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Cubozoans (Cnidaria, Cubozoa) in the western Caribbean Sea: new and additional records of *Carybdea xaymacana*, *Alatina alata,* and *Tamoya* cf. *haplonema*

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Abstract

The cubozoans, a small group of medusozoans with 50 nominal species, have been under research, leading to uncertainty about the validity of some specimens. This study aims to confirm the species found in the western region of the Caribbean Sea. We conducted a review, utilizing specimens from samples collected, zooplankton collection, and collected citizen science data. Specimens of four taxa (two species, one genus, and one order) were identified, and 42 data were compiled for the western coast of the Caribbean Sea (Mexico, Belize, Honduras, Netherlands). Notably, specimens previously identified as *Carybdea marsupialis* in the local collections were confirmed to be *Carybdea xaymacana*, and further studies on *Tamoya* spp. are needed to confirm the specimens' identification. Further morphological and molecular studies are needed from localities in the western Atlantic. This study is a first step to address other aspects of conservation and monitoring of cubozoans in the western Caribbean Sea.

Key words: box jellyfish, Medusozoa, taxonomy

Introduction

Cubozoans (class Cubozoa Werner, 1973) constitute a small group of medusozoans comprising 50 nominal species distributed worldwide (Collins 2024). However, other authors suggested 47 valid species, three species *dubia* (*Carukia shinju* Gershwin, 2005; *Malo bella* Gershwin, 2014; *Tamoya ohboya* Collins, Bentlage, Gillan, Lynn, Morandini & Marques 2011), and one species *inquerendum* (*Tamoya prismatica* Haeckel, 1880) (Straehler-Pohl 2019). Seven species were described for the Caribbean area, of which *T. ohboya* was confirmed invalid by Straehler-Pohl (2020), and the *inquirendum* species *T. prismatica* (Straehler-Pohl 2019). Therefore, only five are considered valid in the Caribbean Sea (Straehler-Pohl 2019, Collins 2024): *Alatina alata* (Reynaud, 1830), *Carybdea xaymacana* Conant, 1897, *Tamoya haplonema* F. Müller, 1859, *Tripedalia cystophora* Conant, 1897, and *Chiropsalmus quadrumanus* (F. Muller, 1859).

The taxonomy of these species has been studied in detail (see Acevedo *et al*. 2019; Straehler-Pohl 2019), and the life cycle of three species (*A. alata*, *T. cystophora*, *C. xaymacana*) is known (Werner 1971; Arneson & Cutress 1976; Carrette *et al*. 2014; Straehler-Pohl & Jarms 2022). Therefore, it is necessary to address the gaps in knowledge, such as the life cycle of *T. haplonema* and *C. quadrumanus*, and the toxicological aspects after corroborating the identity of the species. Especially because the toxins vary depending on the species and the environmental conditions to which they are exposed (Klompen *et al*. 2021; O'Hara *et al*. 2021). The Caribbean Sea, a semi-enclosed basin of the western Atlantic Ocean, is a tropical and nutrient-poor region with its boundaries defined by the coasts of Central and South America on two sides and the Antilles Island chain on the other two (Miloslavich *et al*. 2010). Its western coast, formed by the Atlantic coast of Venezuela, Colombia, Central America, and Mexico (Quintana Roo state) (Wilkinson *et al*. 2009), is a highly dynamic region characterized by extensive mangrove forests, seagrass beds, and

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coral reefs under high pressure from activities related to the tourism industry (Rioja-Nieto *et al*. 2019; Spencer *et al*. 2022). The cubozoan studies conducted in the western Caribbean Sea have addressed several different aspects, including, for example, checklists (Segura-Puertas *et al*. 2003; Gasca & Loman-Ramos 2014; Ehemann *et al*. 2015), ecological aspects (Larson 1982; Suárez-Morales *et al*. 1999a, 1999b; Canché-Canché & Castellanos-Osorio 2005; Canepa *et al*. 2014), taxonomy (Collins *et al*. 2011; Lewis *et al*. 2013; Durán-Fuentes *et al*. 2018; Acevedo *et al*. 2019; Straehler-Pohl 2019; Sansores-Flores *et al*. 2023), and toxicology (Milla *et al*. 2000; Sánchez-Rodríguez *et al*. 2006; Morales-Landa *et al*. 2007; Algaze *et al*. 2015; Lazcano-Pérez *et al.* 2017).

The cubozoan species in this region are stinging. For *A. alata* and *Tamoya* species, their stinging causes severe pain but is not lethal (Straehler-Pohl 2019), but for *C. xaymacana* and *Tamoya* sp., we could not define the specific degree of stinging due to a lack of specific information and taxonomic uncertainty. In 1999, dermatitis was observed in individuals exposed to contact with the tentacles of *C. xaymacana* (as *C. marsupialis*) (Milla *et al*. 2000). Currently, tourist service personnel mention that they and tourists have not experienced severe stings for cubozoans; only redness for several days in the sting area (Jonguitud, F. pers. comm. 2024). In this respect, as well as in the taxonomy of these organisms, the information obtained through citizen science allows for increased knowledge of their diversity and distribution on a scientific basis (e.g. Rojas-Cruz *et al*. 2023; Rocha *et al*. 2024) and could also contribute to the monitoring of the damage they can cause to bathers and tourist areas through stings. The validity of some cubozoan records from the Caribbean Sea has been called into question. For example, the species *T. ohboya* is currently classified as valid by some authors (Collins *et al*. 2011), but as a *dubium* species by others (Straehler-Pohl 2019). Additionally, a recent study found many similarities between *T.* cf. *haplonema* sequences from the Atlantic Ocean of the USA and those of *T. ohboya* from the Caribbean coast, suggesting that the two sets of sequences may be associated with a single species rather than two and that additional research is required to properly delineate species within this genus (Lewis *et al*. 2021) not considering Straehler-Pohl (2020) who confirmed *T. ohboya* as invalid species by obvious morphological characters. Moreover, recent studies have confirmed that *Carybdea marsupialis* (Linnaeus, 1758) is not distributed in this area (see Acevedo *et al*. 2019; Straehler-Pohl 2019; Sansores-Flores *et al*. 2023). Notwithstanding, the aforementioned studies have considered only specimens from a few localities like Spain, Algeria, Tunisia, Puerto Rico, Jamaica, Panama, Bermuda, and the northeast Mexican Caribbean, respectively. Furthermore, there has been no comprehensive review of specimens that have been identified as *C. marsupialis* on the western Caribbean coast. In this context, the present study, following a detailed morphological review and comparison of specimens sampled, zooplankton collection specimens, and citizen observations, the cubozoan taxa recorded in the western Caribbean coast were corroborated, and the presence of *C. xaymacana* was confirmed in Mexico and Belize.

Material and methods

In this study, we identified cubozoan samples (N=7) from the western Caribbean coast (Mexico and Belize). The samples were collected with surface horizontal trawls, oblique trawls or manually, and preserved in ethanol (96%) or formaldehyde (4%) (Table 1). We also revised additional samples from the Collection of Zooplankton at El Colegio de la Frontera Sur (ECOSUR).

