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First record of the box jellyfish *Tripedalia cystophora* (Cnidaria: Cubozoa: Tripedaliidae) in the Gulf of Mexico

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Abstract.—Although observations of the box jellyfish *Tripedalia cystophora* have been widely documented since it was first recorded in Jamaica in 1897, to date there are no published reports of its occurrence in the Gulf of Mexico. Eighteen specimens of *Tripedalia cystophora* (Cubozoa: Tripedaliidae), 12 and 6, respectively, were collected from a mangrove waterway near Bonita Springs, Florida, in 2010 and a brackish canal in Englewood, Florida, in 2015. Additional records from Tampa Bay (2007–2015) and Everglades City (2015), Florida, were documented with photography. Within the past few years, new records of *T. cystophora* from other localities, including Hawai'i, northern Australia, and the east coast of Florida, have been reported. This study represents the first published report of the species from the Gulf of Mexico. Several other species of cubozoans have been reported from the Gulf region, but the presence of three pedalia at each corner of the swimming bell (12 tentacles total), its small size up to 13 mm, and the presence of sexually dimorphic gonads, markedly distinguishes it from other cubozoan taxa.

Keywords: box jellyfish, *Tripedalia cystophora*, Tripedaliidae, Cubozoa, Gulf of Mexico, distribution

Tripedalia cystophora Conant, 1897 is a small (maximum bell height ca. 12–13 mm) box jellyfish (Cnidaria: Cubozoa) that inhabits tropical and subtropical mangrove systems (Conant 1897, Kramp 1961, Ekins & Gershwin 2014). Since its description from Jamaica in 1897, the species has been the subject of several phylogenetic and developmental studies (Werner 1973, Laska-Mehnert 1985, Bentlage et al. 2010, Gurska & Garm 2014). Its elaborate copulation strategies have been well documented (Werner 1971, 1973, Stewart 1996), making it an excellent cubozoan for laboratory and field studies examining paternity, sexual selection, and the potential involvement of visually-guided behavior related to mat-

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ing. *T. cystophora* is one of three species in the family Tripedaliidae (Order: Carybdeida), along with *T. binata* Moore, 1988 and *Copula sivickisi* (Stiasny, 1926), all of which are sexually dimorphic and produce spermatophores (Lewis & Long 2005, Bentlage et al. 2010, Bentlage & Lewis 2012, Straehler-Pohl et al. 2014). While spermatophore transfer from male to female is well documented in *T. cystophora* and *C. sivickisi*, (Werner 1973, Lewis & Long 2005, Underwood et al. 2013), details remain unclear for *T. binata*. Furthermore, *T. cystophora* has long been used as a model for elucidating the biomechanics, physiology, and evolution of the complex lens-eyes characteristic of all box jellyfish (Nilsson et al. 2005, Garm et al. 2007, Garm & Mori 2009). The most recent study of this species used a genomics approach to investigate cubozoan opsin diversification (Liegertová et al. 2015). Despite extensive research on these various aspects of the species' biology and the description of two types of nematocysts (Orellana & Collins 2011), the venom components of the nematocysts are yet to be described. Unlike other box jellyfish that are notorious for painful and sometimes debilitating stings (Russell et al. 1984, Brinkman & Burnell 2009, Bentlage et al. 2010), there are no documented human stings by *T. cystophora* despite the extensive number of publications on this species. Furthermore, *T. cystophora* has never been listed among dangerous box jellyfish in the scientific literature (e.g. Williamson et al. 1996), suggesting that its sting is mild to humans.

