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Tentacle autotomy: an additional mode of asexual reproduction in *Ricordea yuma* (Cnidaria, Anthozoa, Corallimorpharia)

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ABSTRACT

This paper presents a new mode of asexual reproduction of *Ricordea yuma*. Seventeen instances of tentacle autotomy (the deliberate shedding of tentacles) were observed in the tropical corallimorpharian, *Ricordea yuma*, over a four-month period. Of these, seven were deemed to have successfully completed transformation into polyps complete with mouth and tentacles. The majority of tentacles were able to attach to the bottom of the tissue culturing plates they were transplanted into for monitoring. Attachment appeared to have been made via intricate webs made of discharged cnidae, presumed to be spirocysts. Given that tentacle autotomy has been previously reported in both Scleractinia and Actiniaria, this strategy is likely to be used in other corallimorpharian species and may be an important strategy used to quickly clone themselves, monopolize habitats and outcompete other benthic inhabitants.

❑ *clonal, development, replication, polyp, genetically identical*

Corallimorpharians are a distinct group of Anthozoans, superficially described as fleshy and uncalcified solitary polyps similar to sea anemones (order Actiniaria). Morphologically (den Hartog 1980) and genetically (Lin *et al.* 2016) however, corallimorpharians are more closely related to hard corals (Order Scleractinia). There are currently 48 accepted species of corallimorpharians, divided into four families; Corallimorphidae, Discosomidae, Sideractinidae, and Ricordeidae (WoRMS 2022). Corallimorpharians inhabit a broad range of marine habitats, with members adapted to living in both tropical and temperate waters, but also a variety of depths ranging from the shallow intertidal zone down to extremes depths of over 4 km (Fautin 2009; Eash-Loucks 2010).

Corallimorpharians are formidable adversaries of Scleractinia corals and have been shown to not only prevent the recruitment and settlement of coral larvae (Langmead & Chadwick-Furman 1999a) but also smother and kill establish coral colonies in aggressive antagonistic interactions using specialised tentacles and mesentery filaments (Chadwick 1987; Chadwick & Adams 1991; Miles, 1991; Langmead & Chadwick-Furman 1999a, 1999b; Kuguru *et al.* 2004). Despite only being able to travel across benthic surfaces at maximum speeds of 14 mm per month (Chadwick & Adams 1991), corallimorpharians are able to monopolise reef substrate, spatially outcompete hard corals, and cause significant phase shifts in coral assemblages around the world (Muhando *et al.* 2002; Work *et al.* 2008 2018; Carter 2014; Alvin *et al.* 2021). In addition to the dispersal of planktonic larvae via sexual reproduction (Chadwick-Furman *et al.* 2000), corallimorpharians are also able to reproduce asexually. Some corallimorpharians, such as *Corynactis californica,* have been shown to produce up to 94 genetically identical polyps in a single year (Chadwick & Adams 1991). This prolific rate of replication gives corallimorpharians a competitive advantage on space-limited reefs.

There are five modes of asexual reproduction described within the literature for corallimorpharians. These modes include pedal laceration (den Hartog 1980; Chadwick & Adams 1991), marginal budding (Chadwick-Furman & Spiegel 2000; Lin *et al.* 2013), inverse budding (Chen *et al.* 1995; Chadwick-Furman & Spiegel 2000), longitudinal fission (den Hartog 1980; Chadwick & Adams 1991; Chen *et al.* 1995; Chadwick-Furman & Spiegel 2000) and two-mouth fission (Chen *et al.* 1995).

Each mode of asexual reproduction is primarily centered around the corallimorpharians exceptional regenerative capabilities. As its name suggests, pedal laceration occurs when a portion of the pedal disc, whilst firmly attached to the substrate, is stretched and torn free from the primary polyp (Chia 1976). The resulting lacerated piece then proceeds to regenerate and develop into a new, independent yet genetically identical polyp, complete with a mouth and tentacles (Chia 1976). In marginal budding, portions of the polyps margin, incorporating parts of the body column, pedal, and oral discs, are pinched to form buds which are then detached from the primary polyp, before developing into fully formed secondary polyps (Chadwick-Furman & Spiegel 2000). Similar to that of marginal budding, inverse budding is also achieved through the development of a bud, however, in this mode, a bud is formed when a portion of the pedal disc is raised from the substrate, inverted, and fused together (Chen *et al.* 1995). Over the course of a month, the tissue connecting the bud to the primary polyp constricts and the bud is severed and floats away (Chen *et al.* 1995). Longitudinal fission, which has been reported to occur over the space of a week, involves a polyp quite literally bisecting itself longitudinally through the mouth, exposing internal pharynx and mesentery filaments, to create two separate polyps (Chen *et al.* 1995; Chadwick-Furman & Spiegel 2000). This mode is not to be confused with the slower process of two mouth fission, however, which involves a polyp firstly developing a second mouth and then pinching to cause a divide in the space between the two mouths (Chen *et al.* 1995), or transverse fission (though not reported in Corallimorpharia), where the polyp separates to form two polyps from both the upper and lower parts of the original body (Fautin 2002).