TABLE 1. Characteristics of the samples collected in the western Caribbean coast. ECOSUR: El Colegio de la Frontera Sur, NA: not applicable, UNAM: Universidad Nacional Autónoma de México. *specimen with DNA sequence.

Country	Locality	Trawls	Sampling method	Data (month/ year)	Institute samples
Mexico	Puerto Morelos	NA	net with a telescopic handle	11/2023	UNAM*
		horizontal	330 µm mesh conical plankton net	12/2001	ECOSUR
	Mahahual	horizontal	303µm mesh frame trawl net	12/1990	ECOSUR
	Xcalak	NA	net with a telescopic handle	12/2006	ECOSUR
	Southern Quintana Roo	oblique	335µm mesh Mocness net	01/2007	ECOSUR
Belize	Front of Hopkins	oblique	335µm mesh Mocness net	01/2007	ECOSUR
	Northeast Caye Raguana	oblique	335µm mesh Mocness net	01/2007	ECOSUR

The iNaturalist cubozoan records were compiled from the first data to those published in July 2024 (https://www.inaturalist.org/observations/?place_id=any&subview=map&taxon_id=68095). For the search, we used the term "Box Jellies" (Class Cubozoa) and filtered only the data for Western Caribbean countries. Both "research degree" and "need identification" data were used. Additionally, some records were obtained through personal communication and occasional Blackwater Cozumel Scuba Diving Center group encounters with cubozoans. The compiled data were reviewed one by one to corroborate the identification of the specimens in the photos and the coordinates.

The specimens were identified with the support of taxonomic descriptions and compilations available in the literature (e.g. Straehler-Pohl 2019, Gibbons *et al*. 2022). For each specimen identified to species and genus level, we provide information such as the number of its corresponding figures, material examined (collected samples, zooplankton collection of ECOSUR, and citizen science), and nematocysts. For the material examined, we included a code, sampling site (locality, state, country, and geographic coordinates), sampling depth (m); collection date (month and year); temperature (°C); salinity (PSU); number of specimens; and standard bell measurements (BH, IPS, both in cm), when there is more than one specimen, the measurements are separated by a slash. In the absence of data, the corresponding sections have been omitted. For citizen science (Blackwater Cozumel) the information refers to the observation made, not the specimen itself. This is because, on occasion, multiple photographs were provided for each specimen, and there was no way of knowing which one corresponded to which specimen.

The bell standard measurements employed in this study were those outlined by Straehler-Pohl (2014) and Acevedo *et al*. (2019): bell height (BH)=length between bell turn-over (velarium excluded from measurement) and top of apex; interpedalial diameter (IPD)=distance between opposite pedalia (outer pedalial wing edges) at the level of the bell turn-over. Nematocyst measurements are provided as min–max; L=length of capsule in µm, W=width of the capsule at the widest point in µm, and standard deviation, and when feasible, five nematocysts were measured for bell, pedalia, and tentacle. Nematocyst identification follows Mariscal (1974), Östman (2000), and Gershwin (2006). Photographs were taken with a digital camera, a Canon Eos Rebel T3i. From a single specimen recently collected and preserved in ethanol (Table 1), it was possible to extract the mitochondrial gene 16S using the C&B1(F) and C&B2(R) primers (Cunningham & Buss 1993). The sequences were deposited in BoldSystem. We use BLAST searches against NCBI's GenBank to compare the sequence.

Results

The specimens reviewed belonged to four taxa, two species, one genus, and one order were identified. A total of 8 records were obtained from samples collected, 5 from the zooplankton collection, and 29 from citizen science. All records correspond to four countries: Mexico (25), Belize (10), Honduras (6), and the Netherlands (1). The year 2023 was notable for the highest number of cubozoans recorded (10). In addition, December stood out as the month with the highest number of data for these organisms (9). It is noticeable that the number of records increases in the months of the cold season (October–January) and in the transition between the dry and rainy seasons (June) (Fig. 1).

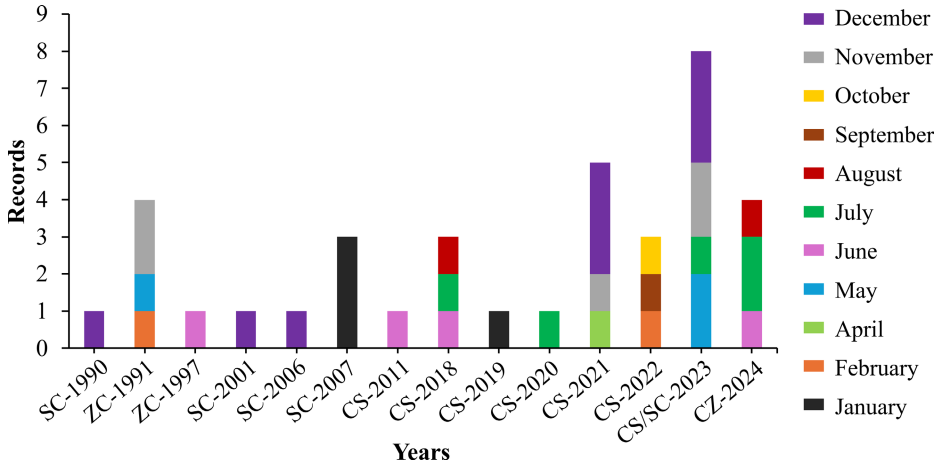

FIGURE 1. Number of cubozoan records from 1990 to 2024 on the west coast of the Caribbean Sea. CS=Citizen science, CSA=Collected sample, ZC=Zooplankton collection. In this graph, records that did not have the month or year were not considered.

The citizen science data, the iNaturalist records (Table S1) corresponded mostly to photos taken from the shore of specimens swimming in the water (15 records), whereby it was impossible to identify at the species level, except for a suggestion of identification at the species level, which due to the locality, the morphology observed in the image and the material reviewed from samples and the zooplankton collection, was identified as *C. xaymacana*. Of the 15 iNaturalist records, 14 were identified as part of the order Carybdeida and 1 of the order Chirodropida, according to the number of tentacles per pedalium. Blackwater Cozumel data retrieved 11 records, of which 10 were identified as *A. alata* and 1 as *Tamoya* sp. Personal communication data also corresponded to the latter genera.

Systematic account

Class Cubozoa Werner, 1973

Order Carybdeida Lesson, 1843

Family Alatinidae Gershwin, 2005

Genus *Alatina* Gershwin, 2005

***Alatina alata* (Reynaud, 1830)**
Figs. 2A–D, 3A–I

Collected samples: XC_38, Xcalak, Quintana Roo, Mexico, 18°16’14.7”N, 87°50’04.5”W; 1 m; December 2006; 2 adult specimens, BH=5.4/5.4 cm, IPD=4.0/3.4 cm. MCS_1, Mexican Caribbean Sea, Mexico; 1 juvenile specimen, BH=1.2 cm, IPD=0.9 cm. SQR_96_1, Southern Quintana Roo, Mexico; January 2007; 1 adult specimen, BH=8.2 cm, IPD=5.6 cm. BEL_65_1, Front of Hopkins, Belize; 16°41’34.1”N, 87°29’25.1”W; 25–50 m; January 2007; 1 juvenile specimen, BH=1.3 cm, IPD=1.1 cm.

