------------------------------|---------------------------------------|--------------------------------------|------------------------------------------|--------------------------|
| C. confusa                  | California (cold)             | up to 32.0 mm; densely scattered with white nematocysts of irregular shapes | epaulette; single rooted, single short-stemmed, brush-shaped | 2 roots per octant; 1 canal per root, multiple branched | scattered with round to oval warts and white nematocyst bands | with thorn-like appendage |
| C. cuboides Haeckel, 1880   | Hawaii (tropical)             | up to 30.0 mm; scattered with small, colourless, nematocyst warts from apex to bell margin | epaulette; single rooted, multiple short-stemmed, short branches, brush-shaped | 2 roots per octant; 1 canal per root, biforked to multiple branched, with wide lateral lobations | lined with rows of white nematocyst warts | rounded, without appendage |
| C. irregularis              | French Polynesia (tropical)   | up to 20.0 mm; no nematocyst warts scattered over the apex and bell of preserved specimens (might be rubbed off) and no data on living specimens | epaulette; single rooted, multiple long, flask-shaped, thick stems, brush-shaped | 2 roots per octant; 1 canal per root, simple to branched, with slight lobations | No data | rounded, without appendage |
| C. marsupialis Linnaeus, 1758| Mediterranean Sea (temperate) | up to 40.5 mm; sparsely scattered with few, whitish nematocyst warts from apex to bell margin | epaulette; single rooted, multiple (8–10) stemmed | 3 roots per octant; 1 canal per root, simple to biforked or branched, slightly lobed | lined with nematocyst freckles, smaller warts scatter on outer half | rounded, without appendage |
| C. murrayana Haeckel, 1880  | South Africa, West Africa (cold to tropical) | up to 82.0 mm; densely scattered with white nematocyst warts from apex to bell margin | epaulette; single rooted, multiple (about 20) long-stemmed, tree-shaped | 2 roots per octant; 2–4 canals per root, complexly branched, with complex lobes | densely scattered with irregular, white nematocyst warts and brownish marks | volcano-shaped, upwards turned |
| C. proenypus (Haeckel, 1880) | Japan, South Korea, Chinese Seas (temperate to tropical) | up to 35.0 mm; scattered with tiny, colourless, nematocyst warts from apex to bell margin | horizontal linear; multiple rooted, multiple (10–15), long-stemmed, brush-shaped | 3 roots per octant; 1 canal per root, complexly branched, slightly lobed | scattered with tiny, round, white nematocyst warts or bands | volcano-shaped, appended sharp peak |
| C. rassoni Haacke, 1886     | Australia (cold to temperate) | up to 35.0 mm; scattered with colourless, nematocyst warts from apex to bell margin | horizontal linear; multiple rooted, multiple (12–15), short-stemmed, brush-shaped | 2 roots per octant; 1 canal per root, triforked | scattered with large, white to light brown nematocyst warts or bands | rounded, without appendage |
| C. saymacana Conant, 1897   | Caribbean Sea (tropical)      | up to 24.0 mm; scattered with tiny colourless nematocyst warts from apex to bell margin | epaulette; single rooted, single short-stemmed, brush-shaped | 2 roots per octant; 1 canal per root, simple to biforked | lined with white, irregular, nematocyst bands, scattered tiny warts | volcano-shaped to triangular |
| C. wayamba sp. nov.         | Sri Lanka (tropical)          | up to 29.0 mm; scattered with microscopic nematocyst warts from apex to bell margin (no prominent warts therefore, smooth appearance with the naked eye) | epaulette; single rooted, multiple (3–5), short-stemmed, both short and long branches, brush-shaped | 2 roots per octant; 1 canal per root, broadly biforked, with narrow lateral lobations | seldom lined with single row of white nematocyst clusters | rounded, without appendage |
h, 2020, Acevedo et al. 2019). Hence, it is important to compare the combination of such characteristics between the valid species of *Carybdea* when determining their taxonomic identity (Table 2).

*Carybdea rastonii* and *Carybdea prototypus* (Haeckel, 1880) [*Procharagma prototypus* Haeckel, 1880 = *Carybdea brevipedalia* Kishinouye, 1891] can clearly be distinguished from the Sri Lankan specimens due to the possession of horizontal linear gastric phacellae (Gershwin & Gibbons 2009, Acevedo et al. 2019, Straehler-Pohl 2020) while the Sri Lankan specimens possess the epaulette-shaped gastric phacellae (Fig. 2K).

