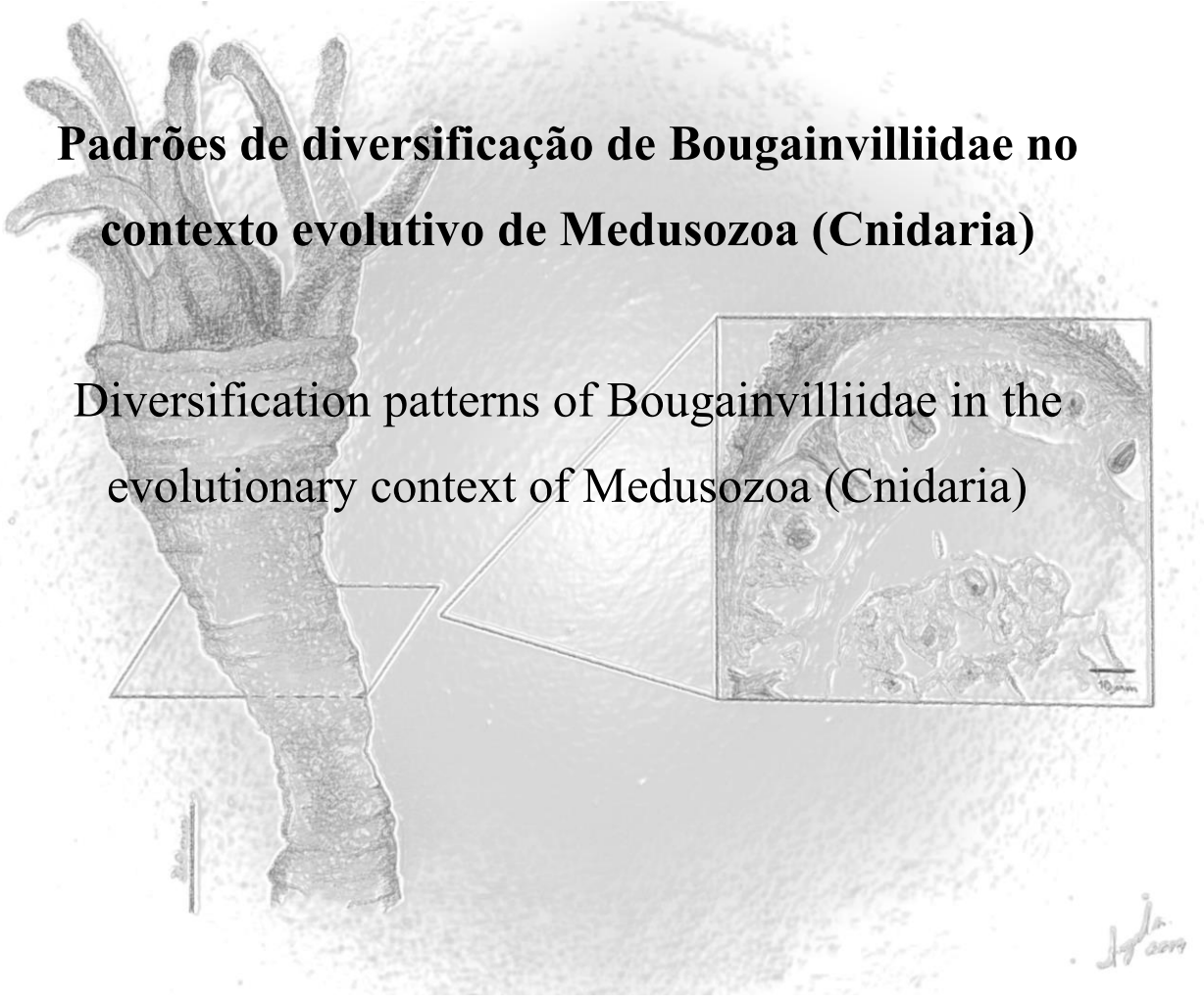
María de los Angeles Mendoza Becerril



Padrões de diversificação de Bougainvilliidae no contexto evolutivo de Medusozoa (Cnidaria)

Diversification patterns of Bougainvilliidae in the evolutionary context of Medusozoa (Cnidaria)

São Paulo

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Diversification patterns of Bougainvilliidae in the evolutionary context of Medusozoa (Cnidaria)

Tese apresentada ao Instituto de Biociências da Universidade de São Paulo, para a obtenção de Título de Doutor em Ciências, na Área de Zoologia.