The species has a widespread, pantropical to subtropical distribution. Within 40 years of the original description from Jamaica (Conant 1897), *T. cystophora* was reported from the eastern Pacific and Coral Triangle (Stiasny 1926, Thiel 1936). In the past 4 years, the reported range of the species has expanded to include records from the east coast of Florida (Orellana & Collins 2011), northern Australia, (Ekins & Gershwin 2014), and Hawai'i (Crow et al. 2015). Ekins and Gershwin (2014) reviewed the geographic distribution of the species, listing various Atlantic, Pacific, and Indian ocean localities and, like prior authors, suggested that these reports represent recent introductions rather than oversight of earlier extensive surveys conducted in those localities. Our new record of the species is the first in the Gulf of Mexico Large Ecoregion, an area differing from neighboring regions (e.g., Caribbean) based on its distinct biota, genetic breaks between it and bordering regions, extensive freshwater drainage, currents, and other abiotic factors (Kumpf et al. 1999, Felder & Camp 2009, Fautin et al. 2010). Furthermore, the northernmost records for *T. cystophora*, presented herein, lie on the fringe between the Northern Gulf and Floridian subregions, which is the northern latitudinal limit of mangroves and a transition to oyster reef and saltmarsh dominated habitats (Fautin et al. 2010). Our report therefore likely represents the northernmost limit of *T. cystophora* in the Gulf of Mexico and perhaps the Atlantic Ocean.

Materials and Methods

The specimens were identified as *Tripedalia cystophora* based primarily on: 1) the presence of four groups of tentacular pedalia, one at each corner of the bell; 2) three pedalia per group; and 3) each pedalium with one tentacle (Conant 1897).

In September 2010, numerous *T. cystophora* medusae were noticed swarming near red mangroves (*Rhizophora mangle*) in a waterway adjacent to Estero Bay near Bonita Springs, Florida. Twelve exemplars (bell height 5.5–13 mm), including males and females, were collected by a resident and delivered to the Florida Gulf Coast University's Vester Field Station in Bonita

Springs, where they were held in a small aquarium for observation. The samples were separated into three lots: 2 lots were prepared in 5% formalin/seawater solution and 1 lot in 95% ethanol for future molecular studies. Material was deposited into the National Museum of Natural History, Smithsonian Institution (USNM). The following year, a large number of medusae were seen swarming at the Vester Field Station in August 2011 (Lasley et al. 2016).

On July 15, 2015, six *T. cystophora* medusae (bell height 4.8–9.5 mm) were collected in a brackish canal parallel to East 3rd Street, Englewood, Florida (Fig. 1). The canal feeds into Rock Creek ca. 1.5 km from the creek's mouth at Lemon Bay. Specimens were caught near *Rhizophora mangle* roots roughly one hour before sunset (20h25; with low tide (–0.1 ft) at 20h47). One exemplar (Fig. 1A) was determined to be female based on the presence of large eggs and embryos circulating in the gastrovascular cavity. The other specimens appeared to be post-spawned adults given their mature size but lack of gonads, so the sex could not be verified (Fig. 1B–F). After live transport to the Fish and Wildlife Research Institute, St. Petersburg, Florida, each specimen was photographed (Figs. 1, 2), measured, preserved in 10% formalin/seawater solution, and deposited into the Institute's marine collection (FSBCI). Prior to preservation in formalin, one tentacle from each specimen was removed and stored in 95% EtOH for future molecular study. Preserved specimens from Englewood were examined using a Zeiss Discovery V8 SMZ-168 stereoscope with manual 8x zoom. Live color photos were taken using a Nikon D7100 DSLR with 60 mm AF Micro-Nikkor f2.8D and the Nikon R1C1 strobe package. Specimens were photographed from above in a shallow aquarium with a black velvet background. Measurements of bell height and bell width are provided below under material examined in the following format (bell height × bell width).

Additional specimens were observed but not collected at Smacks Bayou (2007) and between Cockroach Bay and Anna Maria Island (2011), Tampa Bay, Florida (Sheri Parks pers. obs.); and Everglades City, Florida (2015; including identifiable females) (Anders Garm pers. comm.). Specimens from Smacks Bayou, St. Petersburg and Everglades City, Florida were photographed, the images providing reliable identification of the specimens as *T. cystophora* (Lasley et al. 2016).