Zooplankton collection: ECO-CH-Z_00203, northwest Cozumel, Quintana Roo, Mexico; 20°41’00”N, 86°16’00”W; 0–5 m; November 1991; 28°C; 36 PSU; 1 juvenil specimen, BH=0.6 cm, IPD=0.7 cm; as *Carybdea alata*. ECO-CH-Z_00211, northwest Chinchorro Bank, Quintana Roo, Mexico; 18°29’05”N, 87°36’00”W; 0–5 m; February 1991; 35 PSU; 1 juvenil specimen, BH=0.5 cm, IPD=0.4 cm; as *Carybdea marsupialis*. ECO-CH-Z_00226, northwest Cozumel, Quintana Roo, Mexico; 20°41’00”N, 86°16’00”W; 0–5 m; November 1991; 28°C; 36 PSU; 1 adult specimen, BH=3.1 cm, IPD=2.5 cm; as *Carybdea alata*. ECO-CH-Z_00227, Sian Ka’an Biosphere Reserve, Quintana Roo, Mexico; 19°34’03”N, 87°20’04”W; 0–5 m; May 1991; 27.5°C; 36 PSU; 1 juvenil adult BH=1.4 cm, IPD=0.9 cm; as *Carybdea marsupialis*.

Citizen science (Blackwater Cozumel): Cozumel, Quintana Roo, Mexico; 2023; Obs. Frida Yolotzin Jonguitud. Cozumel, Quintana Roo, Mexico; November & December 2021, May & December 2023, June 2024; Obs. Robert Stansfield. Cozumel, Quintana Roo, Mexico, 20°27’59.5”N, 86°59’24.2”W; 0–3 m; August 2024; 31°C; Obs. Frida Yolotzin Jonguitud.

Nematocysts: bands along the length of the tentacles, undischarged, oval, heterotrichus microbasic p-euriteles 21–23 μm ± 1.8 x 13–14 μm ± 0.4 and undischarged holotrichus isorhizas 14–15 μm ± 0.5 x 13–14 μm ± 0.4.

Family Carybdeidae Lesson, 1843

Genus *Carybdea* Péron & Lesueur, 1810

***Carybdea xaymacana* Conant, 1897**
Figs. 4A–I

Collected samples: MH_2_1, Mahahual, Quintana Roo, Mexico, 18°43’22”N, 87°42’00”W; 9 m; December 1990; 27°C; 36 PSU; 1 adult specimen, BH=2.4 cm, IPD=2.2 cm. PM_A_1, Puerto Morelos, Quintana Roo, Mexico,

20°52’0.00’’N, 86°51’0.00’’W; December 2001; 3 juvenile specimens, BH=0.5/0.4/0.5 cm, IPD=0.3/0.4/0.4 cm. BEL_77_1, Northeast Caye Raguana, Belize, 16°22’31.3”N, 88°01’55.0”W; 0–100 m; January 2007; 1 juvenil specimen, BH=1.6 cm, IPD=1.8 cm. PM_1,2, Puerto Morelos, Quintana Roo, Mexico, 20°52’05.3”N, 86°52’00.9”W; 1 m; November 2023; 28.8°C; 36.5 PSU; 8 adult specimens, BH=2.9/2.3/2.4/2.6/2.3/2.3/3.0/2.5 cm; IPD=2.7/2.3/2.5/2.5/2.4/2.4/3/2.4 cm.

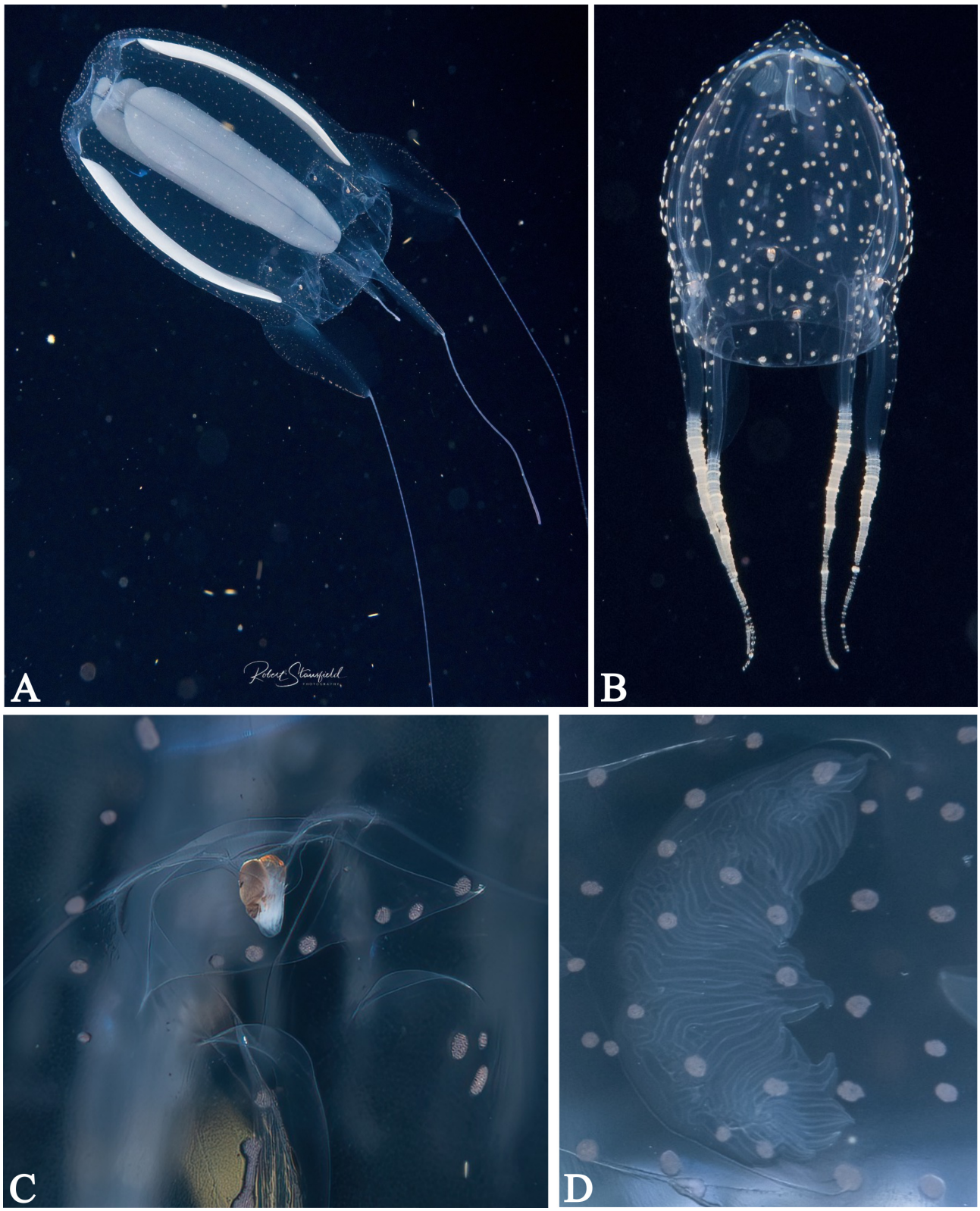

FIGURE 2. *Alatina alata* (Reynaud, 1830) from citizen science. A) Adult medusa; B) Young medusa; C) Rhopalial niche openings T-shaped; and D) Gastric phacella crescentic-shaped. Photos: Stansfield, 2024 (Blackwater Cozumel).