Orientador: Prof. Dr. Antonio Carlos Marques

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Comissão Julgadora:

Prof(a). Dr(a).

Prof(a). Dr(a).

Prof(a). Dr(a).

Prof(a). Dr(a).

Prof. Dr. Antonio Carlos Marques

Aos meus grandes mestres da vida toda, meus pais.

A mis grandes maestros de toda la vida, mis padres.

Aparentemente no había nada
sólo el agua, algunas veces en protesta,
resonante e impenetrable,
otras sólo tranquila y apacible.

Aparentemente no había nada
sólo la inmensa niebla que guardas,
hasta que descubrí un mundo nuevo
y llegué a donde jamás había soñado.

Aparentemente no había nada
sólo secretos y misterios
reflejados en tus violentas
y espumosas olas.

Aparentemente no había nada
sólo tu manto azul,
acompañado de coros y mareas
que me avivaron hasta llegar aquí.

Aparentemente no había nada,
sólo arena y agua entre rocas,
resguardo de pequeños tesoros,
visibles ante sabias miradas.

Aparentemente no había nada,
sólo un infinito y majestuoso horizonte
donde se pierde el sol
y nacen nuevos sueños.

Aparentemente, não tinha nada
só água, as vezes em protesto
ressonante e impenetrável;
outras vezes somente tranquila e em paz.

Aparentemente, não tinha nada
só o imenso nevoeiro que guardas,
somente quando descobri um novo mundo
foi que cheguei onde nunca tinha sonhado.

Aparentemente, não tinha nada
só segredos e mistérios
refletidos nas suas violentas
e espumosas ondas.

Aparentemente, não tinha nada
só um manto azul,
acompanhado de coros e marés
vivificando me para chegar aqui.

Aparentemente, não tinha nada,
só areia e água entre as rochas,
resguardo de pequenos tesouros,
visíveis para um sábio olhar.

Aparentemente, não tinha nada,
só um horizonte infinito e majestoso
onde perde-se o sol
e novos sonhos nascem.

Mendoza-Becerril M.A.

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Índice

Capítulo – 1

Introdução geral

Medusozoa (Cnidaria) inclui as classes Staurozoa, Cubozoa, Scyphozoa e Hydrozoa, cujas relações filogenéticas estão baseadas em morfologia, ciclos de vida e marcadores moleculares (Marques & Collins, 2004; Collins et al., 2006; Van Iten et al., 2006, 2014). Hydroidolina é um grupo de Hydrozoa que inclui "Anthoathecata", Leptothecata e Siphonophorae (Cartwright et al., 2008), sendo "Anthoathecata" e Leptothecata os mais ricos em espécies e, conjuntamente, formando o grupo não monofilético classicamente chamado de hidroides (Daly et al., 2007; Mapstone, 2014). Hydroidolina é caracterizado pela presença de estatocistos de origem ectodérmica (Collins et al., 2006; Daly et al., 2007). Seu ciclo de vida geralmente possui dois estágios mais claros de desenvolvimento morfológica e ecologicamente distintos, nomeadamente, o pólipo e a medusa (Russell, 1953; Cornelius, 1995). Os pólipos de Hydroidolina podem ser solitários ou coloniais, e as colônias podem ser polimórficas (Daly et al., 2007).

Siphonophorae é caracterizado por uma organização colonial holopelágica (exceto a família Rhodaliidae) com alto grau de polimorfismo (cf. Mapstone, 2014). Leptothecata é caracterizado por um exoesqueleto envolvendo os hidrantes (= hidroteca) e gonóforos (= gonotheca), majoritariamente coloniais, em que os tentáculos estão dispostos em uma coroa (Cornelius, 1995; Marques & Collins, 2004). Finalmente, "Anthoathecata" é um grupo não monofilético (Cartwright et al., 2008; Cartwright & Nawrocki, 2010), caracterizado pela ausência de um exoesqueleto sobre os hidrantes (Allman, 1871; Calder, 1988) ou, em alguns casos, de qualquer estrutura exoesquelética (Daly et al., 2007). Representantes de "Anthoathecata" são coloniais ou solitários, com tentáculos dispostos em uma ou duas coroas ou dispersos no corpo do hidrante (Calder, 1988).