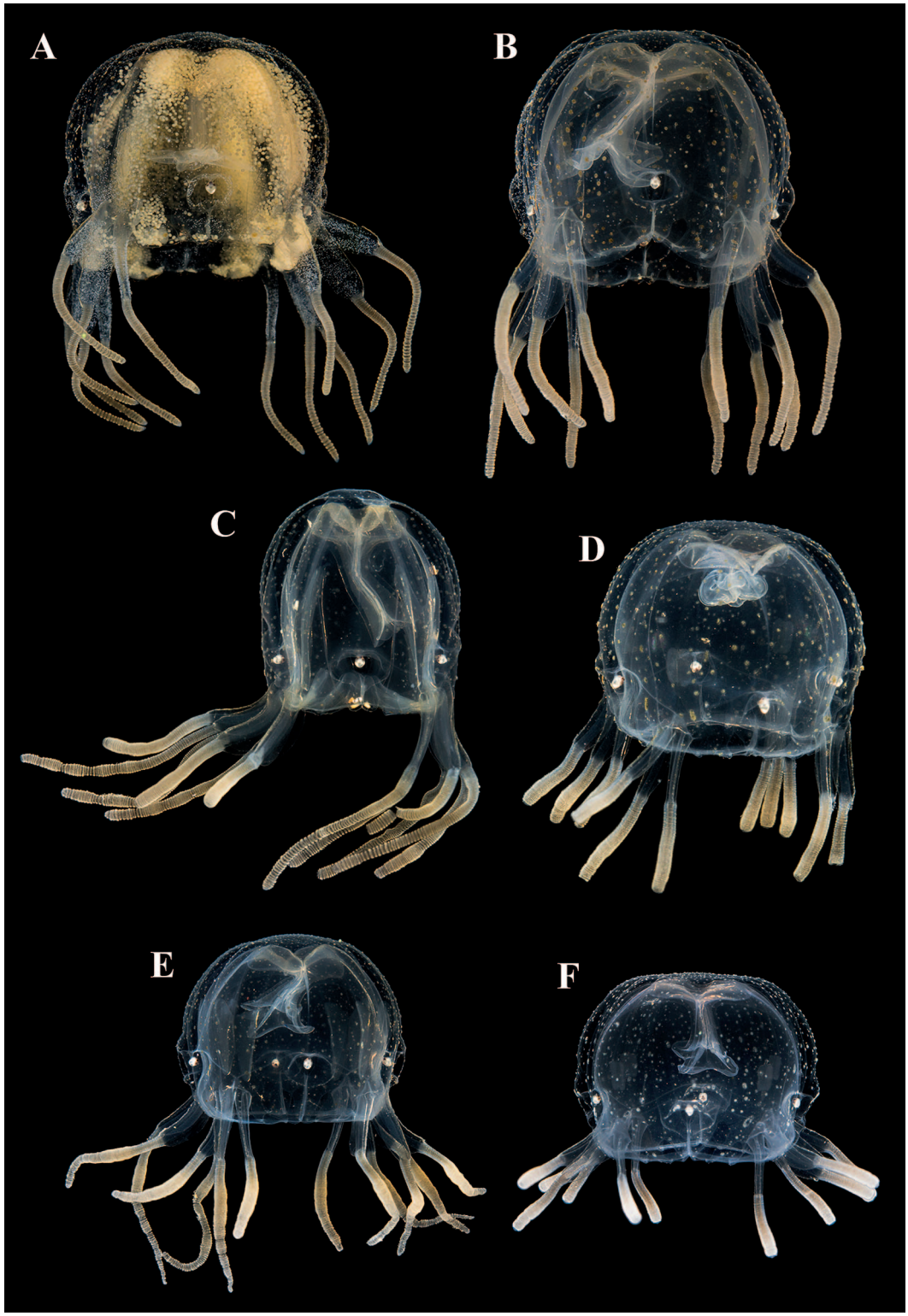
Systematics

Phylum Cnidaria Verrill, 1865
Class Cubozoa Werner, 1973
Order Carybdeida Gegenbaur, 1857
Family Tripedaliidae Conant, 1897
Genus *Tripedalia* Conant, 1897
Tripedalia cystophora Conant, 1897

Material examined.—12 medusae: 1 gravid female (5.5 mm × 7.7 mm), gastrovascular cavity filled with planulae, suggesting recent (within days) fertilization, 1 unsexed (9.5 mm × 13 mm) in formalin (USNM 1204759); 3 unsexed in 95% ethanol (USNM 1204760); 4 mature females (8.33 × 12 mm – 10 × 13 mm), 2 mature males (9 × 12.6 mm), 1 unsexed (10 mm x 14 mm) in formalin (USNM

