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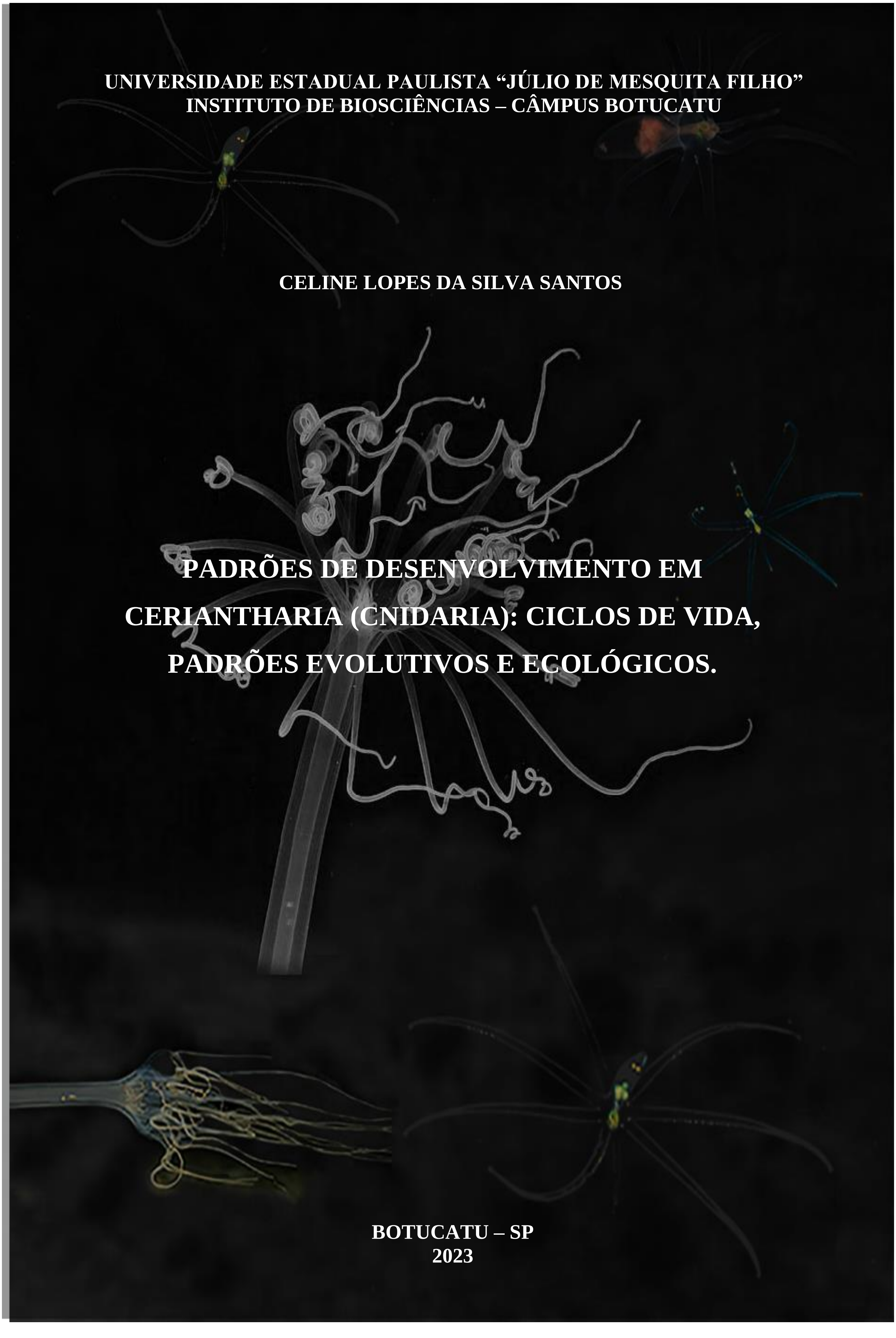

UNIVERSIDADE ESTADUAL PAULISTA "JÚLIO DE MESQUITA FILHO"
INSTITUTO DE BIOSCIÊNCIAS – CÂMPUS BOTUCATU

CELINE LOPES DA SILVA SANTOS

PADRÕES DE DESENVOLVIMENTO EM CERIANTHARIA (CNIDARIA): CICLOS DE VIDA, PADRÕES EVOLUTIVOS E ECOLÓGICOS.