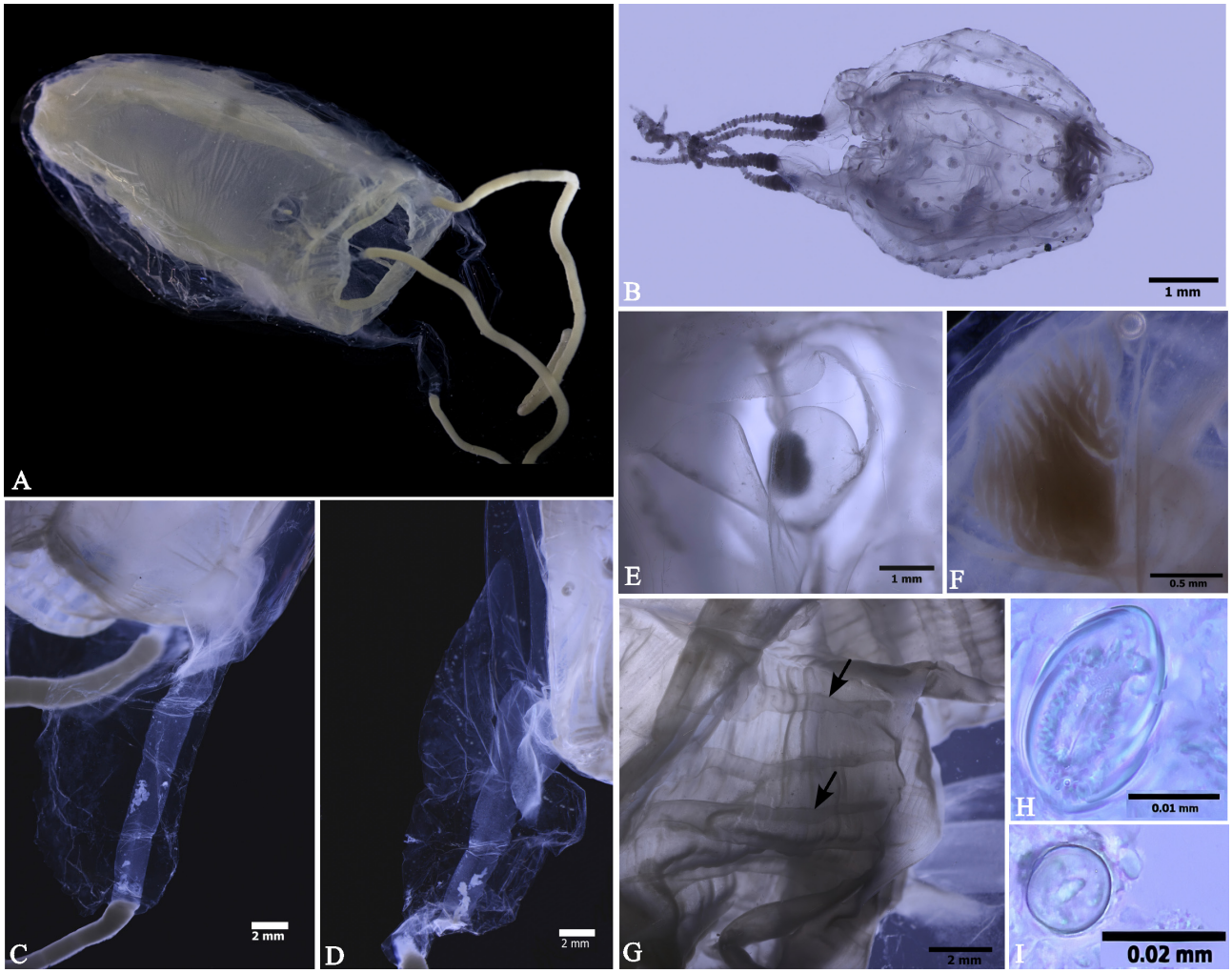

FIGURE 3. *Alatina alata* (Reynaud, 1830) preserved. A) Adult medusa; B) Young medusa; C) pedalium; D) Knee-bend slightly volcano-shaped; E) Rhopalial niche openings T-shaped; F) Gastric phacellae crescentic-shaped; G) Velarial canals (black arrow); H) Undischarged microbasic heterotrichus; and I) Undischarged holotrichus isorhizas nematocyst of the tentacles.

Zooplankton collection: ECO-CH-Z-02242, Bahía de la Ascension, Quintana Roo, Mexico, 19°47'01.0"N, 87°26'07.9"W; 5.8 m; June 1997; 30°C; 35 PSU; 1 juvenil specimen, BH=0.1 cm; IPD=0.1cm; as *Carybdea marsupialis*.

Citizen science (iNaturalist): Quintana Roo, Mexico, 20°16'41.9"N, 87°22'50.9"W; June 2018; Obs. Donají Graham.

Nematocysts: thin bands along the length of the tentacles, undischarged, euryteles 37–39 µm ± 0.8 x 13–14 µm ± 0.4 and warts scattered exumbrella, undischarged, spherical isorhizas 10–11 µm ± 0.5 x 10–11 µm ± 0.5.

DNA Sequence with accession numbers MEDUS187–25 had a greater than 90% identity with JN700978.1 Genbank number access (*C. xaymacana*).

Family Tamoyidae Haeckel, 1880

Genus *Tamoya* Mueller, 1859

Tamoya sp.

