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UNIVERSIDADE ESTADUAL PAULISTA "JÚLIO DE MESQUITA FILHO"
INSTITUTO DE BIOCÊNCIAS DE BOTUCATU

TUBES OF CERIANTHARIA (CNIDARIA; ANTHOZOA): A MARINE HABITATION



FROM ITS CONSTRUCTION TO ITS GUESTS

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**TUBES OF CERIANTHARIA (CNIDARIA; ANTHOZOA): A MARINE HABITATION
FROM ITS CONSTRUCTION TO ITS GUESTS**

PhD thesis presented to the Universidade Estadual Paulista (UNESP), Instituto de Biociências, Botucatu, as a requirement for obtaining the degree of Philosophiae Doctor in Biological Sciences in the field of Zoology.

Supervisor: Sérgio Nascimento Stampar.

Funding: CAPES – process number: 88887.301759/2018-00, and CNPq – process number: 141329/2020-3.

C415t Ceriello, Hellen
Tubes of Ceriantharia (Cnidaria; Anthozoa) : a
marine habitation. From its construction to its guests
/ Hellen Ceriello. -- Botucatu, 2022
118 p. : il., tabs., fotos

Tese (doutorado) - Universidade Estadual Paulista
(Unesp), Instituto de Biociências, Botucatu
Orientador: Sérgio Nascimento Stampar

1. behavior. 2. bioconstruction. 3. eDNA. 4. marine
biodiversity. 5. metagenomics. I. Título.

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DEDICATÓRIA

Esta tese sobreviveu à Pandemia de COVID-19. Dedico este trabalho ao meu primo Lambão, Junior Barbalia, que infelizmente não teve o mesmo destino que esta tese. *“Uma vez me perguntaram “por que você trata bem até aqueles que não gostam de você e são falsos?” A resposta foi simples e direta: o mal não está em mim”* (desconheço o autor, mas soa exatamente como você).

AGRADECIMENTOS

Com exceção da dedicatória, toda esta tese foi escrita em inglês, mas as pessoas a quem este campo é destinado, em sua grande parte, apenas entendem o português ou nem foram alfabetizadas ainda — por motivos de “está cursando o maternal” — e sendo assim, esta seção será escrita inteiramente em português. Porque é para elas. Porque é para que elas saibam, hoje e futuramente, o quanto foram importantes para mim nesta jornada e que sem elas este trabalho não seria possível de forma alguma. É sério.

Agradeço a Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) – n° de processo 88887.301759/2018-00, e Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) – n° de processo 141329/2020-3 por terem financiado esta pesquisa, e ao meu orientador, Sérgio N. Stampar, não somente por ter me guiado ao longo dos últimos anos nesta saga acadêmica e me inserido no âmbito da pesquisa, mas, principalmente, por ter me apresentado a este encantador grupo de belos e intrigantes animais os quais tive a imensa alegria de conhecer e conviver, e que me proporcionaram grandes descobertas. Aliás, obrigada a cada animal que participou da minha jornada, especialmente Brigitte e Jezionél, e que tanto me ensinaram para que eu pudesse ensinar aos outros. Foi muito gostoso aprender com vocês. *“Animais são parte importante do sistema da natureza e carregam uma faísca divina. Uma humanidade iluminada não age com crueldade”* (Shmuel Lemle).

Pai e mãe, obrigada por terem me resgatado de situações angustiantes e me acolhido quando mais precisei, me aturando na cozinha, a qual dominei e designei como “meu escritório”, dia e noite, enquanto preparava cada trabalho, hoje, presente nessa tese. Obrigada aos meus bixinhos, Ruppertino e Rabito, que não estão mais aqui, mas que me acompanharam durante várias madrugadas de manuscritos, Paolina e Ramiro, por me acordarem antes das 7h da manhã, Raíza, por se preocupar comigo e me dar amor, tornando meus dias menos caóticos e mais tranquilos, e Caroline Vitória, por me ensinar que devagar e sempre a gente chega lá.