Ricordea yuma is one of two species in the corallimorpharian family Ricordeidae (den Hartog 1980; Fautin 2016; WoRMS 2022). Each species is localised to geographically distinct regions however, with *R. yuma* distributed throughout the Indo-Pacific whilst its counterpart, *R. florida* is situated in the Atlantic Ocean (Torres-Pratts *et al.* 2011; Parr 2019). Both species inhabit shallow tropical waters, ranging from the intertidal zone to depths of 54 m (den Hartog 1980), and are typically found in either colonial aggregations or as solitary polyps (LaJeunesse 2002; Muhando *et al.* 2002; Torres-Pratts *et al.* 2011; Parr 2019). To date, only pedal laceration (den Hartog 1980) and marginal budding (Lin *et al.* 2013) have been observed in Ricordeidae. Here we present strong evidence of a new mode of reproduction in *Ricordea yuma*, which may also be present in other corallimorpharians.

METHODS

In November 2020, mature *Ricordea yuma* polyps (ranging 6 – 10 cm in diameter), from an established population were moved into a 235 L observation tank to monitor for possible spawning. Polyps were originally collected from the Great Barrier Reef locally off the Cairns coast several years prior. The observation tank was kept free of substrate and was connected to a 60,000 L recirculating marine tank system (average temperature 27° C and salinity of 33%), with a flow-through exchange rate of approximately 150 litres per hour.

In January 2021, during normal husbandry checks, a disassociated tentacle, matching the colouration of the *R. yuma* polyps was found on the bottom of the observation tank. There did not appear to be any physical signs of damage or trauma to any of the *R. yuma* polyps. External visual inspections at this time also revealed that polyps no longer appeared to have the well-developed gonads that were previously observed.

Over the course of the next four months, a total of 17 free tentacles were found. Each tentacle, which was negatively buoyant and easily found on the bottom of the observation tank, was gently collected with a pipette and transferred into 5 ml of fresh seawater in a six-well tissue culturing plate for monitoring.

Plates were kept indoors at a constant ambient room temperature of approximately 24 – 25 °C, and exposed to a light intensity of 292 lux (measured with a digital light meter; 0.01-50000 lux range; 5 % accuracy) provided by artificial cool-white, fluorescent lighting on a 12:12 h light/dark cycle. Fifty percent water exchanges were performed on each well twice weekly. Tentacles were monitored over the course of the next five months. All inspections were performed periodically under a dissecting microscope and photographed. Cnidae webs were examined and photographed from below on an inverted microscope so as to not disturb the developing polyps. Unfortunately, the scale at which the cnidae were observed did not allow for thorough cnidae classification to be confidently carried out.

OBSERVATIONS

While all 17 tentacles showed signs of transformation, a total of seven tentacles were deemed to have successfully transformed into polyps, defined here as having a mouth and tentacles. The procession of the transformation into a polyp can be summarised; 1. settlement, and the development of 2. an oral disc, 3. mouth, and finally 4. tentacles (Fig. 1). There was significant variation in the rate of transformation, ranging from 29 to 67 days after collection.

All but one tentacle appeared to successfully attach to the bottom of their well. Of the tentacles that did appear to attach to the bottom of the wells, ten of these were observed to have formed a web of discharged cnidae (Fig. 2). Evidence of these cnidae webs were first observed within 2-19 days after the collection of the tentacles.

Ten of the seventeen polyps died before they had completed the polyp transformation. The causation of death in these polyps remains unknown, as all polyps were treated the same. However, for several of these deceased polyps, it was noted that these tentacles appeared to develop brown abscesses and/or had an algal bloom in their well. The earliest death occurred five days after tentacle detection. Conversely, of these tentacles that did not survive to reach polyp stage, the longest survived for 47 days. Interestingly, this was the sole tentacle that did not attach to the bottom of the plate.

