UNIVERSIDADE FEDERAL DE SANTA CATARINA
CENTRO DE CIÊNCIAS FÍSICAS E MATEMÁTICAS
PROGRAMA DE PÓS-GRADUAÇÃO EM OCEANOGRAFIA

Fernanda Maria Marques Soares

Conectando o presente ao passado: uso de TimeTree e Paleobiology Database para a discussão da evolução das algas calcárias crostosas (Corallinophycidae, Rhodophyta)

Florianópolis

2023

Fernanda Maria Marques Soares

Conectando o presente ao passado: uso de TimeTree e Paleobiology Database para a discussão da evolução das algas calcárias crostosas (Corallinophycidae, Rhodophyta)

Dissertação submetida ao Programa de Pós-Graduação em Oceanografia da Universidade Federal de Santa Catarina como requisito parcial para a obtenção do título de Mestra em Oceanografia.

Orientador(a): Prof. Paulo Antunes Horta, Dr.

Florianópolis

2023

Soares, Fernanda Maria Marques
Conectando o presente ao passado – uso de TimeTree e Paleobiology Database para a discussão da evolução das algas calcárias crostosas (Corallinophycidae, Rhodophyta) / Fernanda Maria Marques Soares ; orientador, Paulo Antunes Horta Jr, 2024.
46 p.

Dissertação (mestrado) - Universidade Federal de Santa Catarina, Centro de Ciências Físicas e Matemáticas, Programa de Pós-Graduação em Oceanografia, Florianópolis, 2024.

Inclui referências.

1. Oceanografia. 2. Algas calcárias. 3. Paleobiogeografia. 4. Fósseis. I. Horta Jr, Paulo Antunes. II. Universidade Federal de Santa Catarina. Programa de Pós-Graduação em Oceanografia. III. Título.

Fernanda Maria Marques Soares

Conectando o presente ao passado – uso de TimeTree e Paleobiology Database para a discussão da evolução das algas calcárias crostosas (Corallinophycidae, Rhodophyta

O presente trabalho em nível de Mestrado foi avaliado e aprovado, em 10 de novembro de 2023, pela banca examinadora composta pelos seguintes membros:

Prof. Frederico Tamega, Dr.
Universidade Federal Fluminense

Prof. Alberto Lindner, Dr.
Universidade Federal de Santa Catarina

Prof. Paulo Antunes Horta Jr, Dr.
Universidade Federal de Santa Catarina

Certificamos que esta é a versão original e final do trabalho de conclusão que foi julgado adequado para obtenção do título de Mestra em Oceanografia.

ICP-Edu
Documento assinado digitalmente
Pedro de Souza Pereira
Data: 09/02/2024 14:42:20-0300
CPF: ***.759.524-**
Verifique as assinaturas em https://v.ufsc.br

Coordenação do Programa de Pós-Graduação

GOV.BR
Documento assinado digitalmente
PAULO ANTUNES HORTA JUNIOR
Data: 09/02/2024 12:10:08-0300
CPF: ***.346.816-**
Verifique as assinaturas em https://v.ufsc.br

Prof.(a) Paulo Antunes Horta Jr, Dr.(a)
Orientador(a)

Florianópolis, 2024

A todos àqueles que passaram pela pandemia, que perderam entes queridos e tentam superar a dor da perda desse período que ainda é cheio de incertezas.

AGRADECIMENTOS

A minha mãe e irmã, por sempre me apoiarem e acreditarem mais em mim do que eu mesma.

Aos meus tios José Marques e Milta, por serem grandes incentivadores na minha formação acadêmica.

A Yasmin Dutra e a Patrícia Martins, por serem minhas amigas/irmãs, que mesmo com mais de 2.500 km de distância, se fizeram presente em todo o percurso.

As grandes amigas que fiz no mestrado. Amanda, Andressa, Cláudia, Emilly, Giovanna, Lyllyan, Mariana e Tayná, muito obrigada pela parceria, vocês fizeram a diferença nesta caminhada.

Aos amigos que fiz no Laboratório de Ficologia (LaFic). Obrigada a todos, sem exceção, pois são pessoas maravilhosas, trabalham bastante e muito bem. Sendo uma incubadora de ótimas ideias e experimentos.