Obrigada ao meu ex-vizinho, Bruno, à Dona Tereza e ao Sr. Jorge por terem me abrigado em Botucatu, alimentado deliciosamente, incluindo

maçãzinhas da Turma da Mônica, cuidado, e arranjado caronas para eu ir à UNESP diariamente sem precisar subir as infinitas ladeiras dessa cidade. Eu, minhas pernas e minhas costas agradecem imensamente. Obrigada, Sinval, da portaria da UNESP Assis, você nem sabia, mas nunca falhou em me dar um abraço matinal que eu tanto precisava. Obrigada, também, a toda a equipe de manutenção da UNESP Assis por ter embarcado comigo nos meus experimentos malucos e me ajudado a executá-los com ideias maravilhosas. Agradeço, também, a quem eu já não mais mantenho contato, mas que no início desta proposta de doutorado e parte de seu desenvolvimento, auxiliou-me com experimentos, revisou meus textos e me ajudou a melhorá-los. Então, obrigada por isso.

Agradeço demais ao ilustre Gustavo-Gabriel por todas as nossas reuniões semanais que acabaram sendo terapêuticas de tão construtivas. De jeito nenhum teria sanidade mental para superar certas situações acadêmicas e seguir em frente com clareza se não fosse por esses momentos reveladores, por essas conversas e desabafos. Ainda, sou-lhe deveras grata por topar participar de minhas pesquisas confusas e me ajudar a entender meus próprios dados, quando não gerá-los do zero também. MUITÍSSIMO obrigada, Jovem.

Um agradecimento especial à minha pitôca, Olívia, — a neném mais linda do quintal — pela inocência, felicidade, amor, risadas, energia, por ter me ajudado a plantar e a regar nossas plantinhas, bem como vigiar, incansavelmente e com muito afinco, a hortinha contra as formigas que tentaram destruí-la no Outono de 2022, e também por me motivar a pular corda o que, surpreendente e inesperadamente, me gerou várias epifanias e insights que foram colocados neste estudo. Mas, principalmente, obrigada por me ensinar tanto e trazer tanta alegria e leveza aos meus dias; algo imprescindível para a confecção desse trabalho.

Muito obrigada a todos os pesquisadores que colaboraram com a elaboração de cada artigo e manuscritos meus até aqui e que, tão gentilmente, dividiram sua expertise comigo. Sem vocês esta tese não seria a mesma.

“Malfeito feito!”

(Mapa do Maroto)

**TUBES OF CERIAANTHARIA (CNIDARIA; ANTHOZOA): A MARINE HABITATION
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Abstract

This study assessed marine biodiversity of microbes and metazoans found in ceriantharian tubes via species characterization, using both species traditional recognition and metagenomics of environmental DNA (eDNA) methods, and it also described ceriantharian tube-building behavior patterns. Using the traditional method for species characterization, 14 taxa of crustaceans were identified, including one novel species, *Podocerus carmelina* **sp. nov.**, found in *Ceriantheomorpha brasiliensis* tubes (Mello-Leitão, 1919) (n = 3) and in unidentified tubes (n = 5). Also, two new location records for previously known crustacean species were reported as well as an identification key for *Podocerus* species with type localities in the Atlantic Ocean was provided. Analyses of eDNA metagenomics in tubes of *C. brasiliensis* (n = 2) and *Ceriantheopsis lineata* Stampar, Scarabino, Pastorino & Morandini, 2015 (n = 2) showed that these ceriantharian tubes are composed of 79% microbial families and 21% metazoan families. Moreover, tubes from different locations presented a higher metazoan diversity than the microbial that nearly remained unaltered, indicating that, although microbial families are abundant in ceriantharian tubes, they are uniform throughout different locations. The ceriantharian tube-building research revealed that *Botrucnidifer norvegicus* Carlgren, 1912 can build ramified tubes housing two polyps, adult *C. brasiliensis* lacks substrate selection mechanisms and sediment capture, is able to build more than a single tube throughout life, usually vertically oriented, and its behavior may differ from the species *Isarachnanthus nocturnus* (den Hartog, 1977) and *Cerianthus vogti* Danielssen, 1890. The ceriantharian tube is critical in controlling the internal water pressure in ceriantharians in addition to providing protection. In conclusion, this research demonstrated that, other than biodiverse microhabitats, ceriantharian tubes are potential tools for basic research and biodiversity surveys, driving studies of ecology, behavior, life cycles and cnidae toxicity.

