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Occurrence of the hydromedusa *Moerisia cf. inkermanica* (Hydrozoa, Moerisiidae) in the ballast water of oil tankers in the Gulf of Mexico

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Abstract

The introduction of non-native species is a constant concern around the world since it represents one of the main threats to biodiversity, impacting negatively on native populations, some of them with commercial importance. Hence, monitoring these introductions is fundamental to the management and conservation of the biodiversity of a region. Herein, we report the presence of *Moerisia cf. inkermanica* in the ballast water of oil tankers loaded at the Cayo Arcas oil terminal. The taxonomy of *Moerisia* members is uncertain due to the lack of comprehensive morphological descriptions and the few molecular data available. So, we provide a detailed morphological comparison among its congeners. The taxonomic identity of the specimens was determined based on the length of the perradial lobes of the manubrium, the number of tentacles, and the features of their nematocyst rings. Some Moerisids are considered invasive in different localities of the world. However, this genus had not been reported in coastal ecosystems of the Gulf of Mexico over the years until now. Sampled tankers came from different ports of the region, mainly from the northern Gulf of Mexico. Therefore, we encourage systematic monitoring of these ecosystems to recognize the establishment of this species as invasive in the region, know its population dynamics over time, and evaluate the possible ecological impacts that could exert on native populations.

Introduction

The Gulf of Mexico is a semi-closed basin of the Atlantic Ocean that provides diverse ecosystem services related to its biodiversity, biological productivity, and geological features (Fautin *et al.*, 2010). Among the ecosystem services that generate greater economic benefits are oil extraction and tourism (Shepard *et al.*, 2013). Hence, maritime transport has been constant in the Gulf of Mexico throughout history (Botello *et al.*, 1997), impacting some ecosystems due to the introduction of non-native species (Graham *et al.*, 2003; Brockinton *et al.*, 2022). In the last few years, the presence of some non-native invertebrates in the Gulf of Mexico has been reported; some examples include *Phyllorhiza punctata* (Graham *et al.*, 2003; Ocaña-Luna *et al.*, 2010), *Blackfordia virginica* (Ocaña-Luna *et al.*, 2021), *Tubastraea coccinea* (Fenner and Banks, 2004; Derouen *et al.*, 2020), *Penaeus monodon* (Wakida-Kusunoki *et al.*, 2013), and the bryozoans *Hippoporina indica*, *Arbopercula bengalensis*, *Sinoflustra annae*, and *Celleporaria pilaefera* (McCann *et al.*, 2007). Unfortunately, few studies have evaluated their potential economic and ecological impact in the region (Graham *et al.*, 2003), so the status of their populations and their establishment as invasive species is uncertain.

The Hydromedusae of *Moerisia* Boulenger, 1908 distributes in tropical and temperate regions of the world, including continental water bodies (GBIF, 2024). Little is known about their taxonomy due to the lack of reports with detailed morphological descriptions and the few molecular data associated with these reports (Restaino *et al.*, 2018), causing the taxonomic boundaries of the group to be uncertain (Rees, 1958; Calder, 2010; Nawrocki *et al.*, 2010). This genus includes seven valid species (Schuchert, 2024), of which *M. inkermanica* Paltchikowa-Ostroumowa, 1925 and *M. lyonsi* Boulenger, 1908 are more frequently reported in the literature (e.g., Purcell *et al.*, 1999; Ma and Purcell, 2005; Nascimento *et al.*, 2019). *M. inkermanica* was described for the first time in the Bay of Sevastopol, Black Sea (Paltchikowa-Ostroumowa, 1925). Since then, it has been recorded in several localities around the world, mainly in the Atlantic Ocean (see Schuchert, 2010; Nogueira, 2012; Restaino *et al.*, 2018). The nearest record to the Gulf of Mexico was in Barnegat Bay, New Jersey (as *Moerisia* sp. Restaino *et al.*, 2018). This species is considered invasive in some localities (e.g., Nogueira, 2012; Killi *et al.*, 2020), so having a record of its presence in a new region is fundamental to knowing the possible impacts that it could generate on the native biodiversity.

Reports about invasive hydrozoans are frequent around the world (e.g., *Gonionemus vertens*, *Blackfordia virginica*, *Cordylophora caspia*; Bardi & Marques, 2009; Folino-Rorem *et al.*, 2009; Marchessaux *et al.*, 2017). These reports are of importance since hydrozoans are key consumers of zooplankton, and under certain environmental conditions, they can generate massive local



aggregations with high abundance (*blooms*), negatively impacting native populations, some with commercial importance (Rees and Gershwin, 2000). Thus, identifying the invasion pathways, vectors, and source localities is key to understanding their ecological impact and conducting correct management (Reusch *et al.*, 2010). *B. virginica* and *C. caspia* are the only non-native hydrozoans recorded in the Gulf of Mexico, yet their invasion monitoring in coastal zones of the Gulf has been scarce (Rioja, 1959; López-Ochoterena and Madrazo-Garibay, 1989; Álvarez-Silva *et al.*, 2003; Pruski and Miglietta, 2019; Ocaña-Luna *et al.*, 2021). Moreover, other unrecorded non-native species likely exist in this region because of the constant maritime transport, the influence of ocean currents, and the scarcity of studies about coastal hydrozoans. Here, we report the occurrence of *M. cf. inkermanica* in the ballast water of oil tankers loaded at the Cayo Arcas oil terminal, giving a comprehensive morphological description through its comparison with its congeners.