Ao meu companheiro Wellington por todo o amor e compreensão. E toda a sua família, que desde o início me acolheram e se tornaram a minha família também.

Agradeço também os amigos de trabalho no IBAMA, foram muito compreensivos com as demandas finais dessa dissertação.

Ao prof. Alberto Lindner e prof. Frederico por aceitarem compor a banca a fim de contribuir para o melhoramento deste trabalho, bem como a prof. Kalina Brauko e prof. Paulo Pagliosa por também se disponibilizar para a compor a banca e pelas contribuições de forma individual.

Ao prof. Paulo Horta, meu orientador e amigo, muito obrigada. Apesar de tantas idas e vindas durante esta caminhada, você sempre me trouxe novas perspectivas sobre as algas calcárias, fazendo com que isso se tornasse uma paixão pra mim. Obrigada pela paciência e por todo suporte. Você com certeza faz e ainda fará muita diferença na natureza e na vida das pessoas.

A Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) e ao Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) por conceder bolsa por 16 meses e 2 meses, cada.

No mais, a todos que fizeram parte disso o meu muito obrigada!

RESUMO

O Filo Rhodophyta, representado pelas algas vermelhas, que compreende uma ampla diversidade de organismos fotossintetizantes eucariontes, incluindo cerca de 7.000 espécies distribuídas em aproximadamente 800 gêneros. Essas algas são predominantemente marinhas, embora existam alguns representantes de água doce. Elas variam em forma, desde unicelulares até multicelulares, e podem ser encontradas em uma ampla faixa de latitudes, abrangendo desde regiões tropicais até polares. As algas calcárias (AC) possuem corpos multicelulares que secretam carbonato de cálcio em sua parede celular, formando estruturas calcárias que colonizam substratos duros, como rochas e corais. Essa estrutura calcária confere resistência e proteção contra a herbivoria, além de favorecer a preservação no registro fóssil. Diante disto, foram utilizados os recursos *TimeTree* e *Paleobiology Database*. A distribuição das AC em ambientes subantárticos e antárticos, onde essas algas desempenham um papel fundamental na formação e manutenção dos ecossistemas, adaptando-se às condições extremas dessas regiões. No **Capítulo 1**, foram abordados dados paleobiológicos para identificar períodos geológicos e árvores filogenéticas das algas calcárias crostosas. Os resultados mostraram que estes organismos da classe Florideophydae tiveram diversificação de espécies antes mesmo da grande extinção em massa, durante o o período Jurássico. Os resultados apresentados no **Capítulo 1** revelam qual o tempo estimado dos seus registros fósseis a partir de recursos web, descrevendo a filogenia e distribuição das algas calcárias crostosas, recontando sua história ecológica e evolutiva. Os objetivos específicos incluem a identificação de impactos geológicos na Terra, a simulação da distribuição das AC ao longo do tempo geológico e a investigação da diversificação dessas algas em diferentes períodos geológicos.

Palavras-chave: algas calcárias. paleobiogeografia. filogenética. fósseis.

ABSTRACT

The Rhodophyta phylum, represented by red algae, comprises a wide diversity of eukaryotic photosynthetic organisms, including around 7,000 species distributed in approximately 800 genera. These algae are predominantly marine, although there are some freshwater representatives. They vary in shape, from unicellular to multicellular, and can be found in a wide range of latitudes, ranging from tropical to polar regions. Calcareous algae (CA) have multicellular bodies that secrete calcium carbonate in their cell walls, forming calcareous structures that colonize hard substrates, such as rocks and corals. This calcareous structure provides resistance and protection against herbivory, as well as favoring preservation in the fossil record. Given this, the TimeTree and Paleobiology Database resources were used. The distribution of CA in subantarctic and Antarctic environments, where these algae play a fundamental role in the formation and maintenance of ecosystems, adapting to the extreme conditions of these regions. In **Chapter 1**, paleobiological data were discussed to identify geological periods and phylogenetic trees of crustose calcareous algae. The results showed that organisms from the Florideophydae class had species diversification even before the great mass extinction, during the Jurassic period. The results presented in Chapter 1 reveal the estimated time of their fossil records from web resources, describing the phylogeny and distribution of crustose calcareous algae, recounting their ecological and evolutionary history. Specific objectives include identifying geological impacts on Earth, simulating the distribution of CA over geological time and investigating the diversification of these algae in different geological periods.