Figs. 5A–F

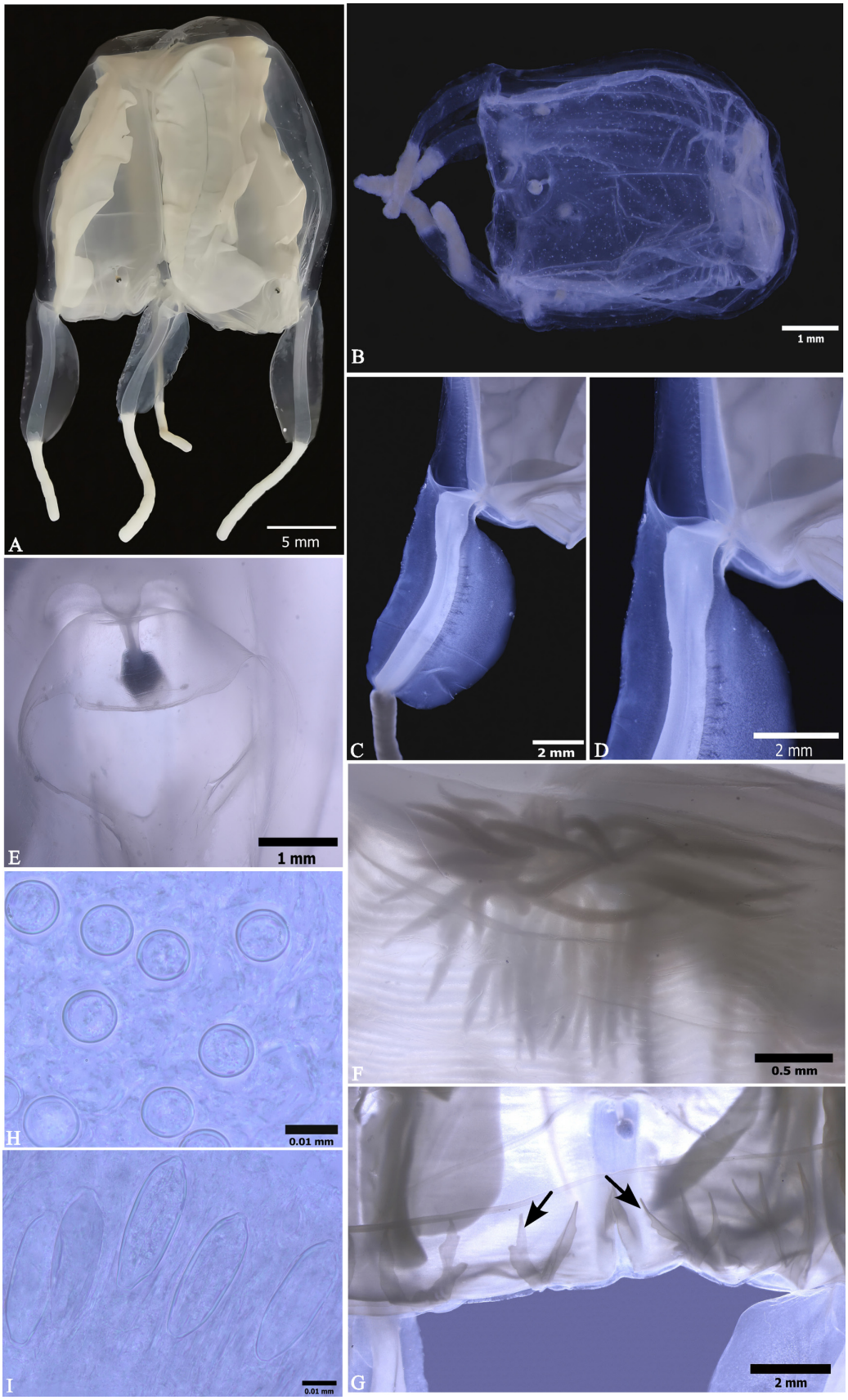

FIGURE 4. *Carybdea xaymacana* Conant, 1897 preserved. A) Adult medusa; B) Young medusa; C) Pedalium; D) Knee-bend rounded volcano-shaped; E) Rhopalial niche openings heart-shaped; F) Gastric phacella epaulette-shaped; G) Velarial canals (black arrow); H) Undischarged spherical isorhizas nematocyst of warts scattered exumbrella; and I) Undischarged euryteles nematocyst of the tentacles.

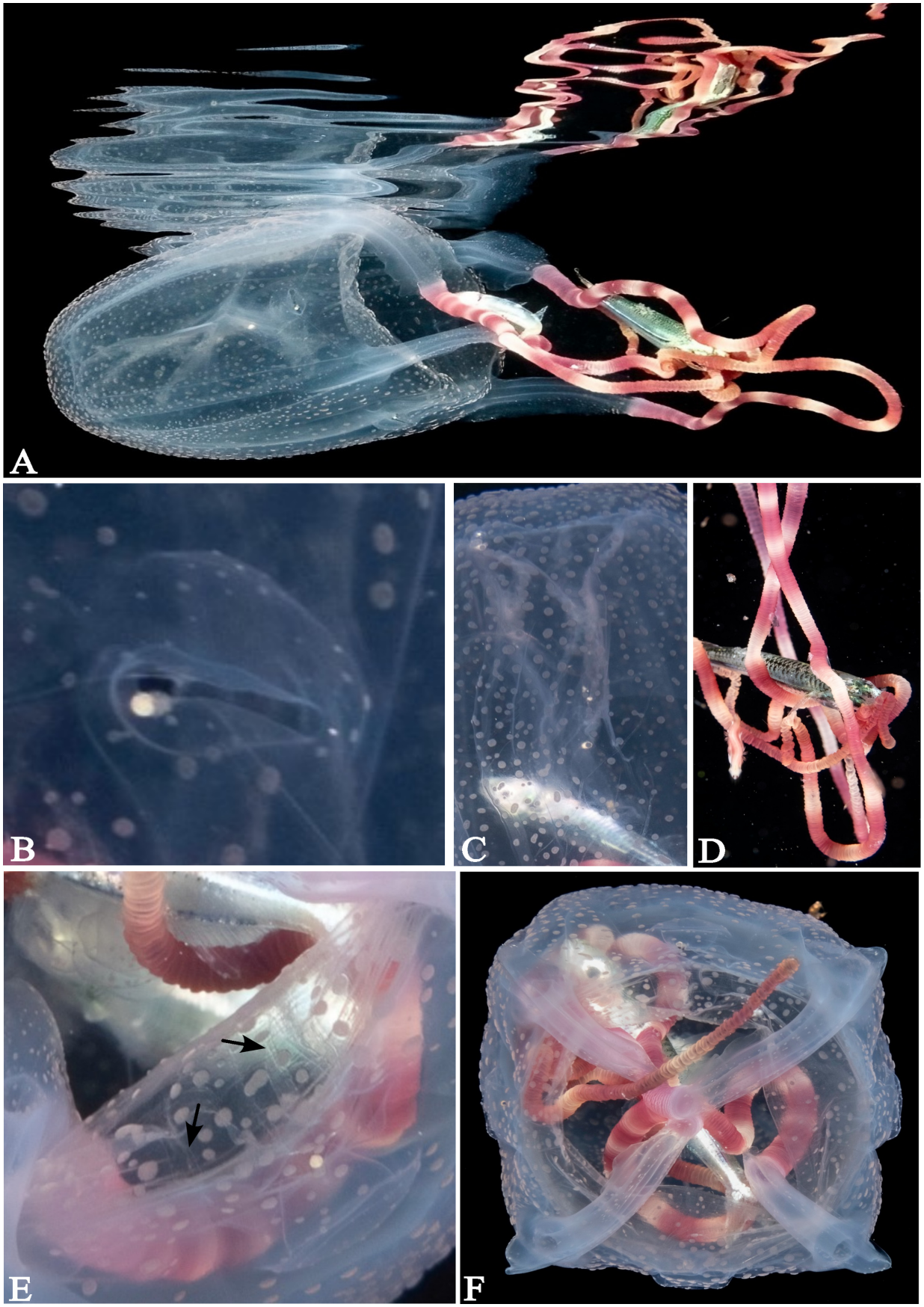

FIGURE 5. *Tamoya* sp. from citizen science. A) Adult medusa; B) Rhopalial niche opening frown-shaped; C) Vertical gastric phacella; D) Tentacles with red and orange bands; E) Velarial canals (black arrow); and F) Nematocyst warts scattered over the velarium. Photos: Stansfield, 2023 (Blackwater Cozumel).

