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Cassiopea andromeda (Cnidaria, Scyphozoa) in the subtropical eastern Atlantic

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Abstract

This study provides the first records of the upside-down jellyfish *Cassiopea andromeda* (Forskål, 1775) in the eastern Atlantic supported by molecular analysis. Specimens were observed, recorded, and sampled in an inland aquaculture facility in September 2023 in Tenerife Island (Canary Islands). This new record officially demonstrates the geographical expansion of *C. andromeda*, and the introduction of a new potential invasive species in the Macaronesia oceanic island system.

Introduction

Cassiopea Péron & Lesueur, 1810, a distinct Scyphozoa genus, has been receiving growing interest attributed to its role as a model system for bioindicators (Epstein *et al.*, 2016; Harris *et al.*, 2020) and symbiotic associations (Ohdera *et al.*, 2018), its geographical extension, and its proliferation/invasive events (Stampar *et al.*, 2020; Mammone *et al.*, 2021). Often, the introduction and the invasive events of *Cassiopea* have been attributed to *Cassiopea andromeda* disregarding the outdated taxonomic knowledge and the high phenotypic variability observed in this genus. Molecular analyses are thus needed for reliable taxonomic identifications (Holland *et al.*, 2004; Morandini *et al.*, 2017; Maggio *et al.*, 2019). To date, *C. andromeda* (*sensu lato*) has been recorded in the tropical and subtropical Atlantic (e.g. Brazil, Mexico, California, Cabo Verde) (Daglio and Dawson, 2017; Moro *et al.*, 2020; Stampar *et al.*, 2020), in the Mediterranean Sea (Schembri *et al.*, 2010), and in the Indo-Pacific (e.g. French Polynesia, India, Sri Lanka) (Kayal *et al.*, 2013; Prasade *et al.*, 2016; Karunarathne *et al.*, 2020), and is often considered invasive due to its high proliferation rate and potential impact on tourism (stinging) and ecosystem (Bayha and Graham, 2014).

We present here the first report, supported by molecular analysis, of *C. andromeda* (Forskål, 1775) in the eastern Atlantic.

Materials and methods

Several *Cassiopea* cf. *andromeda* specimens with different umbrella sizes were sighted at the aquaculture facilities of the Oceanographic Center of the Canary Islands (Tenerife, 28°29′58.758″N, 16°11′46.8276″W) in April 2023. Specimens were observed in two types of inland culture tanks with an open system water supply: a 500 m^3 raceway tank used as a reserve tank and a shallow tank (16 m^2 and 0.5 m height) used for maintenance of the echinoderm *Coscinasterias tenuispina* and the anemone *Exaiptasia diaphana*, which are used for a test of Integrated Multi-Trophic Aquaculture. In September 2023, four specimens were randomly collected from the latter tank. Two specimens were preserved in formaldehyde (5%) for morphological analysis using identification keys provided by Jarms and Morandini (2019). The remaining two specimens were preserved in 98% ethanol.

One 16S rDNA sequence, available in GenBank (accession number PP496631), was determined for one of the *Cassiopea* preserved in ethanol. Its genomic DNA was extracted with the 'QuickExtract™ DNA Extraction Solution'. Polymerase chain reaction (PCR) included a mixture of 0.25 µl of DNA template, 0.4 µl of each primer (primers SHA and SHB designed by Cunningham and Buss, 1993), 6.5 µl of 'Supreme NZYTaq II 2x Green Master Mix' (Nzytech, Lisbon, Portugal), and 5.25 µl of H_2O, subjected to the following conditions: 95°C for 5 min (one cycle), followed by 34 cycles consisting of 94°C for 30 s, 46.5°C for 40 s, and 72°C for 45 s, and a final extension at 72°C for 5 min. After checking the success of the PCR through an electrophoresis run in agarose gel, the PCR product was purified using 'AMPure XP' (Beckman Coulter, Inc.) and later subjected to Sanger sequencing. The taxonomic identity of the 16S barcode generated was then confirmed through a 'Nucleotide Blast' search in GenBank (https://blast.ncbi.nlm.nih.gov/). Finally, we then retrieved all the 16S barcodes of

Figure 1. *Cassiopea andromeda* specimens observed and sampled on Tenerife Island: (A) live specimen in the tank; (B) preserved specimen, (C) marginal lappet. Credit: (A) Alejandro Escánez; (B, C) Sonia K.M. Gueroun.