Keywords: calcareous algae. paleobiogeography. phylogenetics. fossils.

LISTA DE FIGURAS

LISTA DE TABELAS

SUMÁRIO

1 **INTRODUÇÃO GERAL**

O Filo Rhodophyta, representado pelas algas vermelhas, é composto por organismos fotossintetizantes eucariontes, com cerca de 7.000 espécies descritas que estão distribuídas por aproximadamente 800 gêneros (GUIRY, 2017). São predominantemente marinhas (GRAHAM *et al*., 2009), com alguns poucos representantes de água doce (BELLINGER e SIGEE, 2015). Possuem desde formas unicelulares até multicelulares, com distribuição em todas as latitudes, desde regiões tropicais até polares.

As algas vermelhas apresentam ausência de flagelos em todo o seu ciclo de vida, sua parede celular é composta por celulose e inúmeros polímeros de galactanas sulfatadas (ágar e carragenanas), substâncias de reserva armazenadas no citoplasma na forma de amido das florídeas, cloroplastos com tilacóides isolados e ligações celulares. Em sua estrutura há pigmentos fotossintetizantes acessórios, ficobiliproteínas, que ficam armazenados em forma de ficobilissomas. A luz refletida na cor azul é associada a duas formas de ficocianina (R-ficocianina e aloficocianina) e a luz refletida na cor vermelha a três formas de ficoeritrina, que por sua predominância confere a cor vermelha a essas algas (GRAHAM *et al*. 2009, LE GALL *et al*., 2015; VAN DEN HOEK *et al*. 1995, Lee 2008).

Dentre as Rhodophyta, ganham destaque as algas calcárias (AC), que podem ser encontradas nos mais diversos habitats, compreendendo desde a zona entremarés até habitats mesofóticos, como a 268m de profundidade nas Bahamas (BASSO *et al*., 2015; JOHNSON; KÜBLER, 2010; LITTER; LITTER, 1985). Dentre estes organismos são reconhecidas formas articuladas, que possuem porções não calcificadas no talo permitindo flexibilidade, e formas completamente calcificadas (AMANCIO, 2007; NUNES *et al*., 2008).

As AC possuem corpo multicelular composto por células que secretam carbonato de cálcio em sua parede celular como parte de processos químicos e metabólicos, e sua deposição contínua de carbonato forma estruturas calcárias que colonizam substratos duros, como rochas, corais e conchas de moluscos, entre outros. Quando este crescimento é crostoso, estas algas são conhecidas como Algas Calcárias Crostosas (ACC) (HOEK, 1982, HURD *et al*., 2014, RIOSMENA-RODRÍGUEZ; NELSON *et al*., 2015; WYNNE, 2011).

A estrutura de sua parede celular impregnada com carbonatos de cálcio e magnésio, formando cristais de calcita, lhes confere resistência e capacidade de colonizar diferentes substratos, como rochas, conchas, recifes de coral e outras algas (BROOM *et al*., 2017), sendo ela responsável por cerca de 90% do peso seco destas algas (OLIVEIRA, 1997; WOELKERLING *et al*., 1993), servindo como característica estratégica, pois além de conferir proteção contra a herbivoria, também favorece sua preservação no registro fóssil, como por exemplo as espécies *Halysis sp.*(485 Ma) e *Solenopora sp*. (471 Ma) (Tabela 1).

Tabela 1 – Alcance máximo baseado apenas em fósseis de algas vermelhas do grupo das Corallinophycidae: base do Whiterockian até o topo do Holoceno ou 471,80000 a 0,00000 Ma. (Continua)