→

Fig. 1. *Tripedalia cystophora*. Lateral view of live specimens. A, ripe female (7.8 mm × 9.2 mm) (FSBCI 129558, 1); B, sex undetermined (9.5 mm × 11.4 mm) (FSBCI 129558, 2); C, sex undetermined (8.1 mm × 9.5 mm) (FSBCI 129558, 3); D, sex undetermined (4.8 mm × 6.5 mm) (FSBCI 129558, 4); E, sex undetermined (7.6 mm × 9.4 mm) (FSBCI 129558, 5); F, sex undetermined (5.2 mm × 7.9 mm) (FSBCI 129558, 6).



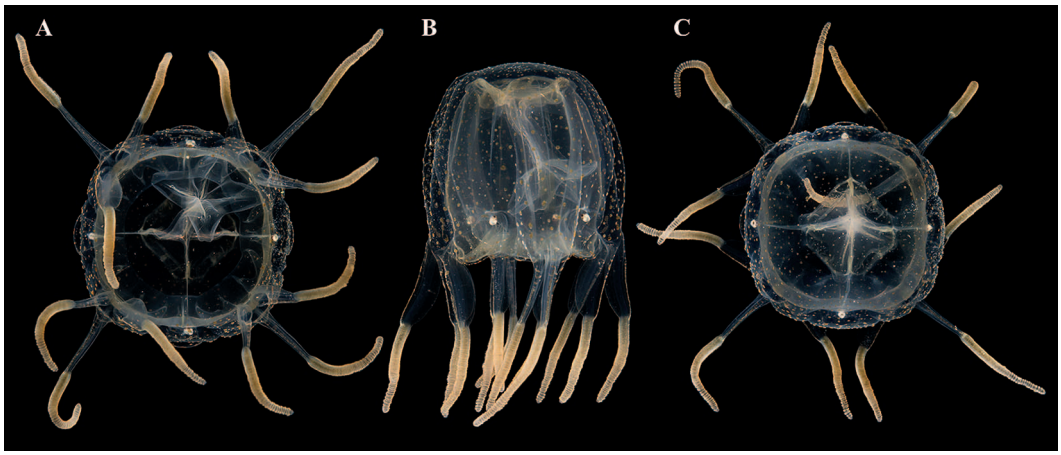


Fig. 2. *Tripedalia cystophora*. A–C, ventral, lateral, and dorsal views, respectively of live specimen, sex undetermined (9.5 mm × 11.4 mm) (FSBCI 129558, 2).

1205451) – collected from red mangroves near Bonita Springs, Florida, Gulf of Mexico (26°22′53″N 81°50′08″W), USA, coll. C. Ritter, 7 September 2010, daylight hours.

6 medusae: 1 female, 5 sex undetermined (4.8 × 6.5 mm – 9.5 × 11.4 mm) (FSBCI 129558, 1–6) – collected from red mangroves, in canal parallel to East 3rd Street, Englewood, Florida, Gulf of Mexico (26.941419, –82.335328), USA, coll. M. Vorkapic, R. Lasley, 15 July 2015.

Range.—*Tripedalia cystophora* occurs in tropical and subtropical mangrove habitats between 32°N and 28°S latitude. In the Atlantic, the species has been reported from Jamaica, Puerto Rico, the Bahamas, and the east coast of Brazil (Morandini & Marques 1997); the east coast of Florida (Orellana & Collins 2011); and the Gulf of Mexico (this report). Pacific Ocean specimens have been reported from Japan (Uchida 1970); Costa Rica (Rodríguez-Sáenz & Segura-Puertas 2009); northern Australia, Thailand, and Indonesia (Ekins & Gershwin 2014); and Hawai'i (Crow et al. 2015). Indian Ocean specimens have been reported from Aldabra Atoll, Seychelles (Ekins & Gershwin 2014).