C. andromeda available in GenBank, aligned these with two sequences of Cassiopea *xamachana* (sister species, used as outgroup) and the new 16S barcode of *C. andromeda* from the Canary Islands, and generated a maximum-likelihood phylogenetic tree through the PHYML server (http://atgc.lirmm.fr/phyml/).

Results

Cassiopea specimens showed an exumbrella disc-shaped with a bell diameter varying from 10 to 5.4 cm for the preserved specimens and 2 cm for the specimens used for molecular analysis; 16 rhopalia; five short and blunt marginal lappets between each rhopalium (Figure 1C); eight dichotomous oral arms that were longer (10 cm specimen) or shorter (5.4 cm specimen) than the bell radius; colour of the club-shaped vesicle was variable from white (Figure 1A, B) to dark brown and blue, mainly with a brown umbrella.

The 16S sequence determined for one of the *Cassiopea* from the Canary Islands revealed 100% identical to 16S sequences of *Cassiopea andromeda* collected in Florida (Daglio and Dawson, 2017; Muffett and Miglietta, 2023) and sister to one 16S haplotype known from the Pacific Ocean and the Red Sea (Figure 2).

Discussion

The present study constitutes the first confirmed record of *Cassiopea andromeda* in the eastern Atlantic, supported by DNA barcoding with the 16S rDNA marker. While the specimens in the aquaculture tank were sighted in April 2023, reaching a density peak in September 2023, Citizen Science (https://redpromar.org) reported the presence of *Cassiopea* specimens in August 2023 on a beach (8 m depth) less than 2 km to the east of the current study location. Another recent sighting occurred in February 2024 (same location, 5 m depth), suggesting the persistence of *C. andromeda* during winter and a potential population establishment in the Canary Islands. Although *C. andromeda* has recently been documented in Cabo Verde based on morphological analysis (Moro *et al.*, 2020), the identification of the *Cassiopea* species solely based on morphological traits cannot be reliable (Gamero-Mora *et al.*, 2022), as is often the case with several scyphozoan species (Bayha *et al.*, 2017; Lawley *et al.*, 2021; Moura *et al.*, 2022). Among the ten valid species in the *Cassiopea* genus, only *Cassiopea frondosa* presents unique traits and can be precisely identified. For the remaining species, morphological traits are too plastic and occur in more than one nominal species, rendering morphology-based identifications unreliable (Jarms and Morandini,