Intervalo de tempo	Ma	País ou estado	Número original de identificação da coleção
Drumiano	513.0 - 505.0	Canada (British Columbia)	*Wahpia* sp.
Termociano - Floiano	485.4 - 470.0	China (Jianxin)	*Halysis sp*. (154811)
Arenig	478.6 - 466.0	Canada (Newfoundland e Labrador)	*Halysis sp*. (80772) *Solenopora sp*., *Halysis sp*. (80774)
Whiterockian	471.8 - 457.5	EUA (Vermont)	*Solenopora sp*. (103298)
Chazyan	468.1 - 460.9	EUA (Vermont)	*Solenopora sp*. (175904 175905)
Llanvirnian - Llandeilian	468.1 - 460.9	South Korea (Kangweondo (Gangwon-do))	*Solenopora sp*. (198260)
Whiterock	468.1 - 460.9	Canadá (Newfoundland e Labrador)	*Solenopora sp*., *Halysis sp*. (45283)
Darriwilian	467.3 - 458.4	China	*Halysis sp*. (211603)
Llanvirn	466.0 - 460.9	Canada (Newfoundland e Labrador)	*Halysis sp*. (80003 80004)
Llanvirn	466.0 - 460.9	EUA (Virginia)	Solenopora sp. (34738)
Chazy	466.0 - 457.5	Canada (Quebec)	*Parachaetetes sp*. (45281) *Solenopora compacta* (172352) *Solenopora sp*. (80006 175234)

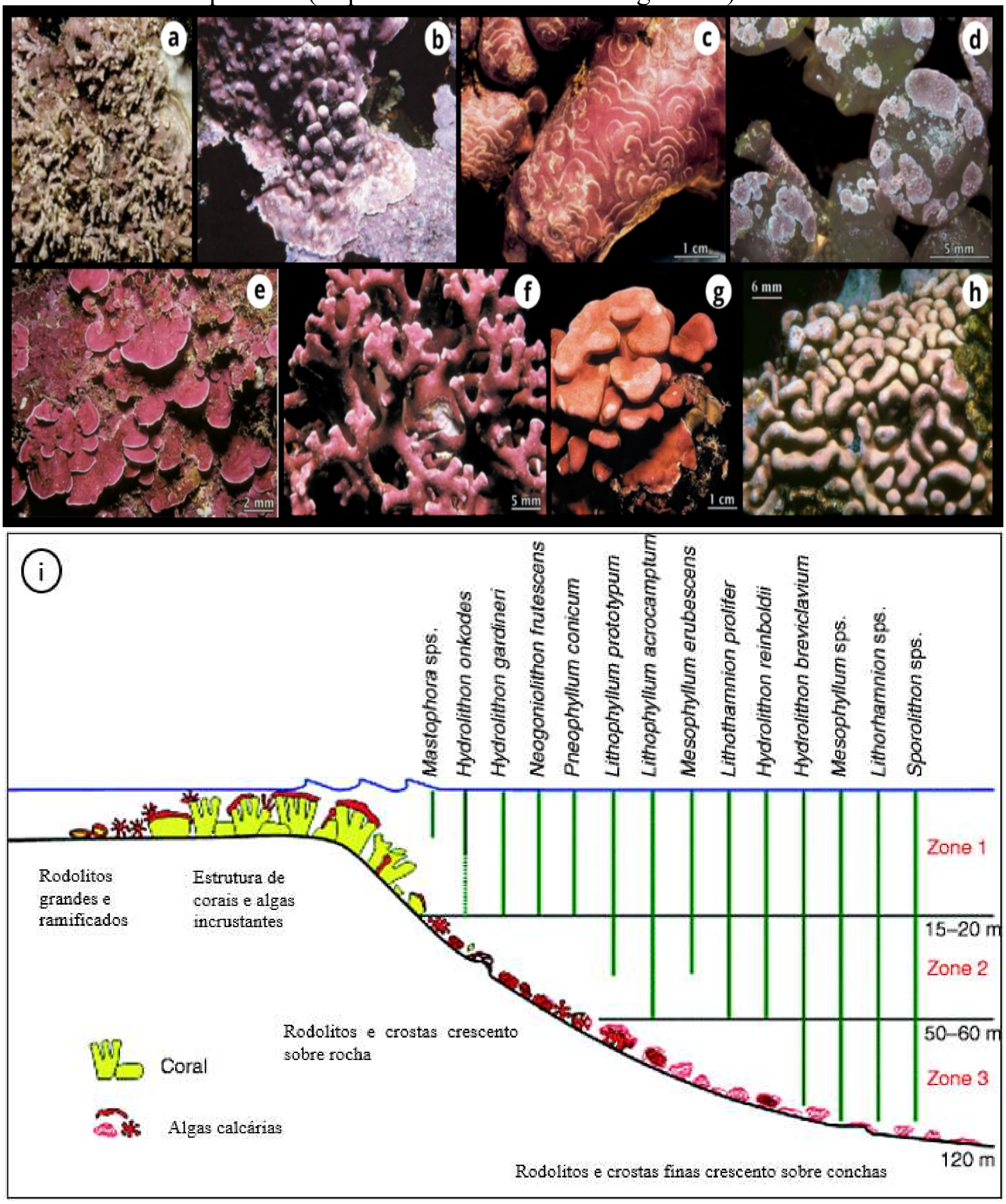
Tabela 1 – Alcance máximo baseado apenas em fósseis de algas vermelhas do grupo das Corallinophycidae: base do Whiterockian até o topo do Holoceno ou 471,80000 a 0,00000 Ma.
(Conclusão)