Materials and methods

Zooplanktonic samples were obtained from 30 tankers (three tanks per tanker) loaded at the Cayo Arcas oil terminal between 18 June and 6 July 2005 (the Cayo Arcas oil terminal is used as a port for the tankers loading oil for exportation; Figure 1) conducting vertical trawls from the bottom to the surface of each tank (90 tanks) using a conical net of 30 cm in diameter and 300 μm of clear mesh. Sampling was initially intended to collect as many zooplanktonic groups as possible for morphological analyses, so the samples were fixed in a 10% formalin solution buffered with sodium borate. Then, the samples were analysed in

the laboratory, sorting the specimens of *Moerisia* from the rest of the material. Standard measurements were recorded (i.e., the width and height of the umbrella and number of tentacles) of the best-preserved specimens ($n=29$). Four specimens were deposited in the Regional collection of 'Cnidarios del Golfo de México y Mar Caribe Mexicano', based at the Universidad Nacional Autónoma de México, Facultad de Ciencias, Unidad Multidisciplinaria de Docencia e Investigación-Sisal, Yucatán (Catalogue numbers for two vials with three and one specimens: YUC-CC-254-11-001660, YUC-CC-254-11-001661). For each tanker, the port of origin was recorded. The depth of the tanks ranged between 1.7 and 20 m (8 m on average). Temperature ($^{\circ}\text{C}$) and salinity (ups) were recorded in each tank with a multi-parametric YSI-85 (± 0.01) (Table 1). Additionally, we surveyed the available genetic data in GenBank (Clark *et al.*, 2016) using the term '*Moerisia*', assessing the locality where the samples were collected and the barcode marker used in order to provide a thorough summary of the available information (morphological and molecular) among the species of the genus.

Results

SYSTEMATICS (according to Schuchert, 2024)

Class HYDROZOA Owen, 1843

Subclass HYDROIDOLINA Collins, 2000

Order ANTHOATHECATA Cornelius, 1992

Suborder CAPITATA Kühn, 1913 (sensu stricto)

Family MOERISIIDAE Poche, 1914

Moerisia cf. inkermanica Paltschikowa-Ostroumowa, 1925
(Figure 2)