BOTUCATU – SP
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PADRÕES DE DESENVOLVIMENTO EM CERIANTHARIA (CNIDARIA): CICLOS DE VIDA, PADRÕES EVOLUTIVOS E ECOLÓGICOS.

Tese apresentada à Universidade Estadual Paulista (UNESP), Instituto de Biociências, Botucatu, como requisito para a obtenção do título de Doutora em Ciências Biológicas (Zoologia)
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1. Cnidários - Desenvolvimento. 2. Venenos de Cnidários. 3. Toxinas. 4. Transcriptoma. 5. Organismos marinhos - Evolução.

Palavras-chave: Anemonas de tubo; Estagios de desenvolvimento; Evolução; Toxinas putativas; Transcriptoma.

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RESUMO

Nas últimas décadas, a subclasse Ceriantharia tem se encontrado no centro das discussões evolutivas em Cnidaria. Este clado é um dos menos abundantes na classe Anthozoa, com cerca de 54 espécies formalmente descritas. Provavelmente, a carência no conhecimento sobre aspectos básicos da ecologia e ontogenia desse grupo reforçam a incerteza evolutiva sobre a subclasse. Atualmente, muitas inconsistências, sejam elas de ordem taxonômica, sistemática ou da história evolutiva dos ceriantários, circundam esse clado. O presente estudo tem como objetivo discutir aspectos ligados ao ciclo de vida, as rotas alternativas e as implicações dessa complexidade ontogênica, para a família Arachnactidae, a nível morfológico e transcriptômico. Nossos dados mostram a ocorrência de indivíduos larvais de *I. nocturnus* na região norte do Brasil sendo capazes de ocupar habitats com influencia estuarina. Ademais, nós discutimos a validade da espécie *Ovactis brasiliensis* descrita somente com base em caracteres das formas larvais. Nós registramos uma nova espécie do gênero *Arachnanthus* para o Atlântico Sul, o primeiro registro de ocorrência desse gênero para essa região, bem como o seu ciclo de vida apresentando uma larva planctônica de vida curta e discutimos um comportamento de locomoção inédito para ceriantários adultos. Ainda, nossos resultados apontam para um arsenal de toxinas bem maior expressado pelos genes no período larval em comparação ao estágio adulto e que o pólipo da nova espécie de *Arachnanthus* exibe uma abundância maior de toxinas putativas em relação ao já descrito para a família *Arachnactidae*. Por fim, nossas análises identificaram uma maior quantidade de transcritos sendo expressos no estágio larval em comparação ao adulto e a maioria desses transcritos estava associada a processos biológicos.

Palavras-chave: Anêmonas de tubo. Ciclo de vida. Toxinas. Transctiptoma. Arachnactidae.

LOPES, Celine da Silva Santos. **Development patterns in Ceriantharia (Cnidaria): life cycle, evolutionary and ecological patterns.** 2023. 115 p. Tesis (Doctorate degree in Biological Sciences – Zoology). – Universidade Estadual Paulista "Júlio de Mesquita Filho (UNESP), Bioscience Institute, Botucatu, 2023.