Citizen science (Blackwater Cozumel and pers. comm.): Cozumel, Quintana Roo, Mexico; December 2023; Obs. Robert Stansfield. Cozumel, Quintana Roo, Mexico; 2023, 2024; Obs. Bud Gillan. Bonaire Island, Netherlands; 2023, 2024; Obs. Bud Gillan.

The specimen photographed in December 2023 was feeding on the fish larva of the genus *Jenkinsia* (Fig. 5A, D, F).

Discussion

In the present study, two orders (Carybdeida and Chirodropida) were identified, to order Carybdeida corresponded 2 species and 1 genus out of the 5 valid species for the Caribbean Sea (see Straehler-Pohl 2019). Of the order Chirodropida only one record, corresponding to iNaturalist, was obtained and it is likely that it corresponds to *C. quadrumanus*, which is the only species of the order recorded from western Caribbean (see Lira *et al.* 1989, Straehler-Pohl 2019). Of the western Caribbean Sea coastline, data on the presence of box jellyfish were available for seven countries: Mexico, Belize, Honduras, Panama, Colombia, Venezuela, and Netherlands (Bonaire) (Gershwin 2006; Collins *et al*. 2011; Acevedo *et al*. 2019; Chuard *et al*. 2019; Llorente-Vega *et al*. 2024; this study). Since 1990, the highest presence of these box jellyfish has reached two peaks, from May to July and from November to January, with December being the month with the highest recorded presence.

Before the publication of the studies that elucidated the taxonomy of some cubozoans (e.g., Straehler-Pohl & Jarms 2005; Gershwin 2005, 2006; Bentlage 2010; Lewis *et al*. 2013, Lawley *et al.* 2016; Acevedo *et al*., 2019, Straehler-Pohl 2019, Gibbons *et al*. 2022), the identification of Carybdeida species like *Alatina alata* (former *Carybdea alata*: Gershwin 2005) and *Carybdea xaymacana* (former *Carybdea marsupialis*: Gershwin 2005) on Mexican coasts was mainly based on the shape and position of the nematocysts in the jellyfish's bell in the 1990s and 2000s (Celis, L. pers. comm. 2024). Advances in both morphological and molecular aspects of this group of organisms have allowed us to corroborate the species present on the west coast of the Caribbean.

We could only obtain citizen science data on *Tamoya* sp., so it was impossible to corroborate several taxonomically important features to identify it at the species level. The characters we identified in the photographs are consistent with those observed in the literature for *T. ohboya* by Collins *et al*. (2011), who also recorded it in Cozumel at 0.76 m depth, based on citizen science data of Daniel Crothers (Collins A. pers. comm. 2024). Moreover, this species is widely distributed in the Caribbean Sea. There have been 118 documented sightings, mostly on Bonaire Island (Gillan B. pers. comm. 2024). However, *T. ohboya* is considered an invalid species, as there are no significant morphological or genetic differences between *Tamoya haplonema* and *Tamoya prismatica*, both recorded in the Caribbean (Straehler-Pohl 2019). Whereas there are so far three valid species of the genus, *T. ancamori* from Africa, *T. haeckeli* from Asia, and *T. haplonema* from the Americas (Straehler-Pohl 2019, 2020; Morandini A. pers. comm. 2024). The observations in the Caribbean may correspond to *T. haplonema*.

Therefore, further morphological and molecular studies are needed from localities in the western Atlantic, which should lead to a better understanding of the cubozoans, such as their life histories, distribution patterns, and toxins. Although no bloom events have been observed in the western Caribbean Sea, the socio-economic impacts should also be considered, as stings from these box jellyfish have been reported. Knowing and identifying the specimens are essential components of any biodiversity assessment, and this is the first step in monitoring, developing conservation strategies, measuring the effect of global change, and managing the potential impacts (Donaldson *et al*. 2016; Sheth & Thaker 2017). In addition, it is necessary to make scientific information accessible to civil society and encourage the training of specialists in the group. Thus, publicly accessible data on platforms such as iNaturalist will continue to grow and can be corroborated for scientific use.

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Author contributions

Raquel Inés Villalobos-León analyzed the data, prepared figures, authored and reviewed article drafts, and approved the final draft. María A. Mendoza-Becerril conceived and designed like to analyze the data, prepared tables, authored and reviewed drafts of the article, and approved the final draft.

References

Acevedo, M.J., Straehler-Pohl, I., Morandini, A.C., Stampar, S.N., Bentlage, B., Matsumoto, G.I., Yanagihara, A., Toshino, S., Bordehore, C. & Fuentes, V.L. (2019) Revision of the genus *Carybdea* (Cnidaria: Cubozoa: Carybdeidae): clarifying the identity of its type species *Carybdea marsupialis*. *Zootaxa*, 4543 (4), 515–548. https://doi.org/10.11646/zootaxa.4543.4.3

Arneson, A.C. & Cutress, C.E. (1976) Life history of *Carybdea alata* Reynaud, 1830 (Cubomedusae). *In*: Mackie, G.O. (Ed.), *Coelenterate ecology and behavior*. Plenum Press, New York, New York, pp. 227–236. https://doi.org/10.1007/978-1-4757-9724-4_24

Algaze, I., Mercado, J. & Arroyo, P. (2014) Irukandji-like syndrome in the Caribbean Sea, Puerto Rico: case report. *Wilderness & Environmental Medicine*, 26 (1), 95. https://doi.org/10.1016/j.wem.2014.09.026

Bentlage, B., Cartwright, P., Yanagihara, A.A., Lewis, C., Richards, G.S. & Collins, A.G. (2010) Evolution of box jellyfish (Cnidaria: Cubozoa), a group of highly toxic invertebrates. *Proceedings of the Royal Society B: Biological Sciences*, 277 (1680), 493–501. https://doi.org/10.1098/rspb.2009.1707

Canché-Canché, V.E. & Castellanos-Osorio, I. (2005) Medusas (Cnidaria) de la Bahía de la Ascensión, Quintana Roo, México (1997). *Hidrobiológica*, 15 (1), 65–72.