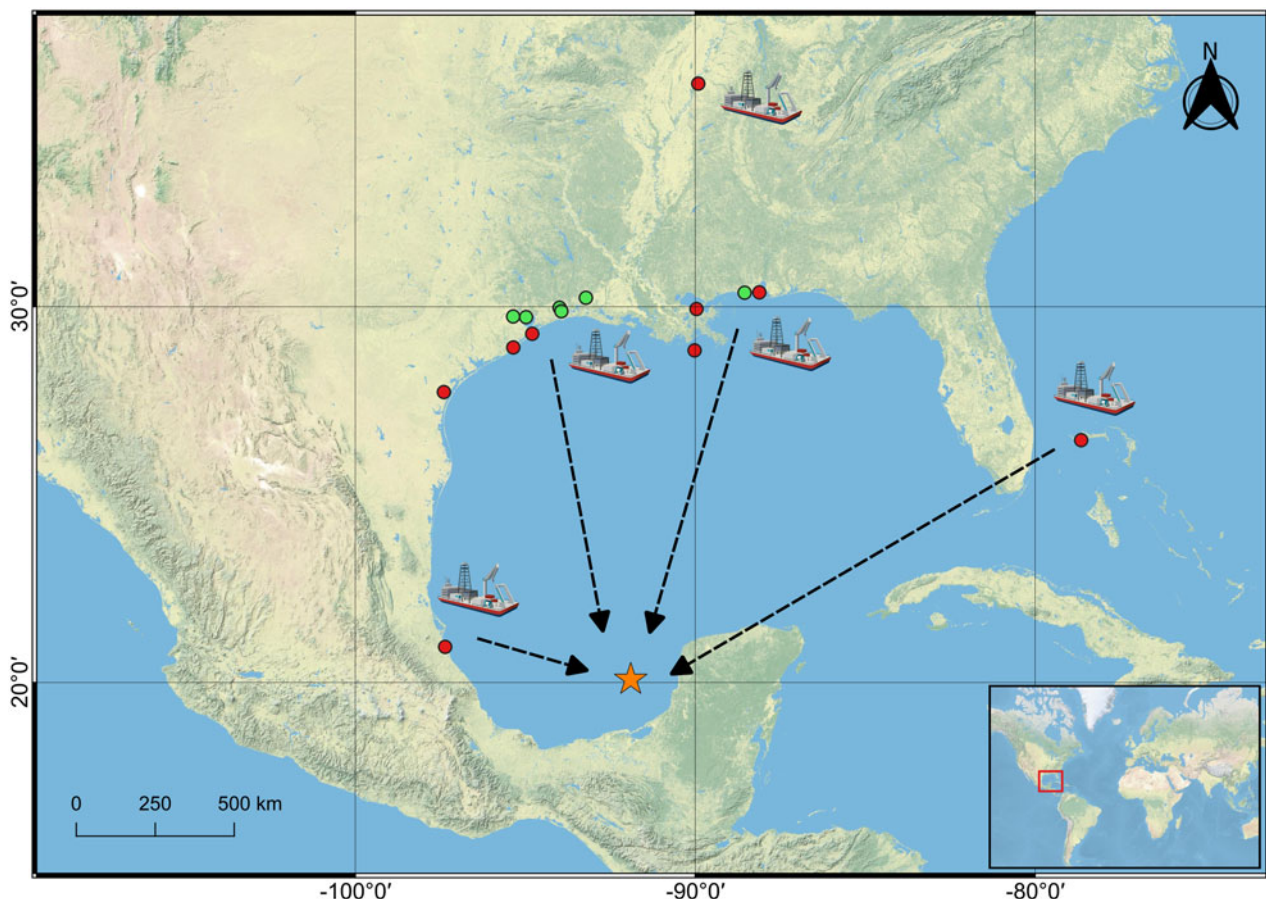


Figure 1. Locations from where the tankers set sailed towards the Cayo Arcas oil terminal (star). Green dots indicate the locations from where the tankers transporting specimens of *Moerisia cf. inkermanica* Paltschikowa-Ostroumowa, 1925 set sailed.

Table 1. Physicochemical features of the ballast water and number of medusae recorded on each tanker. The ID corresponds to each tanker.

ID	Sal ups (mean \pm SD)	Temp °C (mean \pm SD)	Medusae (n)	Water origin	Location of origin
B1	28.7 \pm 0.1	30.9 \pm 0.8	0	Coastal	Mississippi river, AL. U.S.A.
B2	10.4 \pm 0.1	31.1 \pm 0.2	12	River	Baytown, TX. U.S.A.
B3	13.8 \pm 0.1	31.6 \pm 0.7	1	River	Houston, TX. U.S.A.
B4	8.7 \pm 0.6	32.3 \pm 0.3	0	River	Sunil Nederland, TX. U.S.A.
B5	30.3 \pm 0.2	30.3 \pm 0.5	0	Coastal	Freeport, TX. U.S.A.
B6	29.2 \pm 9.3	28.1 \pm 1.3	0	River	Loop, U.S.A.
B7	0.1 \pm 0.1	29.7 \pm 0.2	0	River	Lake St. Charles, LA. U.S.A.
B8	29.4 \pm 0.1	30.4 \pm 0.4	0	Coastal	Corpus Christi, TX. U.S.A.
B9	0.2 \pm 0.1	29.4 \pm 0.5	0	River	Mississippi river, AL. U.S.A.
B10	32.8 \pm 0.4	31.1 \pm 1.0	0	Coastal	Corpus Christi, TX. U.S.A.
B11	20.1 \pm 0.1	30.5 \pm 0.5	0	River	Port Arthur, TX. U.S.A.
B12	14.4 \pm 0.4	32.6 \pm 0.0	0	River	Port Arthur, TX. U.S.A.
B13	9.8 \pm 0.3	31.7 \pm 0.4	58	River	Sunil Nederland, TX. U.S.A.
B14	20.3 \pm 0.1	31.0 \pm 0.3	0	River	Port Arthur, TX. U.S.A.
B15	28.7 \pm 0.1	30.6 \pm 0.5	0	Coastal	Pascagoula, MS. U.S.A.
B16	35.7 \pm 0.4	30.0 \pm 0.0	0	Coastal	Tuxpan, Ver. Mexico
B17	22.1 \pm 0.1	30.8 \pm 0.4	0	River	Lake St. Charles, LA. U.S.A.
B18	15.3 \pm 0.0	30.0 \pm 0.1	0	River	Houston, TX. U.S.A.
B19	14.9 \pm 0.1	31.2 \pm 0.6	1	River	Houston, TX. U.S.A.
B20	28.2 \pm 0.1	29.8 \pm 0.1	1	Coastal	Pascagoula, MS. U.S.A.
B21	0.4 \pm 0.0	30.3 \pm 0.0	0	River	Chalmette, LA. U.S.A.
B22	23.4 \pm 0.0	30.8 \pm 0.0	1	River	Lake St. Charles, LA. U.S.A.
B23	29.0 \pm 0.1	30.1 \pm 0.2	0	Coastal	Pascagoula, MS. U.S.A.
B24	16.6 \pm 0.7	31.8 \pm 0.1	0	River	Houston, TX. U.S.A.
B25	20.1 \pm 0.1	31.8 \pm 0.2	1	River	Port Arthur, TX. U.S.A.
B26	34.2 \pm 1.5	31.5 \pm 1.4	0	Oceanic	Corpus Christi, TX. U.S.A.
B27	33.7 \pm 1.6	30.9 \pm 0.5	0	Oceanic	Freeport, Bahamas
B28	29.3 \pm 0.4	31.3 \pm 1.2	0	Coastal	Pascagoula, MS. U.S.A.
B29	25.3 \pm 0.6	30.3 \pm 0.3	0	Coastal	Mobile, AL. U.S.A.
B30	33.2 \pm 0.5	32.6 \pm 0.1	0	Oceanic	Galveston, TX. U.S.A.