Chazy	466.0 - 457.5	EUA (New York)	*Solenopora compacta* (171705) *Solenopora sp.* (63307)
Chazy	466.0 - 457.5	EUA (Vermont)	*Solenopora sp.* (80821) *Solenopora sp.*, *Solenopora embrunensis* (63297)
Keila	460.9 - 455.8	Estonia	*Solenopora sp.* (197520)
Ashbyan	460.9 - 449.5	EUA (Virginia)	*Solenopora compacta* (33995 33996 33997)
Blackriveran	460.9 - 449.5	Canada (Ontario)	*Tetradium fibratum* (55999)
Blackriveran	460.9 - 449.5	EUA (Tennessee)	*Solenopora compacta* (5331)

Fonte: Tabela gerada automaticamente do período de coleções das algas calcárias ao longo do tempo geológico. 2023 (adaptado). Paleobiology Database, https://paleobiodb.org/.

Esta facilidade das AC nos permite conectar o presente ao passado. Conhecendo a distribuição em diferentes ecossistemas hoje, assim como seu papel ecológico/funcional, podemos reconstruir possíveis condições ambientais em diferentes momentos da história do planeta que tiveram as algas calcárias como testemunhas. Assim como destacado por Braga (2011), as preferências de habitat dos diferentes táxos de AC, as variações na ocorrência e na morfologia de acordo com os níveis de turbulência da água, assim como em função da disponibilidade de nutrientes e luz, conferem às AC o potencial de indicar as condições ambientais em gradientes espaço temporais variados hoje e no passado remoto do nosso oceano (Adey, 1986). A luz é um fator factor que controla a distribuição das espécies AC e, como a intensidade da luz e o comprimento de onda que atinge o fundo do mar dependem fortemente da profundidade, diferentes espécies AC apresentam condições de nicho específicas representando indicadores refinados as condições ambientais como visto no esquema a seguir acompanhado das ilustrações da grande plasticidade morfológica (Figura 1.1).

Figura 1.1 - Diversidade morfo-anatômica das algas calcárias crostosas. Fotos: D. Littler (Littler e Littler, 2013). (a) Alga calcária com crescimento vertical, estratégia de sobrevivência; (b) CCA com crescimento bidimensional; (c-d) Formas de crescimento bidimensionais simples de CCA; (e) CCA de crescimento folioso e gradativo; (f) CCA de crescimento ramificado; (g-h) CCA com crescimento ramificado em forma de nódulos; (i) Variabilidade na ocorrência de diferentes espécies e morfologias de algas calcárias em um gradiente de profundidade de um sistema recifal no pacífico (esquema de acordo com Braga 2011).



Além de diferenciar espécies, a grande plasticidade morfológica do grupo também é observada dentro de suas espécies, e isso, provavelmente, está igualmente relacionado à hidrodinâmica local e outras condições ambientais (BOSENCE, 1976; PEÑA; BÁRBARA, 2008a). Esta alta plasticidade morfológica, dificulta a identificação das espécies coralinas pois muitas vezes o taxonomista carece de caraterísticas distintivas, ou diagnósticas (WRAY, 1977; KANGWE, 2005; STENECK, 1986). No entanto, isso vem sendo superado, pois, as técnicas moleculares têm permitido um avanço crescente no conhecimento da diversidade das algas calcárias nas últimas duas décadas, muitas vezes confirmando os antigos paradigmas baseados em dados anatômicos/ morfológicos ou biogeográficos, mas também trazendo novidades em todos os níveis de classificação. No contexto da diversidade de espécies, presenciamos o reconhecimento de espécies crípticas no que antes se reconhecia como sendo uma só unidade taxonômica, como pode ser visto no caso de *Mesophyllum erubescens*, (SISSINI *et al*. 2014) e de *Calrskottsbergia antartica* (ATHANASIADIS, 2019).