In mid-May, it was noted that surviving polyps were reducing in size. At this time, surviving polyps were between 42 and 89 days post first detection. Attempts were made to relocate polyps (including the tissue culture plates they were attached to) into the main aquarium system, thereby providing them with a constant supply of fresh seawater, natural sunlight, and water temperature (27°C) that has proven favorable for mature polyps. Unfortunately, despite the best efforts to protect the secondary polyps, this relocation was unsuccessful, and all polyps either disappeared or perished within 27 days. Ultimately, the longest surviving polyp, from the first detection to disappearance, was kept for 107 days.

DISCUSSION

The observations presented here of budded tentacles developing into polyps do not fit the descriptions of asexual reproduction that have previously been described for any species within Corallimorpharia. As there were no signs of portions of the pedal or oral disc nor the body column on the fragments, these dissociated tentacles do not align with the descriptions

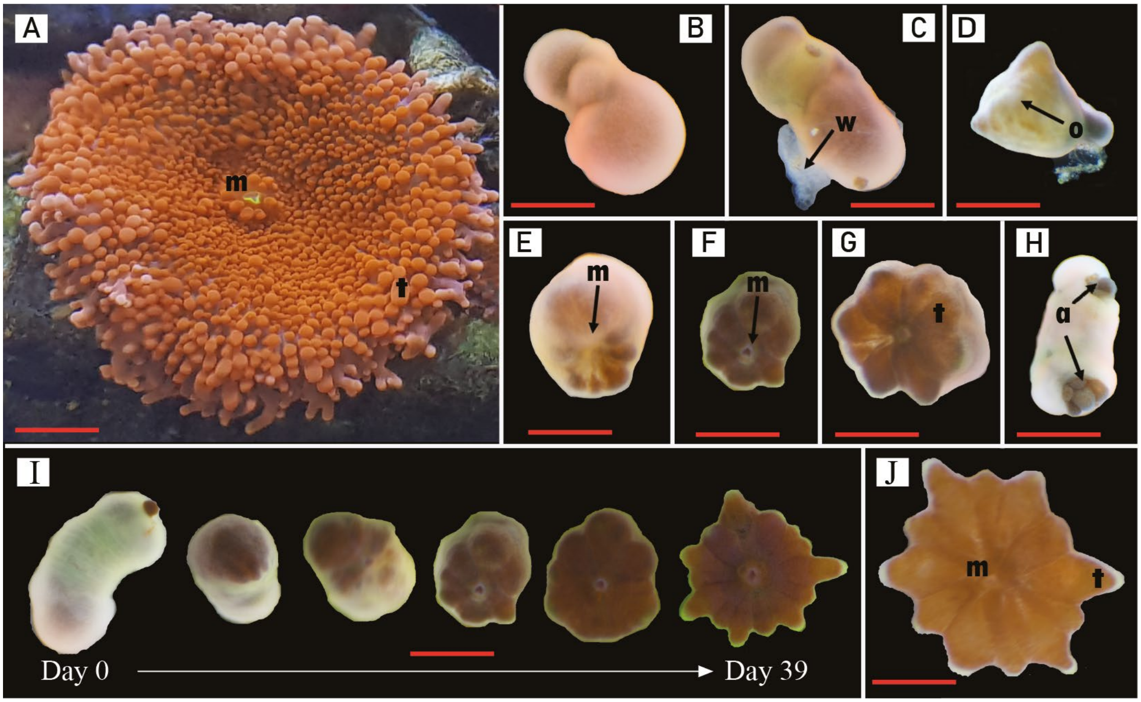

FIG. 1. Growth and developmental stages of *Ricordea yuma* autotomous tentacles. **A**, Adult polyp showing mouth (m) and tentacles (t); **B**, detached tentacle; **C**, tentacle has formed a web (w) of cnidae and has attached the substrate; **D**, flat oral disc (o) has begun to form; **E**, early stages of mouth (m) formation; **F**, mouth (m) is fully developed; **E-G**, tentacles (t) in the initial stages of formation; **H,** abnormal brown abscess (a); **I**, full transition of one autotomous tentacle from first detection (Day 0) to reaching polyp status (Day 39); **J**, a newly formed polyp complete with mouth (m) and tentacles (t). Scale bars approximately: A, 1 cm; B-J, 1 mm; I, transitional timeline not to scale.

provided for pedal laceration or marginal budding in the literature. The observations presented here however do align with a mode of asexual reproduction, tentacle autotomy, that has been previously reported to occur in a range of other orders within Hexacorallia (Scleractiniaria (Toh & Ng 2016) and Actiniaria (Kesava Panikkar 1937; Chia 1976; Cutress 1979; Pearse 2002; Bocharova & Kozevich 2011)), but interestingly also in some Cubozoan (Straehler-Pohl & Jarms 2011) and Scyphozoan (Robinson *et al.* 2019) species. This mode involves the shedding of individual tentacles, via the contraction of a sphincter at the base of the tentacle, from the primary polyp (Kesava Panikkar 1937; Bocharova & Kozevich 2011).