Diagnosis

Moerisid with less than 32 but more than four moniliform tentacles, with rings of nematocysts arranged regularly on tentacles, with a terminal knob; manubrium short, cylindrical, lacking lips, with a quadrangular base and four long periradial lobes, with their distal parts swollen and pendant; gonads surrounding the manubrium and continuing over the periradial lobes.

Description

Medusa with an umbrella slightly wider than high, 3.25 mm width (2 ± 4.5 mm, SD = 0.70), 3.06 mm height (2 ± 4.5 mm, SD = 0.57); mesoglea thick; manubrium slender, not extending beyond the half of the subumbrellar cavity, with a narrow mouth beset with nematocysts, and with appearance of four folded lips; the base of the manubrium is small and quadrangular, with four long periradial lobes, extending nearly to the umbrella margin in the most mature specimens, with their distal parts swollen and pendant; the proximal part of the lobes is divided longitudinally by a median groove that narrows in its distal part; gonads located on the manubrium, continuing over the periradial lobes; four thin

radial canals; margin of umbrella simple, lacking statocysts, and with a marginal ring narrow; in some specimens, the presence of short tentacles-like or vesicles-like structures, arising directly from the umbrella margin were observed; velum thin, covering 1/3 of the subumbrellar cavity; marginal bulbs oval, slightly enlarged, tapering, and clasping the umbrella margin; 15–24 (usually 16) hollow tentacles, moniliform, with numerous nematocyst rings regularly arranged, bearing a terminal knob. Cnidome composed of stenoteles of two size classes and desmonemes; stenoteles of class 1 in the tentacles: $7\text{--}8 \times 8\text{--}10$ μm , stenoteles of class 2 in the mouth: $6\text{--}9 \times 7\text{--}11$ μm ; desmonemes of tentacles: $4\text{--}5 \times 5\text{--}7$ μm ; scarce desmonemes in the mouth: $4\text{--}5$ μm .

Habitat

M. inkermanica usually inhabits brackish waters of shallow depths (Schuchert, 2010). Nevertheless, its wide distribution suggests good adaptability to physicochemical variations, reporting it in estuaries (Nascimento *et al.*, 2019), lakes (Restaino *et al.*, 2018), and marine environments (Killi *et al.*, 2020) around the world. The polyps can tolerate 5–40 psu (‰) salinity and temperatures