Conclusions

Of the seven box jellyfish species reported from the Gulf of Mexico, including those in this study, three have been well documented as long-term inhabitants: 1) *Alatina alata* (Reynaud, 1830) (= *Carybdea alata*) (Larson et al. 1991, Lewis et al. 2013); 2) *Tamoya* sp. (*T.* cf. *haplonema*) Müller, 1859 (Phillips & Burke 1970, Collins et al. 2011); and 3) *Chiropsalmus quadrumanus* Müller, 1859 (Müller 1859, Guest 1959, Phillips & Burke 1970, Gómez Aguirre 1986). In addition to these well-documented taxa, *Alatina grandis* (Agassiz & Mayer, 1902) was reported (as *Carybdea* var. alata) a single time in the Gulf of Mexico (Graham 1998). Furthermore, Hedgepeth's (1954) species checklist of the Gulf of Mexico includes *Carybdea aurifera* Mayer, 1900, and newer checklists (Segura-Puertas et al. 2003, Segura-Puertas et al. 2009) include *Carybdea marsupialis* (Linnaeus, 1758). However, the former corresponds to collections by Mayer (1900) from Tortugas and the latter to reports by Suárez-Morales et al. (1999) from the western Caribbean Sea.

All species reported from the Gulf of Mexico, including *T. cystophora*, belong to

the order Carybdeida except *Chiropsalmus quadrumanus*. *Tripedalia cystophora* is easily distinguished from the other species of Carybdeida by the presence of three pedalia/tentacles at each interradial corner of the bell (versus one in other Gulf species of Carybdeida) (Fig. 2) (Conant 1897, Mayer 1910). *Chiropsalmus quadrumanus* (Chirodropida: Chiropsalmidae), superficially resembles *T. cystophora* in having multiple tentacles at each corner, but *C. quadrumanus* possesses only a single pedalium per corner that is divided into 5–9 branches, each giving rise to a single tentacle (Mayer 1910, Calder 2009).

Conant's 1897 original description of *T. cystophora* does not allude to any type specimens. Furthermore, the legendary F. S. Conant described *T. cystophora* as a species new to science while he was Director at the Johns Hopkins Marine Laboratory at Kingston Harbor, Jamaica (Conant 1897), but there is no indication that Conant deposited any cubozoan specimens into the affiliated Institute of Jamaica Museum (IJM) (Muka 2014) prior to his untimely death in 1897. A Johns Hopkins circulatory published in memory of Conant and his work (Brooks 1900) states that Conant "brought home specimens", but it does not say where they were deposited (Brooks 1900:2). No invertebrate zoology collection currently exists at Johns Hopkins University, bringing the existence of the specimens further into question. Nonetheless, given the completeness of Conant's original description and accompanying illustration of the specimens, there is no doubt about the species' identity as *T. cystophora*, negating the need to erect a neotype in accordance with ICZN Article 75.2 (ICZN). Finally, it has been suggested that the species has been extirpated from its type locality of Kingston, Jamaica (Ekins & Gershwin 2014).

This new record of *T. cystophora* extends the species' known range to the Gulf of Mexico as far north as Tampa Bay. Together with the movement of mangrove systems into higher latitudes (Saintilan et al. 2014) and the possible increase in frequency of jellyfish blooms (Condon et al. 2013), the range expansion of *T. cystophora* and its possible link to climate change and human introduction is worthy of investigation. Molodtsova (2009) reviewed the long history of medusozoan studies in the Gulf. Despite being a small species that can easily blend in with mangrove infrastructure and murky water (Stewart 1996, Garm et al. 2012), the fact that *T. cystophora* was previously never reported in the Gulf of Mexico, despite decades of extensive medusozoan sampling, casts doubt on their prior occurrence in the region. Correspondingly, recent new records of the species in Australia (2014) and Hawaii (2015) are assumed to have resulted from human introductions (Ekins & Gershwin 2014, Crow et al. 2015), and the likelihood of anthropogenic influence and cryptogenesis (introduction from an obscure locality) was addressed in a report on the recent appearance of *Copula sivickisi*, another member of the Tripedaliidae, in the western Atlantic (Bennett et al. 2011), which had been considered strictly an Indo-Pacific species (Lewis et al. 2008). The recently published *T. cystophora* genome, along with future large-scale morphological and molecular studies, could serve as a tool to elucidate the mechanism of dispersal resulting in the apparent recent global range expansion of the species.

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