No campo da filogenia, temos vivenciado grandes alterações na organização e classificação das AC. Os autores Harvey e Woelkerling (2007) propuseram que as ACC fossem agrupadas somente em uma ordem, a Coralinalles, tendo três famílias como representantes: Corallinaceae, Hapalidiaceae e Sporolithaceae, com sete subfamílias (Tabela 2).

Tabela 2 – Classificação da ordem Corallinales (Harvey e Woerkling, 2007).

(Continua)

Família	**Subfamília**	**Gênero**
Corallinaceae	Metagoniolithoideae	*Metagoniolithon*
	Corallinoideae	*Alatocladia, Arthrocardia, Bossiella Calliarthron, Cheilosporum, Chiharaea, Corallina, Haliptilon, Jania, Marginosporum, Masakiella, Serraticardia, Yamadaea*
	Mastophoroideae	*Hydrolithon, Lesueuria, Lithoporella, Mastophora, Metamastophora, Neogoniolithon, Pneophyllum, Spongites*

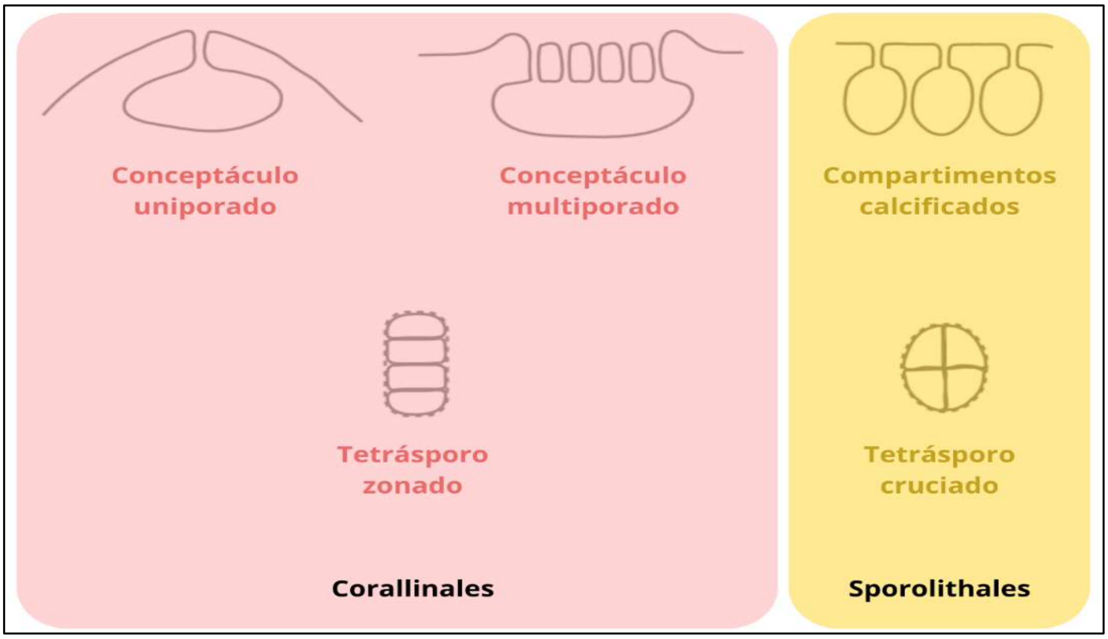
Tabela 2 – Classificação da ordem Corallinales (Harvey e Woerkling, 2007).

(Conclusão)

	Lithophylloideae	*Amphiroa, Ezo, Lithophyllum/Titanoderma, Lithothrix, Paulsilvella, Tenarea*
Hapalidiaceae	Austrolithoideae	*Austrolithon, Boreolithon*
	Choreonematoideae	*Choreonema*
	Melobesioideae	*Clathromorphum, Exilicrusta, Kvaleya, Lithothamnion, Mastophoropsis, Melobesia, Mesophyllum, Phymatolithon, Synarthrophyton*
Sporolithaceae		*Heydrichia, Sporolithon*

Com novas abordagens e intensificação dos esforços para se descrever os representantes do grupo, táxons incluídos em Corallinales foram sendo revistos e ganharam status de ordem. Com o estudo filogenético realizado por Le Gall *et al*. (2010), foi proposto que a família Sporolithacae fosse elevada ao status taxonômico de ordem, sendo assim a ordem Sporolithales, do qual os autores se basearam em características morfológicas e anatômicas que pudessem delimitar uma ordem da outra (Figura 1.2).