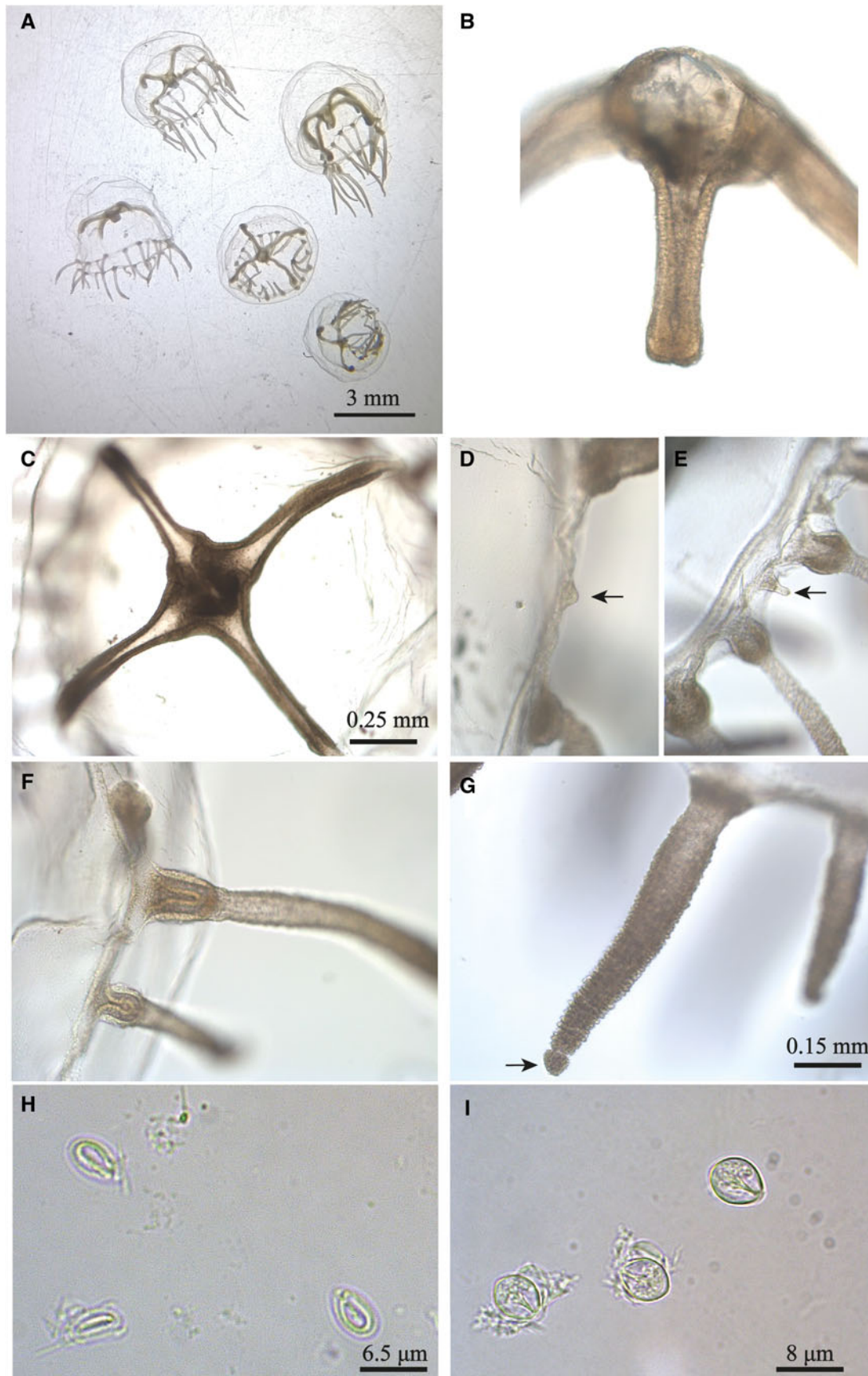


Figure 2. *Moerisia* cf. *inkermanica* Paltchikowa-Ostroumowa, 1925. (A) Complete view of mature specimens; (B) Lateral view of the manubrium; (C) Aboral view of the manubrium and perradial lobes; (D-E) Umbrella margin indicating tentacles at different development stages; (F) Oval clasping bulbs; (G) Moniliform tentacle indicating the terminal nematocyst knob; (H) Desmonemes; (I) Stenoteles.

Table 2. Comparison of the morphological diagnostic features of the valid species within *Moerisia* Boulenger, 1908