Keywords: behavior, bioconstruction, eDNA, marine biodiversity, metagenomics, microhabitat.

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Introduction

Coral reefs are recognized as valuable sources of biological diversity. As such, they play an important role in marine biodiversity as they provide suitable feeding locations and habitats for a wide variety of species [1]. Despite this, competition between reef-dwelling organisms is likely to occur, mainly over recruitment space which is the most disputed resource in coral reefs [2]. The availability of these areas is recognized as a limiting factor for species that rely on reef establishment to complete their life cycle. As a result, the shortage of dwelling spaces, along with the high demand for reefs, may drive the search for alternative settlement habitation structures [2].

In this scenario, some studies on *Ceriantharia* (Cnidaria; Anthozoa), also known as tube-dwelling anemones (e.g. 3–4), suggest that ceriantharian tubes (Fig. 1) can provide suitable habitats for the survival of various marine invertebrate species, acting as alternative substrates for these organisms. The findings in these investigations assist in understanding if such structures have an ecological function similar to that observed in coral reefs, although in a smaller scale, and may thus be designated as rich microhabitats.



Fig. 1 Several tubes of *Ceriantheomorphe brasiliensis*, two of which had polyps extending outwards (Photo: Marcelo Krause).

Although groups such as Bryozoa, Crustacea, Phoronida, Mollusca, and Sipuncula have been observed anchored on the ceriantharian tube [3–4–5–6–7], knowledge on the species that can use this microhabitat is still very limited, particularly when restricted to a macroscopic view. As a result, there is still a biased perception of the variety and ecological significance of these structures.

Currently, it is estimated that the number of worldwide known species is considerably lower than the real biological variety in the planet, reflecting the gap of biodiversity information while emphasizing the need for more studies that provide registration of the numerous undiscovered species. As shown by some taxonomic studies (e.g. 8–9), there are around 8.7 million eukaryotic species worldwide, although only approximately 1.6 million have been discovered. Furthermore, when it comes to marine animals, records suggest that only 9% of all species on the planet are known [8–10]. Nonetheless, while no precise estimate of the number of prokaryotic species exists, Gilbert et al. [11] found nearly 6 million bacterial taxa at the species or genus level in their investigation and yet they support the idea that this estimate is still lower than the predicted bacterial abundance globally.

Even so, the relevance of biodiversity records extends beyond demonstrating the richness of species in a given space/time to comparing reports of new species with older records, providing an abundance projection of known species, demonstrating the loss of current biodiversity, and estimating future extinction rates [8–9–12]. Some strategies are used to recognize biodiversity, such as species traditional recognition and recognition based on genomic data.

Species traditional recognition

Species traditional recognition focuses on morphological characters which, although effective in the field, have disadvantages. For example, the taxonomy of some worm groups (e.g. Nematoda) is reliant on electron microscopy methods, which are both costly and time-consuming to employ [13–14]. Another issue is that traditional identification may be misleading because species recognition and determination are credited based on the perspective of its identifier [15]. On the other hand, species identification based on molecular

data has gained interest among researchers since its information arrangement allows more consistent identifications [16]. Thus, the methodology in this work was based on environmental DNA (eDNA) metagenomics to identify molecular data from species in ceriantharian tubes and characterize them.

eDNA and Metagenomics

Because of the high phenotypic plasticity found in several species from a number of taxonomic groups, recognizing global biodiversity only by traditional methods has been a major challenge [17]. A greater challenge yet, is attempting to identify a species when it is impossible to visually confirm their presence in a particular environment.

As Gilbert et al. [11] have already pointed out, the diversity of microbial species is vast, as microorganisms can be found in the most diverse ecosystems, making accurate quantification difficult. However, combining eDNA analysis with metagenomics approach enabled a better understanding of the variety of organisms found in a given environment.

The set of genomic DNA of an entire community of organisms obtained from the same site, such as water droplets, soil, and substrates, is referred to as eDNA [18–19–20–21]. Metagenomics, otherwise, refers to the technique that allows eDNA extraction [22].