ABSTRACT

Ceriantharia is a small subclass of the Anthozoa, which has only 54 valid species and in the past decades has been assumed a central space in evolutionary discussions. Probably, the lack of knowledge about ontogenetic and ecology aspects increase the evolutionary uncertainness of this subclass. Currently, many taxonomic, systematics and evolutionary history inconsistences are present in this clade. The study discuss life cycle, alternative routes and implications of these ontogenetic complexities for the Arachnactidae family at morphological and transcriptomic level. Our results evidence the occurrence of larva stages of *I. nocturnus* from North region of the Brazil, occupying habitats with estuarine influences. We discussed the validity of the species *Ovactis brasiliensis* described only based on morphological characters of the larva forms. A new species of the genus *Arachnanthus* from South Atlantic Ocean and its life cycle with a short-time larva were described; the first occurrence record of this genus for the region. The unprecedented locomotion behavior of the ceriantharian adult was discussed. Our data revealed a higher putative toxin arsenal expressed by genes in the larval stages of the *Arachananthus* sp1 than adult phase. The polyp of the new species presented more abundant number of toxins than earlier registered for the family Arachnactidae. Additionally our analyses identified great number of transcripts expressed by the larva than polyp; most of transcripts was related to biological process.

Keywords: Tube-dwelling anemones. Life cycle. Toxins. Transcriptome. Arachnactidae.

SUMÁRIO

- Traçar um perfil de toxinas putativas para a fase larval e adulta da espécie *Arachnanthus* sp. 1, bem como apresentar a anotação funcional dos genes expressos em cada fase, propondo uma discussão sobre as implicações evolutivas dentro de Ceriantharia e em Cnidaria.

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DISCUSSÃO GERAL

Ceriantharia é uma subclasse de Cnidaria que em comparação aos outros representantes deste filo, é pouco estudada (eg. Medusozoa: Brekhman et al. 2015, Ceh et al. 2015, Gold et al. 2019; Anthozoa: Utrilla et al. 2019, Karako-Lampert et al. 2014, Moya et al. 2012). Aspectos como a ontogenia e as respostas a níveis gênicos dos diferentes estágios de desenvolvimento ainda são pouco compreendidos (ver Stampar et al. 2015). As análises morfológicas e moleculares realizadas em larvas encontradas no Pará – região Norte do Brasil – evidenciaram um cenário complexo para o gênero *Isarachnanthus*. De acordo com os estudos utilizando o marcador molecular COI, as sequências larvais do Pará apresentaram similaridades significativas com aquelas referentes à espécie *Isarachnanthus nocturnus* (~2% de divergência), corroborando com o cenário hipotetizado por Stampar et al. (2012) de que as larvas de *I. nocturnus* poderiam tolerar as condições ambientais das regiões estuarinas. De fato, recentemente algumas larvas de Ceriantharia (254) foram encontradas novamente na região do Pará sob uma variação relativamente alta de salinidade – 31 a 36 ppt – e de temperatura – 9 a 29ºC (Tosetto et al. 2022). Esse cenário possibilita o início de discussões biogeográficas mais profundas em relação a *I. nocturnus*, uma vez que já é compreendido que larvas como a que essa espécie apresenta estão adaptadas para permanecer por um longo período no ambiente pelágico (cerca de 3 meses), sendo assim essas larvas tem capacidade de dispersão consideravelmente grande (Stampar et al. 2015). Em relação à divergência genética observada entre as regiões COI (1 a 2%) da larva do Pará e de *I. nocturnus*, apesar de ser maior do que a encontrada anteriormente para membros da referida espécie, a distância genética interespecífica observada entre o gênero pode chegar a 9% (Stampar et al. 2012). As construções filogenéticas utilizando as sequências COI de *I. nocturnus, I. maderensis, Isarachnanthus* sp. e das larvas do Pará, demonstraram 3 clados putativos, sendo que *I. nocturnus* e as larvas do Pará foram alocados no mesmo clado. As análises morfológicas das larvas do Pará evidenciaram semelhanças acentuadas com as larvas descritas por van Beneden (1897) como da espécie *Ovactis brasiliensis*. Entretanto, essa espécie foi descrita somente com base na morfologia de indivíduos larvais encontrados na região nordeste do Brasil (cerca de 600km de distância do Norte do Pará) sem menção ao holótipo. Durante o século XIX e início do século XX a massiva descrição de espécies estava em alta e, especificamente em Ceriantharia, muitas espécies foram descritas indiscriminadamente somente com o uso de caracteres morfológicos das formas larvais (van Beneden 1897). Registros como esses resultaram na superestimação do número de espécies na subclasse, afetando severamente o conhecimento da biodiversidade de Ceriantharia e gerando uma extensa lista de espécies. As descrições baseadas em um tipo de análise de apenas um estágio do desenvolvimento de invertebrados com ciclos de vida complexos como os cnidários são bastante problemáticas, devido às mudanças morfológicas que acontecem entre um estágio e outro (van Beneden 1987, Storch et al. 2013, Stampar et al. 2015, Brink et al. 2019). Portanto, com base nesse cenário, nós defendemos que *Ovactis brasiliensis* seja considerada uma *espécie inquirenda*, uma vez também que a análise do material original de van Beneden (1987) é inviável. Além disso, de acordo com as evidências moleculares, a larva encontrada no Pará é um estágio inicial de *I. nocturnus*.