	<i>M. inkermanica</i> Paltschikowa-Ostroumowa, 1925	<i>M. lyonsi</i> Boulenger, 1908	<i>M. pallasii</i> (Derzhavin, 1912)	<i>M. horii</i> (Uchida and Uchida, 1929)	<i>M. carine</i> Bouillon, 1978	<i>M. gangetica</i> Kramp, 1958	<i>M. gemmata</i> (Ritchie, 1915)
Medusa stage							
Umbrella (mm)	Up to 8 wide, 6 high	4.5 wide, 4 high	3 wide, 3.5 high	4–6 high	2.6 wide, 3.3 high	3 wide, 2 high	Not available
Manubrium	Small, cruciform, lacking real lips	Cylindrical, without lips	Short, cruciform, with four weakly defined lips	Short, quadrangular, four-sided mouth armed with nematocysts	Short, quadrangular; mouth cruciform, with four fine lips armed with nematocysts	Small, quadrangular, with a cross-shape mouth, lacking lips	Not available
Perradial lobes	Long, 3/4 of radial canals length, extending nearly to bell margin, divided longitudinally by a median groove that narrows in its distal part; distal portions sac-like and pendent	About 2/3 of the length of the radial canals	About 2/3 of the length of the radial canals	Long, with sac-like terminal parts hanging down in the subumbrella	Very short, not extending beyond the subumbrellar cavity, with smooth gonads running over lobes	Long, extending almost to the ring canal, with gonads running over lobes, in their distal part interrupted by a narrow median line; distal portions sack-like and pendent	Not available
Tentacles (n)	Up to 34, of different lengths, moniliform, with smooth rings of nematocysts regularly arranged, and a terminal knob	Usually 4, rarely 16–22, with prominent rings of nematocysts	Up to 32, of different lengths, with large nematocyst rings	Up to 39	Up to 16 (usually 12), of different sizes, altering short and long tentacles, moniliform, with rings of nematocysts regularly arranged, and a terminal knob	19 of the same length, with numerous nematocyst rings regularly arranged	Not available
Cnidome (µm)	Desmonemes (4–5 × 5–7), stenoteles of two size classes, class 1 in tentacles (7–8 × 8–10), class 2 in the mouth (6–9 × 7–11), mastigophores, ? haplonemes	Three types. Large oval barbed capsules of two size classes (stenoteles), cylindrical capsules, without barbs with the thread coiled around the imaginary longitudinal axis, forming several coils (? mastigophores), and small pip-shaped capsules, devoid of barbs, with the thread thick and short (Desmonemes)	Not available	Stenoteles (6.7–12.5 × 8.2–15.4), Desmonemes (2.9–4.8 × 5.8–8.6), Basitrichous isorhizas (1.9–3.8 × 5.8–8.6)	Composed of stenoteles, desmonemes and euryteles	Not available	Not available
Polyp stage							
Size (mm)	Up to 5	Over 2	~1	1–2	Not available	Not available	0.6–1
Tentacles (n)	4–12	4–8	10–15	4–15, usually more than 12	Not available	Not available	4–12
Podocysts (n)	Up to 5	Lacking, instead, colonial growing with short branched hydrorhiza of stolon-like tubes	Lacking, instead, forming small hydrorhiza	Up to 10	Not available	Not available	1–2

(Continued)

Table 2. (Continued.)

	<i>M. inkermanica</i> Paltschikowa-Ostroumowa, 1925	<i>M. lyonsi</i> Boulenger, 1908	<i>M. pallasi</i> (Derzhavin, 1912)	<i>M. horii</i> (Uchida and Uchida, 1929)	<i>M. carine</i> Bouillon, 1978	<i>M. gangetica</i> Kramp, 1958	<i>M. gemmata</i> (Ritchie, 1915)
Cnidome (µm)	Stenoteles, desmonemes, mastigophores, haplonemes?	Large oval barbed capsules of two size classes (stenoteles), cylindrical capsules, without barbs with the thread coiled around the imaginary longitudinal axis, forming several coils (mastigophores?), and small pip-shaped capsules, devoid of barbs, with the thread thick and short (Desmonemes)	Not available	Stenoteles (5.3– 8.6 × 6.7–10.6), Desmonemes (2.9– 4.8 × 5.0–7.9), Basitrichous isorhizas (1.9–3.8 × 4.8–7.7)	Not available	Not available	Macrocnides 6 × 7– 8 (stenoteles?) and microcnides 3 × 4–5 (desmonemes?)
References	(Uchida and Nagao, 1959; Bouillon <i>et al.</i> , 2004; Schuchert, 2010)	(Boulenger, 1908; Kramp, 1961; Bouillon <i>et al.</i> , 2004)	(Derzhavin, 1912; Kramp, 1961)	(Uchida and Uchida, 1929; Uchida and Nagao, 1959; Calder, 2010)	(Bouillon, 1978; Schuchert, 2010)	(Kramp, 1955, 1961)	(Ritchie, 1915)

from 0–30°C. They grow on reeds, pilings, and among polychaete tubes (Schuchert, 2012).

Remarks

The presence of ocelli is a diagnostic character at the family level (Bouillon *et al.*, 2004; Schuchert, 2010). However, ocelli were not observed in the analysed specimens. We attribute the absence of ocelli to the deterioration of the specimens due to the age of the samples and the preservation method. In addition, the shape of the bulbs varied among the specimens, which can also be attributed to the preservation method. The length of the per-radial lobes varied among the analysed specimens, likely due to the different development stages. Kramp (1938) mentioned the presence of statocysts in the umbrella margin of *M. inkermanica*, whereas Valkanov (1953) states that Kramp's interpretation corresponds to nematocyst capsules (Schuchert, 2010). We observed similar structures to the previously described, concluding that they are marginal tentacles with different developmental stages (Figure 2d, e).