In the last 10 years, the metagenomic approach has been widely used, integrating knowledge in ecological, microbiological, industrial, and health fields [23–24]. In addition to the fact that it is a rather rapid technique to conduct, it also allows the identification of microorganisms using a small amount of material from the most diverse environments, including microhabitats [25].

This approach has a variety of applications, including the identification of microorganisms of importance to the human population without the need for their cultivation in laboratory [25], the registration of species, including unknown organisms [26–27–28], and the recognition of threatened species [29] as well as the monitoring of past and present biodiversity [30], thus assisting in the area of taxonomy.

Currently, metagenomic research employing eDNA has been conducted with fungi, viruses, gastrointestinal microorganisms and microorganisms found

in wounds, bacteria, archaea [31–32–33–34–35–36], and also in aquatic ecosystems, providing a wealth of information on microorganisms that live in these habitats [28–37–38–39–40–41].

As there may be more than a million species in a gram of sediment or in a single drop of water, marine microbial metagenomics is one of the most data-rich fields [18], revealing the immense species variety found in marine ecosystems [42–43]. Moreover, metagenomics often records microbial communities associating with other organisms, such as anthozoans [44–45]. Thus, the qualitative metagenomic analysis of ceriantharian tubes could provide molecular data on species composition heterogeneity, including fragmented specimens, and organic compounds found amidst the sediments adhered to this structure/substrate, similar to the studies by Wei et al. [46] with sediments found in the Yellow Sea in China, and Grassle and Maciolek [47] that were able to estimate species richness found in deep seas through the evaluation of seabed samples.

Marine Bioconstructions

Elevated and often multi-layered structures created by benthic animals, from the aggregation and accumulation of components found both on the seafloor or synthesized by themselves, are common in the marine ecosystem [48]. Because of their building activities, such animals are considered as bioconstructors or ecosystem engineers [49], and structures formed by their activities are referred to as bioconstructions or biogenic reefs [50]. Similar to coral and algae reefs, the ceriantharian tube is a biogenic structure, although soft, produced by "cementing" activities in which small sediment fragments are adhered to cnida filaments produced by the bioconstructor, like in the process of tube bioconstruction by tube polychaetes [51]. Additionally, ceriantharian tubes are built on unconsolidated substrates and may be one of the few alternatives of consolidated structures for species establishment in these habitats [3].

Bioconstructions increase spatial complexity and provide secondary substrates for species establishment throughout several generations, as such structures may be modified and maintained by bioconstructors other than those who built them initially [52–53]. Thus, bioconstructions play an essential role in

terms of species diversity found in marine ecosystems, generating and sustaining biodiversity, and hence contributing to the maintenance of ecosystems' high levels.

It is not uncommon to investigate fauna found in biogenic reefs, and it has been previously done in numerous groups such as algae [54], polychaetes [55–56–57], and cnidarians [58]. However, the use of molecular tools to conduct fauna survey in ceriantharian bioconstructions is unprecedented and has the potential to contribute to the identification of biodiversity in these microhabitats as well as to possibly designate them as biodiversity hotspots.

Is Ceriantharia's tube-building behavior inherited?

Stampar et al. [59] investigated the ultrastructure and ptychocyst production/release for ceriantharian tube construction. However, changes in tube formation in response to diverse substrates were not addressed, and one of the current questions is whether the polyp is likely to select sediments during tube building. If so, is this an intentional or random choice? These guiding questions are rather relevant because the composition of organisms using the tube as a substrate may be modified by the polyp's own performance.

Based on the scenario described above, the goal in this study was to better understand the role of ceriantharian tubes as microhabitats for the management of marine biodiversity. To do so, metazoan and microbial diversity found in ceriantharian tubes of *Ceriantheomorphe brasiliensis* (Mello-Leitão, 1919) and *Ceriantheopsis lineata* Stampar, Scarabino, Pastorino & Morandini, 2015 was identified, the changes in species composition in relation to the ecosystem in which these bioconstructions were built was investigated, and the tube-building behavior of *Botrucnidifer norvegicus* Carlgren, 1912 and *C. brasiliensis* was described based on observations in laboratory and in natural habitat (only the latter).

Objectives

The overall goal in this study was to look into the potential of the ceriantharian tube as marine biodiversity rich microhabitat by describing and

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