Na família Arachnactidae, a maioria dos estudos está relacionado ao gênero *Isarachnanthus* (Molodtsova 2004, Stampar e Morandini 2014, Stampar et al. 2012, DeBiasse et al. 2022). A maioria dos estudos voltados para o gênero *Arachnanthus* foi conduzida entre os séculos XIX e XX e consistiam em trabalhos taxonômicos (Carlgren 1912, 1924, 1937). Nós descrevemos uma nova espécie para o gênero *Arachnanthus* e o ciclo de vida da mesma. Ademais, nós utilizamos a abordagem transcriptômica para analisar a expressão gênica e para traçar o perfil das toxinas inerentes à fase larval e adulta da nova espécie descrita. *Arachnanthus* sp. 1 é uma espécie que está distribuída no Sudoeste do Oceano Atlântico, mais especificamente na costa litorânea do Sul do Brasil e Uruguai. É o primeiro registro do gênero para essa região. A espécie é caracterizada por ter uma actinofaringe pequena em comprimento, um par de mesentérios conectados à sifonóglife, o primeiro par de protomesentérios (P) alcança a metade do comprimento da cavidade gastrovascular, enquanto o primeiro par de metamesentérios é longo, mas não se estende até o final da cavidade gastrovascular. A quantidade de tipos de cnida encontrada nos tentáculos marginais foi relativamente baixa (apenas um). O ciclo de vida é caracterizado por ter uma duração curta com uma larva inicial mais oval, com sete tentáculos marginais cujas pontas eram acastanhadas; e uma larva tardia com um corpo mais cônico, oito tentáculos marginais e com protomesentérios visíveis na cavidade gastrovascular. A larva inicial era bastante ativa e se locomovia pela coluna d’água, quanto mais próximo ao assentamento, a larva ficava menos ativa, apresentando uma locomoção mais contida e períodos sem ingestão de alimentos. Após o assentamento e a construção de um tubo pelo pólipo, ele apresentou com muita frequência um comportamento de locomoção inédito para os ceriantários. Os pólipos deixavam o seus tubos e arrastavam o corpo sobre o sedimento e, muitas vezes se contraiam para dentro do tubo, se retiravam dele e cavavam o substrato, se locomovendo entre o sedimento.

Arachnanthus sp 1. é uma espécie com características morfológicas e comportamentais bem distintas de seus congêneres, além de apresentarem variações morfológicas intra-específicas. Carlgren (1912) destacou algumas variações em caracteres morfológicos, como quantidade de tentáculos, coloração, quantidade de mesentérios, dentre outros. Mais recentemente, Lopes et al. (2019) observou variações intra-específicas em caracteres morfológicos externos e internos das espécies do gênero *Ceriantheomorphe*. Dados não publicados sugerem que essas diferenças morfológicas intraespecíficas pode está relacionado, dentre outros fatores, ao tempo que a larva demora para se assentar. Em Meduzosoa, os ciclos de vida são caracterizados por um padrão metagenético, o qual pode gerar diversas rotas ao longo do desenvolvimento (Ceh et al. 2015, Morandini et al. 2016). Em hidrozoários como *Turritopsis dohrnii* e cifozoários como *Aurelia* sp. um ciclo de vida reverso ainda pode estar presente (He et al. 2015, Matsumoto et al. 2019). Já nos Anthozoa, esses tipos de desenvolvimento não estão presentes. Especificamente em Ceriantharia, observa-se a possibilidade de uma plânula ou cerínula ao longo do desenvolvimento do indivíduo e um período larval pelágico curto ou longo (Nyholm 1943, Uchida 1979, Stampar et al. 2015). Geralmente, a fase larval está relacionada algumas funções, como a de dispersão, enquanto o estágio adulto a outras distintas, como a reprodução (Podolsky and Moran 2006) e estão susceptíveis a diferentes sugestões ambientais, consequentemente os indivíduos durante cada fase desenvolveram respostas a níveis gênicos, comportamentais e morfológicos distintas.