Estudos morfológicos tradicionais classificam representantes de "Anthoathecata" em Filifera e Capitata, cujas sinapomorfias, na fase de pólipo, são os tentáculos filiformes e capitados, respectivamente, ambos espalhados ou em coroas definidas no hidrante (Bouillon, 1985; Petersen, 1990). Essas características não encontram embasamento filogenético, a disposição de tentáculos dispersos pode ocorrer em ambos os grupos e o desenvolvimento de tentáculos capitados apresenta variação nas fases do ciclo de vida de espécies de Capitata (Millard, 1975; Petersen, 1990). Outra sinapomorfia proposta para Filifera foram os nematocistos desmonemos e euritelos microbásicos (Petersen, 1990), caracteres também

demonstrados como plesiomórficos (Marques, 2001), além da ausência de estenotelos (Schuchert, 2012). Estudos moleculares demostram que "Anthoathecata" pode ser compreendido com vários grupos não relacionados, como Aplanulata (anteriormente incluído em Capitata; Collins et al, 2006) e Capitata (Cartwright et al., 2008; Cartwright & Nawrocki, 2010; Nawrocki et al., 2010), além de diversos grupos considerados como "Filifera" (Cartwright et al., 2008; Cartwright & Nawrocki, 2010).

Conforme classicamente interpretados, "Filifera" inclui 26 famílias (Schuchert, 2015, com adição de dados de Calder et al., 2015), das quais três (Bougainvilliidae, Clathrozoellidae e Pandeidae) possuem exoesqueleto envolvendo seus hidrantes (= pseudo-hidroteca) (cf. Millard, 1975; Calder, 1988; Vervoort, 2000; Peña-Cantero et al., 2003; Schuchert, 2007). Dentre essas famílias, Bougainvilliidae destaca-se pela diversidade de sua estrutura exoesquelética e riqueza (110 espécies válidas e 15 gêneros, Mendoza-Becerril & Marques, 2013; Schuchert, 2015; Stepanjants & Chernyshev, 2015). Uma substancial parte de Bougainvilliidae é pouco conhecida, mal descrita e com registros raros. Pouco se sabe sobre o monofiletismo da família (Cartwright et al., 2008; Maronna, 2014), suas relações filogenéticas, indicações de ciclos de vida (Edwards, 1966; Calder, 1971; Schuchert, 1996, 2007), diversidade e morfologia. A "pseudo-hidroteca", por exemplo, é uma particularidade do grupo pouco investigada no que sua composição, morfologia, funcionalidade e evolução.

Nesse contexto de ausência de comparações evolutivas e de diversidade, este estudo teve como objetivos contextualizar historicamente e geograficamente o conhecimento atual sobre Bougainvilliidae, além de fazer uma predição de sua distribuição (Capítulo 2); analisar a estrutura exoesquelética em Medusozoa, comparando variações em origem, estrutura e função, e de seu papel em padrões de diversificação do grupo (Capítulo 3); analisar e comparar a estrutura e composição tecidual e exoesquelética de Bougainvilliidae e outros Hydroidolina (Capítulo 4); e esclarecer a posição filogenética de Bougainvilliidae dentre os "Anthoathecata" (Capítulo 5).

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Capítulo – 2

Synopsis on the knowledge and distribution of the family Bougainvilliidae (Hydrozoa, Hydroidolina)

María de los Angeles Mendoza-Becerril & Antonio C. Marques

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Capítulo – 3

An evolutionary, comparative analysis of the medusozoan (Cnidaria) exoskeleton

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Capítulo – 4

Exoskeletal system of Bougainvilliidae and other Hydroidolina (Cnidaria, Hydrozoa)

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Capítulo – 5

Relações filogenéticas e cenários da evolução morfológica em Bougainvilliidae (Cnidaria, Hydrozoa)

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Capítulo – 6

Discussão geral e conclusões

O conhecimento prévio sobre diversos aspectos de Bougainvilliidae (Hydrozoa, Anthoathecata) era limitado, demandando a necessidade de estudar aspectos sobre sua morfologia e biologia, permitindo formular e/ou testar hipóteses de padrões evolutivos de diversificação e riqueza do grupo.