Several theories have been proposed around the occurrence of autotomous tentacles. It has been proposed that tentacle autotomy is a stress response to physical damage, disturbance, or stressful conditions (Chia 1976; Lawn & Ross 1982; Toh & Ng 2016). However, this was mitigated for in this study through predator exclusion. Alternatively, it has also been theorised that asexual reproduction often occurs independently to periods of sexual reproduction (Kesava Panikkar 1937). Our observations support this theory, as the shed tentacles were first seen after polyps no longer showed obvious signs of well-developed gonads.

The webs that were observed in attached tentacles are believed to be the result of cnidae. Cnidae, are specialised organelles used by cnidarians for prey capture, defence, spatial competition, and adhesion (Mariscal 1974). Although the cnidom (specific compliment of

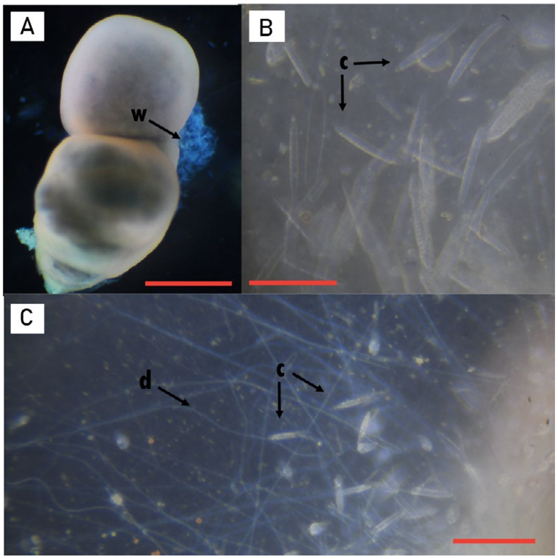

FIG. 2. **A**, autotomous tentacle attached to bottom of the culture plate with a cnidae web (w), viewed from above; **B**, cnidae (c) within the web, viewed from below with an inverted compound microscope; **C**, undischarged (c) and discharged (d) cnidae within the web, viewed from below with an inverted compound microscope. Scale bars approximately: A, 700 µm; B, 80 µm; C, 200 µm

cnidae) of *R. yuma* has not been described, den Hartog (1980) reported that *R. florida*, possessed spirocysts, spirulae (basitrichs), homotrichs (holotrichs), and penicilli (p-mastigophore or p-amastigophore) cnidae types. Given that the fine microfillia on discharged spirocyst threads are known to create an adhesive web-like mesh (Mariscal *et al.* 1977), we conclude that the webs we observed were likely the product of discharged spirocysts located within the epidermal tissue of the tentacles, thus enabling the successful settlement and attachment of budded *R. yuma* tentacles. Future works would seek to examine this cnidae further

Unfortunately, no polyp was successfully maintained longer than 107 days. While the exact reasons for the deaths remain unknown, a combination of the temporary nature of being housed in small volumes of water and also the possibility that there was insufficient lighting and/or temperature within the room, are suspected to be the main drivers behind the mortalities. In future, attempts will be made to mitigate these risks through the use of temperature-controlled water baths, gentle water flow, and designated coral aquaria grow lights. Future work will also involve targeted sampling and characterisation of cnidae within the webs.

In conclusion, the observations presented here are not consistent with the descriptions given for any of the modes of asexual reproduction currently known to occur within Corallimorpharia (den Hartog 1980; Chadwick & Adams 1991; Chen *et al.* 1995; Chadwick-Furman & Spiegel 2000; Lin *et al.* 2013). As they align with details provided for tentacle autotomy seen within Scleractiniaria and Actiniaria (Kesava Panikkar 1937; Chia 1976; Cutress 1979; Pearse 2002; Bocharova & Kozevich 2011; Toh & Ng 2016), we believe that our observations are the first record of this mode of reproduction within Corallimorpharia. Whilst *R. yuma* is the first corallimorpharian to have displayed tentacle autotomy, given that this mode is shared between two other Hexacorallian Orders, it cannot be ruled out that other corallimorpharians may also use this mode of replication. Given the ability of many corallimorpharian species to rapidly monopolise and dominate reef substrate, tentacle autotomy may prove to be an important strategy used by such species to boost their population numbers and instigate inter- and intraspecies aggression with other Anthozoan reef inhabitants.

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