Canepa, A., Purcell, J.E., Belmar, M.B., Acevedo, M., Gentile, M. & Fuentes, V. (2014) Salinity effects on asexual reproduction of *Carybdea* sp. (Cnidaria: Cubozoa). *Journal of Plankton Research*, 36 (2), 585–590. https://doi.org/10.1093/plankt/fbt124

Carrette, T., Straehler-Pohl, I. & Seymour, J. (2014) Early life history of *Alatina* cf. *moseri* populations from Australia and Hawaii with implications for taxonomy (Cubozoa: Carybdeida, Alatinidae). *PLoS One*, 9 (1), e84377. https://doi.org/10.1371/journal.pone.0084377

Chuard, P.J.C., Johnson, M.D. & Guichard, F. (2019) Ocean acidification causes mortality in the medusa stage of the cubozoan *Carybdea xaymacana*. *Scientific Reports*, 9, 5622. https://doi.org/10.1038/s41598-019-42121-0

Collins, A.G. (2024) World List of Cubozoa. Cubozoa. Accessed through: World Register of Marine Species at: https://www.marinespecies.org/aphia.php?p=taxdetails&id=135219 (accessed 15 July 2024)

Collins, A.G., Bentlage, B., Gillan, W., Lynn, T.H., Morandini, A.C. & Marques, A.C. (2011) Naming the Bonaire banded box jelly, *Tamoya ohboya*, n. sp. (Cnidaria: Cubozoa: Carybdeida: Tamoyidae). *Zootaxa*, 2753 (1), 53–68. https://doi.org/10.11646/zootaxa.2753.1.3

Cunningham, C.W. & Buss, L.W. (1993) Molecular evidence for multiple episodes of paedomorphosis in the family Hydractiniidae. *Biochemical Systematics and Ecology*, 21 (1), 57–69. https://doi.org/10.1016/0305-1978(93)90009-G

Donaldson, M.R., Burnett, N.J., Braun, D.C., Suski, C.D., Hinch, S.G., Cooke, S.J. & Kerr, J.T. (2016) Taxonomic bias and international biodiversity conservation research. *Facets*, 1 (1), 105–113.
https://doi.org/10.1139/facets-2016-0011

Durán-Fuentes, J., Gracia, C.A., Osorio, M.C. & Cedeño-Posso, C. (2018) Aporte al conocimiento de las medusas (Cnidaria: Medusozoa) en el departamento del Atlántico, Colombia. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales*, 42 (162), 49–57.
https://doi.org/10.18257/raccefyn.520

Ehemann, N. (2015) Macro-medusas (cnidaria: cubozoa, hydrozoa y scyphozoa) observadas en las costas del estado nueva esparta, venezuela. *Boletín del Instituto Oceanográfico de Venezuela*, 54 (2), 185–190.

Gasca, R. & Loman-Ramos, L. (2014) Biodiversidad de Medusozoa (Cubozoa, Scyphozoa e Hydrozoa) en México. *Revista Mexicana de la Biodiversidad*, 85 (1), 154–163.
https://doi.org/10.7550/rmb.32513

Gershwin, L.A. (2005) *Carybdea alata* auct. and *Manokia stiasnyi*, reclassification to a new family with description of a new genus and two new species. *Memoirs-Queensland Museum*, 51 (2), 501–523.

Gershwin, L. (2006) Nematocysts of the Cubozoa. *Zootaxa*, 1232 (1), 1–57.
https://doi.org/10.11646/zootaxa.1232.1.1

Gibbons, M.J., Morandini, A.C., Straehler-Pohl, I. & Bezio, N. (2022) *Identification guide to macro jellyfishes of West Africa*. FAO, Rome, 181 pp.

Klompen, A.M., Kayal, E., Collins, A.G. & Cartwright, P. (2021) Phylogenetic and selection analysis of an expanded family of putatively pore-forming jellyfish toxins (Cnidaria: Medusozoa). *Genome Biology and Evolution*, 13 (6), evab081.
https://doi.org/10.1093/gbe/evab081

Larson, R.J. (1982) Medusae (Cnidaria) from Carrie Bow Cay, Belize. *In*: Rützler, K. & Macintyre, I.G. (Eds.), *The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize, I – Structure and Comminities*. Smithsonian Institute Press, Washington, pp. 253–269.

Lawley, J.W., Ames, C.L., Bentlage, B., Yanagihara, A., Goodwill, R., Kayal, E., Hurwitz, K. & Collins, A.G. (2016) Box jellyfish *Alatina alata* has a circumtropical distribution. *The Biological Bulletin*, 231 (2), 152–169.
https://doi.org/10.1086/690095

Lazcano-Pérez, F., Arellano, R.O., Garay, E., Arreguín-Espinosa, R. & Sánchez-Rodríguez, J. (2017) Electrophysiological activity of a neurotoxic fraction from the venom of box jellyfish *Carybdea marsupialis*. *Comparative Biochemistry and Physiology*, 191, 177–182.
https://doi.org/10.1016/j.cbpc.2016.10.010

Lewis, C., Bentlage, B., Yanagihara, A., Gillan, W., Van Blerk, J., Keil, D.P., Bely, A.E. & Collins, A.G. (2013) Redescription of *Alatina alata* (Reynaud, 1830) (Cnidaria: Cubozoa) from Bonaire, Dutch Caribbean. *Zootaxa*, 3737 (4), 473–487.
https://doi.org/10.11646/zootaxa.3737.4.8

Lewis, C.L., Ohdera, A.H., Colston, S.M., Collins, A.G., Fitt, W.K., Morandini, A.C., Erickson, J.S. & Vora, G.J. (2021) Fieldable environmental DNA sequencing to assess jellyfish biodiversity in nearshore waters of the Florida Keys, United States. *Frontiers in Marine Science*, 8, 640527.
https://doi.org/10.3389/fmars.2021.640527

Lira, G.I.E., Ziehl, C.M. & Lemus, J.L.C. (1989) *Guía ilustrada de animales marinos venenosos de México y el Caribe*. Noriega, Distrito Federal, 105 pp.

Llorente-Vega, J.L., Nisperuza-Pérez, C.A., Cedeño-Posso, C. & Quirós-Rodríguez, J.A. (2024) First report of *Carybdea xaymacana* Conant, 1897 (Cnidaria, Cubozoa, Carybdeida) in Colombia. *Check List*, 20 (4), 847–852.
https://doi.org/10.15560/20.4.847

Mariscal, R.N. (1974) Nematocysts. *In*: Muscatine, L. & Lenhoff, H.M. (Eds.), *Coelenterate biology–reviews and new perspectives*. Academic Press, New York, New York, pp. 129–178.
https://doi.org/10.1016/B978-0-12-512150-7.50008-6

Milla, L., Segura Puertas, L., Celis, L. & Heimer de la Cortera, E. (2000) Dermatitis por contacto con *Carybdea marsupialis* (cnidaria cubozoa). *Dermatología Revista Mexicana*, 44 (4), 167–170.