Discussion

The morphological characteristics of the specimens analysed in this work match those reported for *M. inkermanica* (Kramp, 1959, 1961; Bouillon *et al.*, 2004), except the cnidome reported by Schuchert (2010), which indicated four types of nematocysts. Due to the scarcity of morphological and molecular information for the members of *Moerisia* (Tables 2 and 3), we decided to tentatively recognize our specimens as *M. cf. inkermanica*. The variation in the cnidome could be considered a diagnostic character for discriminating among the species of *Moerisia*; yet, this information is poorly described for some species, so taxonomic studies describing this aspect are fundamental to improving the knowledge about the taxonomy of this group. The number of marginal tentacles and the length of the perradial lobes of the manubrium are the main characteristics differentiating among the medusae of *Moerisia* (Bouillon *et al.*, 2004; Schuchert, 2010; Jankowski and Anokhin, 2019). In this sense, *M. lyonsi* is distinguished from *M. inkermanica* by the number of tentacles and their prominent nematocyst clusters (Kramp, 1961; Bouillon *et al.*, 2004; Jankowski and Anokhin, 2019). Likewise, the polyp of *M. lyonsi* lacks podocysts (pedal disc), whereas that of *M. inkermanica* presents these structures (Bouillon *et al.*, 2004; Jankowski and Anokhin, 2019). *M. lyonsi* is reported from Egypt (type locality) and in rivers from Virginia, U.S.A. (Calder and Burrell, 1967).

M. carine Bouillon, 1978 can be differentiated from *M. inkermanica* by its short perradial lobes, its marginal tentacles of different sizes (up to 16), and its mouth with well-defined lips and cnidome (Bouillon, 1978). Despite the perradial lobes of the specimens analysed in this study varied in length, no specimens with short lobes as described in *M. carine* were observed (Bouillon *et al.*, 2004), except a juvenile with four tentacles. The polyp of *M. carine* is unknown, so a comprehensive morphological comparison with its congeners is not possible. This species is distributed in Papua New Guinea (type locality) and the Eastern Mediterranean (Schuchert, 2010).

The medusa of *M. horii* (Uchida and Uchida, 1929) resembles that of *M. inkermanica* (Uchida and Nagao, 1959), making it hard to recognize reliable morphological characteristics to discriminate between these species. Their main morphological differences are in the polyp stage. The polyp of *M. horii* is smaller, usually with more than 12 tentacles and up to 10 podocysts (Uchida and Nagao, 1959; Calder, 2010). In addition, three types of nematocysts are reported in *M. horii*, i.e., stenoteles, basitrichous isorhizas, and desmonemes, whereas the specimens of this study only had stenoteles and desmonemes, and those analysed by

Table 3. GenBank accession numbers for the specimens of *Moerisia* Boulenger, 1908 with molecular data and their locality

Taxa	GenBank accession number				Locality	Reference
	28s	18s	16s	COI		
<i>M. inkermanica</i>			MG882122; MG882118		Barneget Bay, USA	Unpublished
<i>M. inkermanica</i>			MG575536; MG575535		New Jersey, USA	(Restaino <i>et al.</i> , 2018)
<i>M. inkermanica</i>	KT757161	KT722408; GQ424340	KT266626		Brazil	(Nawrocki <i>et al.</i> , 2010; Maronna <i>et al.</i> , 2016)
<i>M. inkermanica</i>		KF962289; KF962288; KF962287; KF962286; KF962285	KF962504; KF962503; KF962502; KF962501; KF962500	KF962163; KF962162; KF962161; KF962160; KF962159	China?	Unpublished
<i>M. lyonsi</i>		HM997188			San Francisco estuary, California, USA	(Meek <i>et al.</i> , 2013)
<i>Moerisia</i> sp	AY920801				San Francisco Bay, USA	(Collins <i>et al.</i> , 2006)
<i>Moerisia</i> sp		GU198210; GU198209			San Francisco estuary, California, USA	(Meek <i>et al.</i> , 2013)
<i>Moerisia</i> sp			AY512534		San Francisco Bay, USA	(Collins <i>et al.</i> , 2005)
<i>Moerisia</i> sp			KX355402		Suisun Bay, California, USA	Unpublished
<i>Moerisia</i> sp			MH166778; MH166777; MH166776; MH166775		Pamunkey River, Virginia, USA	Unpublished
<i>Moerisia</i> sp		AF358083			NA	(Collins, 2002)
<i>Moerisia</i> sp			EU876555		NA	(Cartwright and Nawrocki, 2010)

Schuchert (2010) presented two additional types, i.e., mastigophores and haplonemes?