Apesar do estilo de vida diferente, da metamorfose e das condições ambientais distintas, as quais indivíduos na fase larval e adulta estão condicionadas, as nossas anotações funcionais dos transcritos da larva e do adulto de *Arachnanthus* sp. 1 resultaram em um perfil similar entre esses estágios. Em ambos os estágios, a maioria dos genes anotados estavam relacionados a processos biológicos, nestes, na fase larval a maioria dos genes foram incluídos na categoria de processos metabólicos e celulares e no pólipo na categoria de processos metabólicos e regulação biológica. O cenário acima pode estar relacionado ao curto período de tempo que a larva de *Arachnanthus* sp. 1 dispende no ambiente pelágico, que provavelmente diminui a capacidade de dispersão nessa fase e consequentemente as variações ambientais experimentadas pela larva são amenas em comparação às larvas de duração mais longa que pode alcançar distâncias de até 4000km ao longo da costa (ver Stampar et al. 2005). Além disso, o fato de o pólipo apresentar um comportamento de locomoção durante a fase adulta, deixando a proteção do tubo e ficando mais exposto a pressões ambientais, como os fatores abióticos e predadores, poderia também contribuir para os resultados encontrados.

Ao longo da história evolutiva os cnidários desenvolveram estratégias adaptativas responsáveis pelo sucesso evolutivo da linhagem (Babonis and Martindale 2014, Kayal et al. 2018). Uma dessas estratégias foi a síntese de células urticantes, os cnidócitos que possuem diversas funções, dentre elas a captura de presas (Kass-Simon and Scappaticci 2002). Os cnidócitos também são os responsáveis pela produção de veneno e inoculação destes compostos na presa (Macrander et al. 2016). Portanto, o perfil toxicológico dos cnidários pode variar de acordo com as condições ambientais (Sachkova et al. 2020), diferentes tipos de tecidos e quantidade de cnida (Surmm et al. 2019, Ashwood et al. 2021) e entre os estágios de desenvolvimento (Columbus-Shenkar et al. 2018). A partir de análises transcriptômicas, nós encontramos um perfil de toxinas putativas, relativamente similar entre a larva e o adulto. Contudo, algumas diferenças também foram evidenciadas. Nós identificamos um número maior de proteínas similares a toxinas sendo expressas na fase larval (166) em relação à adulta (95). A discrepância significativa na quantidade de possíveis toxinas encontradas em ambas as fases pode estar evidenciando o estilo de vida muito mais dispersivo na fase larval em relação à fase adulta, mesmo com o pólipo apresentando um comportamento de locomoção. Pois, inicialmente, a locomoção observada nos adultos de *Arachnanthus* sp 1. não foi suficiente para que o indivíduo seja capaz de percorrer grandes distâncias. Não foi possível estabelecer a função ecológica do comportamento de locomoção exibido pela nova espécie de Ceriantharia. Entretanto, estudos com outros cnidários mostram que esse tipo de comportamento em indivíduos até então vistos como semi-sésseis, pode estar relacionado à ocupação de locais vazios para se distanciar de organismos altamente tóxicos que podem porventura ser competidores ou até mesmo predadores (Hoeksema and de Voogd 2012). A maioria das toxinas identificadas no estágio larval estava intrínseca a funções hemostáticas e hemorrágicas e no estágio adulto, a maioria foi inerente a funções auxiliares. No geral, o padrão das toxinas identificadas em nossas análises consistiu com o encontrado para os outros cnidários (Jaimes-Becerra et al. 2017). Entretanto, algumas diferenças foram encontradas, por exemplo, a pouca expressão de toxinas com funções neurotóxicas diferente do cenário encontrado para Actiniaria (Macrander et al. 2015).