Miloslavich P., Díaz J.M., Klein E., Alvarado J.J., Díaz C., Gobin J., Escobar-Briones E., Cruz-Motta J.J., Weil E., Cortés J., Bastidas A.C., Robertson R., Zapata F., Martín A., Castillo J., Kazandjian A. & Ortiz M. (2010) Marine Biodiversity in the Caribbean: Regional Estimates and Distribution Patterns. *PLoS One*, 5 (8), e11916.
https://doi.org/10.1371/journal.pone.0011916

Morales-Landa, J.L., Zapata-Pérez, O., Cedillo-Rivera, R., Segura-Puertas, L., Simá-Alvarez, R. & Sánchez-Rodríguez, J. (2007) Antimicrobial, antiprotozoal, and toxic activities of Cnidarian extracts from the Mexican Caribbean sea. *Pharmaceutical Biology*, 45 (1), 37–43.
https://doi.org/10.1080/13880200601026325

O'Hara, E.P., Wilson, D. & Seymour, J.E. (2021) The influence of ecological factors on cnidarian venoms. *Toxicon*, X (9–10), 100067.
https://doi.org/10.1016/j.toxcx.2021.100067

Östman, C. (2000) A guideline to nematocyst nomenclature and classification, and some notes on the systematic value of nematocysts. *In*: Mills, C.E., Boero, F., Migotto A. & Gili, J.M. (Eds.), Trends in hydrozoan biology. IV. *Scientia Marina*,

64 (Supplement 1), pp. 31–46.
https://doi.org/10.3989/scimar.2000.64s131
Rioja-Nieto, R., Garza-Pérez, R., Álvarez-Filip, L., Mariño-Tapia, I. & Enríquez, C. (2019) The Mexican Caribbean: From Xcalak to Holbox. *In*: Sheppard, C. (Ed.), *World seas: an environmental evaluation. Vol. I. Europe, the Americas and West Africa*. Academic Press, San Diego, California, pp. 637–653.
https://doi.org/10.1016/B978-0-12-805068-2.00033-4
Rocha, R.M., Azevedo, F., Oliveira, U., Cardoso, M.N.M., Clerier, P.H.B., Fortes, R.R., Lopes-Filho, M., Miranda, L.S., Moura, R.B., Senna, A.R., Silva, F.M., Stampar, S.N. & Venekey, V. (2024) West Atlantic coastal marine biodiversity: the contribution of the platform iNaturalist. *Aquatic Ecology*, 58 (1), 57–71.
https://doi.org/10.1007/s10452-023-10062-6
Rojas-Cruz, J.E., García-Dimas, J.J., Cruz-Francisco, V.D.L. & Mendoza-Becerril, M.A. (2023) Blue button (Cnidaria: Hydrozoa) distribution and trends in the Mexican Atlantic, based on field surveys and open-access data. *Latin American Journal of Aquatic Research*, 51 (4), 602–609.
https://doi.org/10.3856/vol51-issue4-fulltext-3070
Sánchez-Rodríguez, J., Torrens, E. & Segura-Puertas, L. (2006) Partial purification and characterization of a novel neurotoxin and three cytolysins from box jellyfish (*Carybdea marsupialis*) nematocyst venom. *Archives of Toxicology*, 80, 163–168.
https://doi.org/10.1007/s00204-005-0023-7
Sansores-Flores, L.D., León-Deniz, L.V. & Ahuatzin-Hernández, J.M. (2023) Ocurrence of *Carybdea xaymacana* Conant, 1897 off the Mexican coasts. *Marine Biodiversity*, 53 (50). [published online]
https://doi.org/10.1007/s12526-023-01359-8
Segura-Puertas, L., Suárez-Morales, E. & Celis, L. (2003) A checklist of the Medusae (Hydrozoa, Scyphozoa and Cubozoa) of Mexico. *Zootaxa*, 194 (1), 1–15.
https://doi.org/10.11646/zootaxa.194.1.1
Sheth, B.P. & Thaker, V.S. (2017) DNA barcoding and traditional taxonomy: an integrated approach for biodiversity conservation. *Genome*, 60 (7), 618–628.
https://doi.org/10.1139/gen-2015-0167
Spencer, N., Strobl, E. & Campbell, A. (2022) Sea level rise under climate change: Implications for beach tourism in the Caribbean. *Ocean & Coastal Management*, 225, 106207.
https://doi.org/10.1016/j.ocecoaman.2022.106207
Straehler-Pohl, I. (2014) Critical evaluation of characters for species identification in the cubomedusa genus *Malo* (Cnidaria, Cubozoa, Carybdeida, Carukiidae). *Plankton & Benthos Research*, 9 (2), 83–98.
https://doi.org/10.3800/pbr.9.83
Straehler-Pohl, I. (2019) Cubomedusae. *In*: Jarms, G. & Morandini, A.C. (Eds.), *A World Atlas of Jellyfish. Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg, Special Edition. English Edition*. Dölling und Galitz Verlag, Hamburg, pp. 673–805.
Straehler-Pohl, I. (2020) A new species found in the Collection of the Discovery Expedition from 1925–27: *Tamoya ancamori* sp. nov. (Cnidaria, Cubozoa, Carybdeida, Tamoyidae) from West African waters. *Plankton and Benthos Research*, 15 (3), 189–206.
https://doi.org/10.3800/pbr.15.189
Straehler-Pohl, I. & Jarms, G. (2005) Life cycle of *Carybdea marsupialis* Linnaeus, 1758 (Cubozoa, Carybdeidae) reveals metamorphosis to be a modified strobilation. *Marine Biology*, 147, 1271–1277.
https://doi.org/10.1007/s00227-005-0031-4
Straehler-Pohl, I. & Jarms, G. (2022) Back to the roots, Part 1—Early life cycle data of Rhopaliophora (Scyphozoa, Cubozoa and Staurozoa). *Plankton and Benthos Research*, 17 (1), 1–33.
https://doi.org/10.3800/pbr.17.1
Suárez-Morales, E., Segura-Puertas, L. & Gasca, R. (1999a) A survey of the reef-related Medusa (Cnidaria) community in the western Caribbean Sea. *Gulf Research Reports*, 11, 23–31.
https://doi.org/10.18785/grr.1101.05
Suárez-Morales, E., Segura-Puertas, L. & Gasca, R. (1999b) Medusan (Cnidaria) assemblages off the Caribbean coast of Mexico. *Journal of Coastal Research*, 15 (1), 140–147.
Werner, B., Cutress, C.E. & Studebaker, J.P. (1971) Life cycle of *Tripedalia cystophora* Conant (Cubomedusae). *Nature*, 232 (5312), 582–583.
https://doi.org/10.1038/232582a0
Wilkinson, T.A.C., Wiken, E., Creel, J.B., Hourigan, T.F., Agardy, T., Herrmann, H., Janishevski, L., Madden, C., Morgan, L. & Padilla, M. (2009) *Marine Ecoregions of North America*. Commission for Environmental Cooperation, Montreal, 197 pp.

Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper:

Table S1. Citizen science data