Three species of *Moerisia* are hard to differentiate among their congeners due to their incipient morphological descriptions, the scarcity of records, and the lack of knowledge about their polyp or medusa stages, i.e., *M. pallasi* (Derzhavin, 1912), *M. gemmata* (Ritchie, 1915), and *M. gangetica* Kramp, 1958. Morphological differences between *M. pallasi* and *M. inkermanica* are not evident in the medusa stage (Kramp, 1961; Schuchert, 2010). Unfortunately, since its first description in the Caspian Sea (Derzhavin, 1912), the morphological descriptions of *M. pallasi* have been scarce (e.g., Kramp, 1961), making it difficult to recognize its taxonomic boundaries. The polyp of *M. pallasi* is smaller than that of *M. inkermanica* and lacks podocysts, resembling that of *M. lyonsi*. However, the polyp of *M. pallasi* presents a greater number of tentacles (Derzhavin, 1912; Bouillon *et al.*, 2004). *M. gemmata* was described based on the polyp stage, which is smaller than that of *M. inkermanica* and has up to two podocysts and two types of nematocysts, although both possess the same number of tentacles (Ritchie, 1915). The medusa of *M. gemmata* is unknown, so comprehensive morphological discrimination is complicated. *M. gangetica* was described and differentiated from *M. lyonsi* based on geographical grounds (Kramp, 1955). This species, however, is reported in nearby locations where *M. inkermanica* occurs, presenting similar characteristics in the medusa stage (Kramp, 1955). Moreover, the polyp stage of *M. gangetica* is unknown, making reliable morphological differentiation

impossible. These three species have been suggested as conspecific of some of their congeners (Rees and Thursfield, 1965; Schuchert, 2010); however, this must be addressed with integrative approaches, considering morphological and molecular data of the species from their different type localities. Molecular data regarding Moerisids is scarce, and the available information is related to only two nominal species (*M. inkermanica* and *M. lyonsi*) coming from the USA, Brazil, and China. *M. inkermanica* is the best molecularly known species, although there exist specimens with no specific assignment, which could suggest other undescribed species (Table 3).

Since its first description from the bay of Sevastopol in the Black Sea, *M. inkermanica* has been reported in the Netherlands (Saraber, 1962), the Mediterranean Sea (Schuchert, 2010; Killi *et al.*, 2020), India (Kramp, 1955), France (Bouillon *et al.*, 1969), South Africa (Millard, 1975) and in different localities from Brazil (e.g., Nogueira and Oliveira, 2006; Nascimento *et al.*, 2019; Teixeira-Amaral *et al.*, 2021). Some works hypothesized that its introduction was through maritime transport (e.g., Saraber, 1962; Nascimento *et al.*, 2019). Here, we proved this hypothesis for the Gulf of Mexico since the analysed specimens came from the ballast water of oil tankers. Hence, we encourage attention to the application of protocols that regulate the management of this type of water since other non-native species could be introduced. The presence of juvenile specimens in our samples suggests a budding process, which might explain the prevalence of the species after water exchange since the polyps can be fixed on the walls of the tanks.

Only the tankers coming from the ports of Baytown, Houston, Sunoil Nederland, Port Arthur (TX), Lake St. Charles (LA), and Pascagoula (MS) transported specimens of *M. cf. inkermanica* on their ballast water (Figure 1). Nevertheless, the presence of this species in other ports is not ruled out since we only sampled three tanks per tanker.

Studies monitoring hydrozoan diversity in the Gulf of Mexico are fragmentary. In the southern Gulf, diverse studies have been conducted since the collection of the specimens of this work (2005) reporting different hydrozoan species in coastal ecosystems but not reporting to *M. inkermanica* (e.g., Cortés-Lacomba et al., 2013; Gutiérrez-Aguirre et al., 2015; Ahuatzin-Hernández et al., 2020; López-Torres et al., 2023). In the northern Gulf, fewer studies have been carried out in this field, focusing on phylogenetic aspects (e.g., Pruski and Miglietta, 2019; Miglietta and Pruski, 2023). The monitoring hydrozoan diversity in nearby areas to the ports where tankers transporting *M. cf. inkermanica* set sail is scarce (e.g., Moore, 1962; Burke, 1975, 1976; Harrel, 2002; Pruski and Miglietta, 2019). *M. inkermanica* is considered an invasive species in some regions of the world (Killi et al., 2020), so its establishment in the Gulf of Mexico must be proved by monitoring the different coastal ecosystems of the region, analysing its abundance changes through the seasons of the year, and its impact on the native populations of the Gulf. Only then could it be recognized as an invasive species in this region. We encourage conducting more efforts in this way, aiming to have a better knowledge of the diversity of this group in the Gulf of Mexico, which is crucial to understanding the potential impacts on the native fauna and being able to apply correct management strategies to mitigate these impacts.

Data. All data are provided within the manuscript. Specimens are deposited at the collection of ‘Cnidarios del Golfo de México y Mar Caribe Mexicano’, based at the Universidad Nacional Autónoma de México, Facultad de Ciencias, Unidad Multidisciplinaria de Docencia e Investigación-Sisal, Yucatán.

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Author contribution. UOL, MHR, and MAON conceptualized the sampling. JMAH conceptualized the idea and identified the specimens. All the authors approved the final version of the manuscript.

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