Uma revisão bibliográfica de seus táxons (baseada na classificação seguida por Schuchert, 2007), sob uma perspectiva histórica, caracterizou gêneros e espécies válidos, e desvendou o potencial de distribuição em função da ecologia das espécies mais bem representadas, resultando em cinco padrões possíveis de distribuição latitudinal para pólipos e medusas de Bougainvilliidae (Mendoza-Becerril & Marques, 2013). Conjuntamente, identificamos caracteres diagnósticos usados nas classificações tradicionais da fase polipoide (cf. Millard, 1975; Calder, 1988; Schuchert, 2007), em que o tipo de gonóforo é essencial para caracterização dos táxons e, ante a ausência de gonóforos, os hidroides podem ser aproximadamente determinados pela cobertura de sua pseudo-hidroteca, que é bastante variável e também presente em outras famílias de "Anthoathecata".

A pseudo-hidrotheca é, de fato, um caráter chave na taxonomia de Bougainvilliidae, mas há grandes hiatos sobre sua origem, desenvolvimento, composição e variação morfológica. Além disso, baseado na semelhança morfológica, há pelo menos oito nomes diferentes para a estrutura na literatura (Allman, 1871; Warren, 1919; Brown, 1975; Thomas & Edwards, 1991; Calder, 1988; Stepanjants et al., 2000; Vervoort, 2000; Schuchert, 2007; Cartwright et al., 2008), causando uma inexatidão e ambiguidade na delimitação entre os táxons.

A pseudo-hidroteca faz parte do sistema geral de suporte dos hidroides e, como tal, a universalidade e evolução do exoesqueleto fornecem informações cruciais para compreender a evolução em Medusozoa em si. Nossas análises histológicas e microestruturais de diversos grupos mostrou que a pseudo-hidroteca faz parte do sistema exoesquelético, sendo melhor representada em Bougainvilliidae. Uma análise comparada dos dados de grupos fósseis e atuais deixa claro que há variação na síntese, estrutura e função do exoesqueleto dentre os medusozoários, e que a esqueletogênese retrocede ao Ediacarano, quando processos bióticos, abióticos e fisiológicos atuaram conjuntamente resultando em um exoesqueleto rígido e/ou biomineralizado. No entanto, o exoesqueleto axial córneo (complexo quitina-proteico)

predomina nos pólipos atuais, apresentando a maior variação e complexidade estrutural entre os pólipos de Hydroidolina, grupo para o qual foi descrito um novo tipo de exoesqueleto bicamada.

O exoesqueleto bicamada, carateristico da maioria de Bougainvilliidae, é formado de uma camada externa de glicosaminoglicanos (= exossarco), disposta radialmente em relação a uma camada interna quitino-proteica (= perissarco) e considerada um reforço exoesquelético. Consequentemente, a pseudo-hidroteca, classicamente uma cobertura externa com ou sem detritos que envolve os hidrantes (Allman, 1871; Calder, 1988), é redefinida como um exossarco que envolve o hidrante em diferentes graus e que pode ou não estar associado a material orgânico ou inorgânico.

Concluímos que é essencial estudar o exoesqueleto de forma ampla, não se limitando a estruturas específicas. Com essa perspectiva, e focando em estudos sobre seu desenvolvimento, morfologia e histologia entre diferentes espécies de Bougainvilliidae e de outros Hydroidolina, caracterizamos o desenvolvimento exoesquelético em três sistemas, viz. "síntese molecular", "matriz molecular" e "expressão morfológica", que têm implicações evolutivas e ecológicas importantes.

Os dados levantados permitiram um estudo integrado da evolução de Bougainvilliidae considerando-se dados moleculares e morfológicos, incluindo os novos caracteres exoesqueléticos. As análises identificaram "Bougainvilliidae" e "Bougainvillia" como não-monofiléticos. Por outro lado, propusemos o grupo monofilético Pseudothecata *taxon novum* incluindo os gêneros classicamente assumidos em "Bougainvilliidae" (exceto *Dicoryne*) e algumas outras família. Pseudothecata é grupo irmão de Leptothecata, grupo com exoesqueleto rígido amplamente desenvolvido nas colônias na maioria de seus representantes. Vimos ainda que membros de "Bougainvilliidae" possuem estados exoesqueletais intermediários, na forma de um exossarco.

As evidências apontadas ampliam uma linha de pesquisa sobre a origem e composição em diferentes níveis estruturais, o sinal filogenético do exoesqueleto e possíveis influências de variações batimétricas sobre o mesmo, além de métodos para compreender seu sistema molecular. Entretanto, estudos evolutivos sobre o grupo são imprescindíveis para uma melhor compreensão dos caracteres compartilhados entre "Bougainvilliidae" e outros Medusozoa, que permitirá correlacionar a áreas como conservação e filogeografia.