The nature of the velarial canal system (two velarial canal roots per octant; 2–4 canals per root, with lateral lobations) of *Carybdea murrayana* (*Charybdea murrayana* Haeckel, 1880 = *Carybdea branchi*) is characteristic of the species and its bell is more than double the height of Sri Lankan *Carybdea* specimens (Gershwin & Gibbons 2009, Acevedo et al. 2019, Straehler-Pohl 2020). Also, the number of stems per bundle of gastric phacellae in *C. murrayana* is about four times higher than the present specimens and the long stems are arranged in dense bundles (Gershwin & Gibbons 2009: Table 1, Acevedo et al. 2019, Straehler-Pohl 2020). Therefore, the Sri Lankan specimens can easily be distinguished from this species.

Both the species, *Carybdea confusa* Straehler-Pohl, Matsumoto & Acevedo, 2017, and *Carybdea xaymacanna* Conant, 1897 have two velarial canal roots per octant with one canal per root. Both canals differ in complexity, and they possess appendages in the pedrial canal knee bend and single-rooted, single-stemmed, epaulette-shaped gastric phacellae (Straehler-Pohl et al. 2017: Figs. 1E, I, K, 2S–V, Acevedo et al. 2019: Fig. 1F–I, K–M, Straehler-Pohl 2019: Fig. 2J–L, V–X); thus, the Sri Lankan specimens can certainly be distinguished from them, since the Sri Lankan specimens have two velarial canal roots per octant with equally complex velarial canals (Fig. 2G–H), multiple filament stems per phacellum (Fig. 2L–M), and a lack of appendages in the pedrial bend (Fig. 2E). Moreover, *C. marsupialis* possesses three velarial canal roots per octant (Straehler-Pohl et al. 2017: Fig. 2O, Acevedo et al. 2019: Fig. 1D, Straehler-Pohl 2019a: Fig. 2Q), while the observed specimens from Sri Lanka possess two per octant (Fig. 2G). *Carybdea marsupialis* also has a larger number of filament stems (8–10) per gastric phacellum (Gershwin 2005a: Table 2.5, Gueroun et al. 2015: Fig. 1D), therefore it is also different from Sri Lankan specimens.

*Carybdea irregularis* Straehler-Pohl, 2019 possesses irregularly shaped, simple or complexly branched velarial canals. No canal is the same length as any other over the whole velarium (Straehler-Pohl 2019: Figs. 1L, M, 2N, 3L–O). The Sri Lankan specimens can be differentiated by having nearly equally shaped velarial canals (Fig. 2G) in all octants. Additionally, *C. irregularis* has flask-shaped, thick-stemmed gastric phacellae (Straehler-Pohl 2019a: Figs. 1H, 2O), but these are slender (non-flask-shaped) in the present specimens from the North Indian Ocean (Fig. 2M).

*Carybdea cuboides* (Haeckel, 1880) [*Procharybdis cuboides* Haeckel, 1880 = *C. arborifera* Maas, 1897], described from the central North Pacific region, is morphologically by far the most similar species to the specimens from the North Indian Ocean due to the nature of the pedalial canal knee bend, the number of velarial canal roots per octant, and the shape of the gastric phacellae of both species being similar, with even their bells being almost the same in size. Although both species have two velarial canal roots per octant, and the shape of the gastric phacellae of both species being similar, with even their bells being almost the same in size. Although both species have two velarial canal roots per octant, the canals are typically bi-forked with narrow lateral lobations in the Sri Lankan specimens (Fig. 2G), but bi-forked to multiply-branched with wide lateral lobations in *C. cuboides* (Acevedo et al. 2019: Page 526). The information recorded concerning the number of stems per gastric phacellum of *C. cuboides*, in the description by Maas (1897: Page 86), and the recent revision of the genus
Carybdea done by Acevedo et al. (2019) was not sufficient; however, typical length of those stems is clearly shown in Straehler-Pohl et al. (2017: Fig. 2A, B), Acevedo et al. (2019: Fig. 2C, D), and Straehler-Pohl (2019a: Fig. 2C). Carybdea cuboides usually possesses several short stems per gastric phacellum (Acevedo et al. 2019: Page 526), while in the Sri Lankan specimens, although those stems are short, they are typically few (three to five) in each phacellum (Fig. 2L, M). Branches in the phacellae of C. cuboides are short (Acevedo et al. 2019: Fig. 2D, Straehler-Pohl 2019a: Fig. 2C), but the Sri Lankan specimens have long branches (Fig. 2L, M).

It can therefore be concluded that the present cubomedusan material from Sri Lanka belongs to a new carybdeid species, herewith named Carybdea wayamba sp. nov. The distribution of this new species also complies with Acevedo et al. (2019), because it does not overlap with the inferred distributions of the other eight Carybdea species (Fig. 4).

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