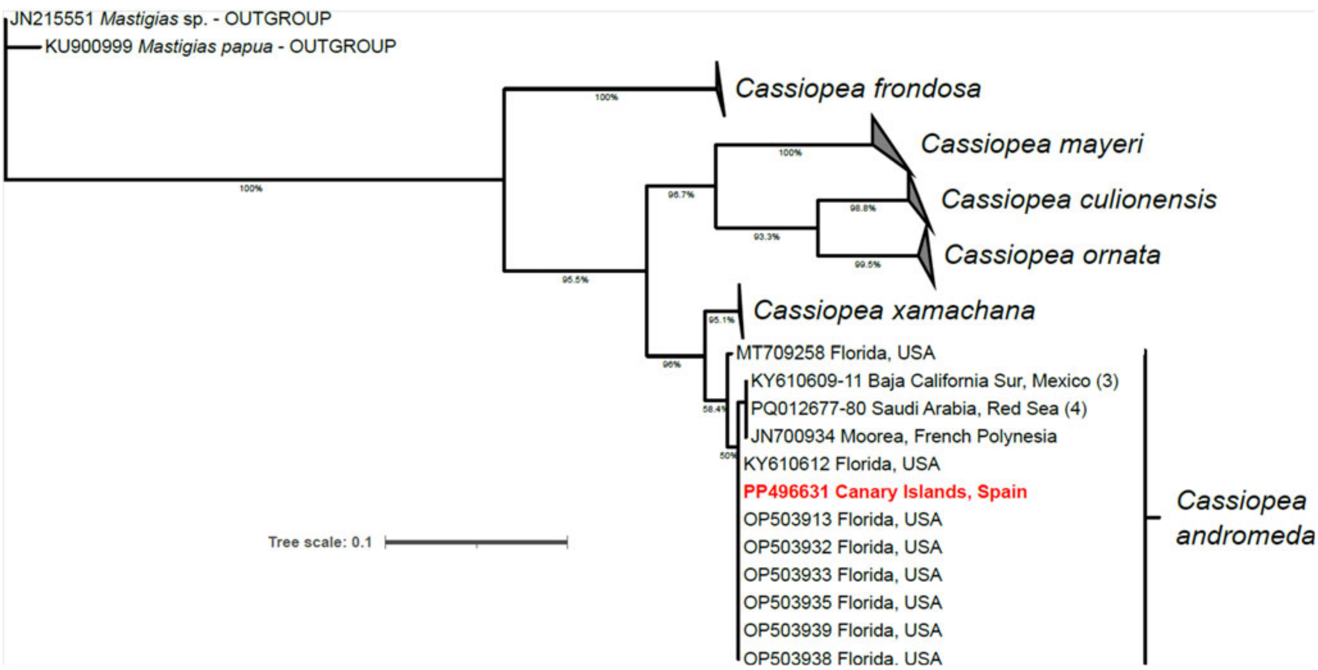

Figure 2. Maximum-likelihood phylogenetic tree, with 1000 repeats of standard bootstrap analysis, including all the available 16S sequences of *Cassiopea*.

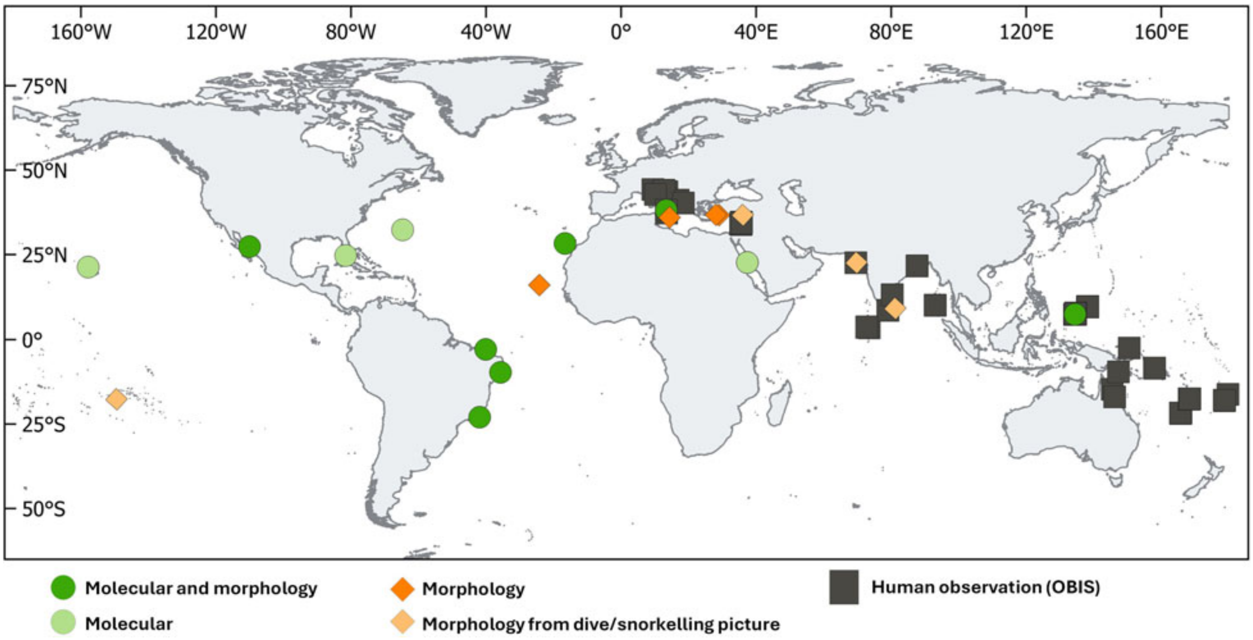

Figure 3. Worldwide records of *C. andromeda* and its identification method in the literature and in OBIS (2024) (black spots) (Holland *et al*., 2004; Çevik *et al*., 2006; Özgür and Öztürk, 2008; Schembri *et al*., 2010; Gülşahin and Tarkan, 2012; Armani *et al*., 2013; Kayal *et al*., 2013; Prasade *et al*., 2016; Gómez Daglio and Dawson, 2017; Maggio *et al*., 2019; Karunarathne *et al*., 2020; Moro *et al*., 2020; Stampar *et al*., 2020; Thé *et al*., 2021; Muffett and Miglietta, 2023).