CONCLUSÃO GERAL

Nossos resultados constribuem significativamente com o conhecimento dos processos inerentes ao desenvolvimento da família Arachnactidae em Ceriantharia. A partir das análises das sequências do DNA barcode – COI, foi possível inferir que as larvas encontradas na ilha de Maiandeua – Pará correspondiam a *I. noctunus*, ampliando as discussões sobre a capacidade de dispersão e tolerância adaptativa dos indivíduos dessa espécie. As sequências apresentaram uma divergência intraespecífica de cerca de 2%. Nas reconstruções filogenéticas realizadas três possíveis clados foram gerados, um deles era composto pelas larvas do Pará + *I. nocturnus*, enquanto os outros abarcaram *I. maderensis* e *Isarachnanthus* sp. A similaridade morfológica entre as larvas do Pará e aquelas descritas por van Beneden (1897) foi demonstrada. Porém, devido à impossibilidade de analisar o holótipo, sugerimos que *Ovactis brasiliensis* seja considerada uma *espécie inquirenda*.

Além disso, nós descrevemos uma espécie nova do gênero *Arachnanthus*, o primeiro registro do gênero para o Uruguai e Sul do Brasil, e registramos o seu ciclo dessa espécie. Os indivíduos adultos de *Arachnanthus* sp 1. apresentaram um par de mesentérios conectados a sifonóglife, o primeiro par de protomesentérios ocupou mais da metade da cavidade gastrovascular e o primeiro par de mesentérios se estendeu até a metade da cavidade gastrovascular. A larva passou cerca de quatro a sete dias no ambiente pelágico até se assentar. O adulto alcançava até 5cm de comprimento corpóreo, a coloração do corpo era leitosa e apresentou um comportamento de locomoção que, até então, não era conhecido para Ceriantharia. No intuito de se locomover, o adulto abandonava o tubo já construído e provavelmente, sintetizou mais de um tubo durante o estágio adulto.

Nós tambpem analisamos o transcriptoma da larva e do adulto de *Arachnanthus* sp. 1. Nossos resultados demonstraram que a proporção de transcritos classificados em cada categoria ‘Gene Ontology’ foi similar em ambos os estágios do ciclo de vida, a maioria deles foram atrelados a processos biológicos. Nós também avaliamos o perfil de possíveis toxinas expressas pela larva e pelo adulto da nova espécie. O adulto apresentou uma abundância muito menor de proteínas similares a toxinas em comparação a larva. Provavelmente, isso evidencia os fatores ambientais, os quais a larva e o adulto estão susceptíveis e as estratégias que o indivíduo em cada estágio precisa desenvolver para garantir a sobrevivência e sucesso reprodutivo.

Por fim, muitas icógnitas persistem em relação ao desenvolvimento de espécies da subclasse Ceriantharia. Os percursos dos estágios de desenvolvimento ainda precisam ser desvendados para grande parte das espécies de ceriantários. Análises voltadas para a função ecológica da locomoção do adulto de *Arachnanthus* sp 1., bem como as implicações evolutivas desse comportamento ainda precisam ser desvendadas. Além disso, é necessário compreender melhor a relação entre expressão gênica, as fases do desenvolvimento em Ceriantharia e fatores ambientais experimentados pelos indivíduos em cada estágio. Adicionalmente, é de grande relevância estudos mais abrangentes no intuito de entender a síntese de toxinas por cada estágio do ciclo de vida das anêmonas de tubo, a variação encontrada mediante as sugestões ambientais e as funções ecológicas dessas toxinas.

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