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Resumo

A família Bougainvilliidae é um grupo de hidrozoários “Anthoathecata” “Filifera” pouco conhecido. Nesse estudo, diversos aspectos da biologia do grupo e de táxons relacionados a ele foram analisados e discutidos. Nossas análises incluem: uma revisão bibliográfica dos táxons de Bougainvilliidae, a partir de um embasamento histórico e geográfico sobre seu conhecimento atual; uma síntese sobre sua estrutura exoesquelética, abrangendo informações de outros medusozoários fósseis e atuais; análises histológicas e microestruturais de pólipos de diversos grupos de Medusozoa; e um estudo integrado da evolução de Bougainvilliidae, considerando-se dados moleculares e morfológicos. Os resultados desvendaram gêneros e espécies válidos, padrões possíveis de distribuição latitudinal para pólipos e medusas de Bougainvilliidae, assim como a universalidade e evolução do exoesqueleto como fonte de informação para compreender padrões de diversificação dentro de Bougainvilliidae e em relação a outros Medusozoa. Além disso, os resultados evidenciam a variação na síntese, estrutura e função do exoesqueleto dentre os medusozoários, apontando que a esqueletogênese retrocede ao Ediacarano, sendo que o exoesqueleto axial córneo (complexo quitina-proteico) predomina nos pólipos atuais e atua como uma estrutura de suporte e proteção, entre outras funções. O exoesqueleto apresenta maior variação e complexidade estrutural entre os pólipos de Hydroidolina, grupo para o qual foi descrito um novo tipo de exoesqueleto bicamada, que é encontrado na maioria dos Bougainvilliidae. Resultados das análises filogenéticas identificam a “Bougainvilliidae” e “*Bougainvillia*” como táxons não-monofiléticos, e demonstram que o grupo monofilético Pseudothecata *taxon novum* inclui os gêneros classicamente assumidos em “Bougainvilliidae” (exceto *Dicoryne*), entre outras famílias de “Anthoathecata”. Neste estudo, ampliamos o nosso entendimento sobre a natureza química e física do exoesqueleto em Medusozoa, estrutura com um valor subestimado na taxonomia do grupo. Concluímos que estudar a “síntese molecular”, “matriz molecular” e “expressão morfológica” do exoesqueleto é essencial para inferências evolutivas e ecológicas, as quais podem ser intrinsecamente correlacionadas com outras áreas biológicas, tais como biologia de conservação e filogeografia.

Abstract

The family Bougainvillidae is a poorly known group of hydrozoans “Anthoathecata” “Filifera”. In this study, several aspects of the biology of this group and other related taxa are analyzed and discussed. Our analyzes include: a bibliographic revision of the taxa comprising the Bougainvilliidae, based on its current historical and geographical knowledge; a synthesis regarding its exoskeletal structure, including information on other extinct and extant medusozoans; histological and microstructural analyzes of polyps of several groups of Medusozoa; and an integrated study on the evolution of the Bougainvilliidae, considering molecular and morphological data. The results validated several genera and species and possible latitudinal distributional patterns for polyps and medusae of Bougainvilliidae, as well as the universality and evolution of the exoskeleton as a source of information to understand its role in the diversification patterns in Bougainvilliidae and with relation to other Medusozoa. Additionally, the results reveal the existence of variation on the synthesis, structure and function of the exoskeleton among the Medusozoa, showing that the exoskeletogenesis dates back to the Ediacaran, since the corneus exoskeleton (chitin-protein complex) predominates today in current polyps and acts as a supporting structure and protection, among other functions. The skeleton has higher variation and structural complexity among polyps of Hydroidolina, taxon from which we described a new type of bilayer exoskeleton, which is found in most of the species of Bougainvilliidae. Results of phylogenetic analyzes identificate “Bougainvilliidae” and “*Bougainvillia*” as non-monophyletic taxa, and showed that the monophyletic group Pseudothecata *taxon novum* includes the classical genera usually inserted in the “Bougainvilliidae” (excluding *Dicoryne*), and other families of “Anthoathecata”. In this study, we increased our understanding of the chemical and physical nature of the exoeskeleton of Medusozoa, a structure whith an underestimate role in the taxonomy of the group. We concluded that the study of the “molecular synthesis”, the “molecular matrix” and the “morphological expression” of the exoskeleton is necessary for evolutionary and ecological inferences, which are intrinsically related to other biological areas, such as conservation biology and phylogeography.