2019; Gamero-Mora *et al*., 2022; Muffett and Miglietta, 2023). Despite this, around half of the scientific literature records of *C. andromeda* worldwide have been determined based on morphological analyses, either from anatomical laboratory approaches or from specimens photographed during dives/snorkelling, decreasing the resolution of the morphological analysis (Figure 3).

The presence of *C. andromeda* in the eastern Atlantic is still unclear. This nominal species, originally described from the Red Sea, was so far DNA barcoded from the Red Sea (only one specimen), the Mediterranean, Brazil, the Caribbean, Florida, and the Pacific Ocean in French Polynesia, Baja California, and Hawaii (Maggio *et al*., 2019; Muffett and Miglietta, 2023). The 16S haplotype of *C. andromeda* we detected in the Canary Islands is only known to occur in Florida (Figure 2) and eventually in Hawaii (cf. Muffett and Miglietta, 2023), but is still unknown to occur in the natural biogeographic range of the nominal species, preventing further explanation on the species introduction into the Atlantic based on molecular methods.

An introduction of the pelagic stage (which, in the *Cassiopea*'s case, would most likely be the ephyrae rather than the medusae, which typically reside on shallow substrates) via oceanic currents is less likely plausible as the main current systems in Macaronesia follow a southward direction and then turn west in the south of the Canary Islands after joining the North Equatorial Current towards the Tropical West Atlantic. A hull fouling-mediated introduction of the polyps is a more probable scenario, especially in the Canary Islands, where the number of ports/marinas and the total marina area have a strong effect on the non-native species richness, alongside the distance from the mainland (Castro *et al*., 2022). In the case at hand, the presence of a nearby harbour next to the aquaculture facility where *C. andromeda* was sighted (<800 m distance), strongly points to the boat-mediated introduction hypothesis.

Thé *et al*. (2021) were the first to identify *C. andromeda* in aquaculture settings, specifically semi-natural ponds for prawn farming on Brazilian mangroves and old salt flat ponds. The present record is the first in artificial marine aquaculture tanks located inland. Aquaculture facilities' nutrient-rich and stable environmental conditions support the development and reproduction of *C. andromeda* (Thé *et al*., 2020, 2021, 2023). The establishment and blooms of jellyfish, including allochthones species, in areas associated with aquaculture activities have been described worldwide in several species (Lo *et al*., 2008; Dong *et al*., 2010, 2019).

An upside-down jellyfish, identified as *C. andromeda* was recorded in the Cabo Verde (Moro *et al*., 2020) in 2019, but only based on general morphology. Assuming that the observed specimen was indeed *C. andromeda*, then its successive observation in Cabo Verde and then in the Canary Islands may constitute another example supporting the 'stepping stone' biogeographical concept along various species (Afonso *et al*., 2013; Schäfer *et al*., 2019; Schäfer, 2023).

Various human activities may facilitate the potential spread of *C. andromeda* in Tenerife and other Canary Islands. The Canary Islands, being major tourist destinations in Europe, have experienced significant degradation of their coastal habitats due to tourism (Riera and Delgado, 2019). This degradation includes the modification of shorelines to create artificial beaches, marinas, and seaports, resulting in the proliferation of artificial structures such as rock walls, breakwaters, dykes, and groynes (Riera *et al*., 2014; Riera and Delgado, 2019). These modified areas, characterized by shallow, sunlit waters, soft bottoms, and often high nutrient levels, provide ideal conditions for the establishment of *C. andromeda* colonies (Duarte *et al*., 2013; Mammone *et al*., 2021; Cillari *et al*., 2022). In addition, human-mediated introduction via the frequent ship traffic between the Canary Islands, other oceanic islands (Madeira, Azores), and the continental shores of Europe and Africa will more likely contribute to its long-distance spread in the eastern Atlantic, alongside the tropicalization of these waters.

Data. The data supporting this study's findings are available from the corresponding author, S. K. M. G., and the author, C. J. M., for molecular data, upon reasonable request.

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Competing interests. None.

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