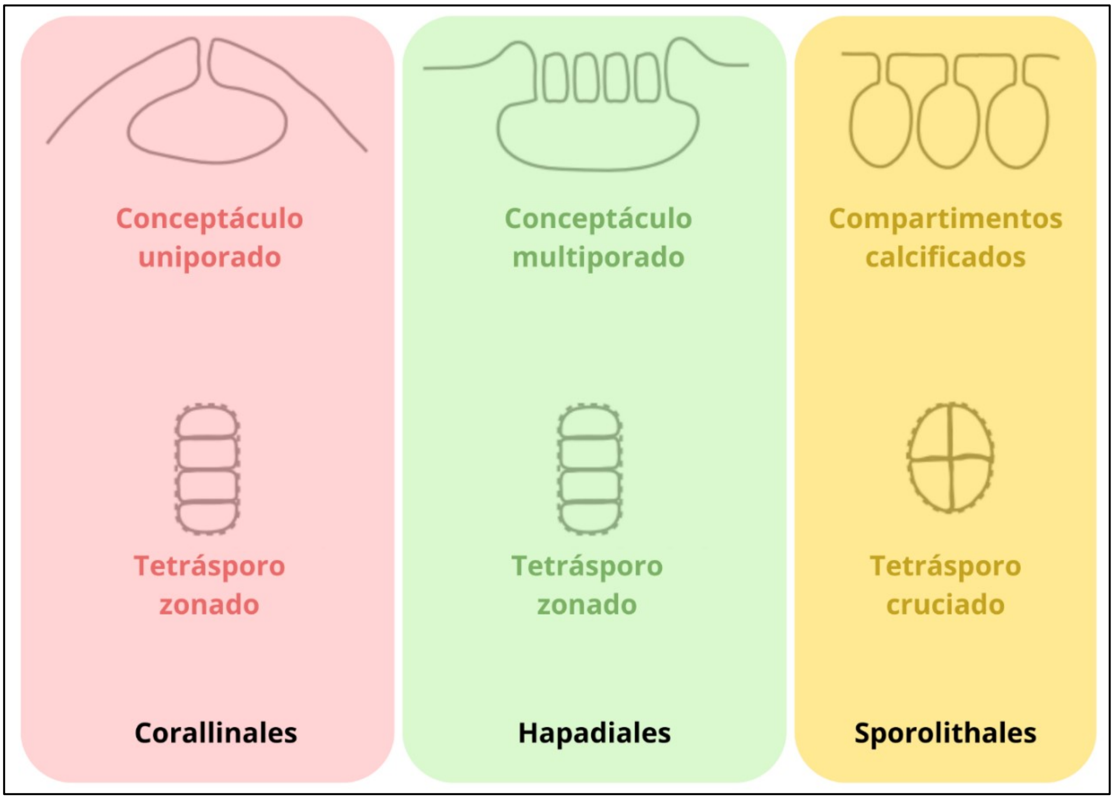
Figura 1.2 – Caracteres morfológicos delimitadores para a divisão entre as ordens Corallinales e Sporolithales.



Fonte: Farr *et al*., 2009 (adaptado).

Atualmente, para o Filo Rhodophyta foram atribuídas quatro ordens, sendo reconhecidas como algas calcárias sensu strito: Corallinales, Hapadiales e Sporolithales (NELSON *et al*., 2015; PENHA *et al*., 2020). A distinção entre as três se dá por seus caracteres morfológicos reprodutivos, especialmente os relacionados à fase tetrasporofítica. Os representantes da ordem i, Corallinales apresentam conceptáculos uniporados sem a presença de *plug* apical nos canais dos poros por onde são liberados tetrasporângios zonados, os representantes da ordem ii. Hapadiales apresentam conceptáculos multiporados com *plug* apical nos canais dos poros por onde são liberadostetrasporângios zonados, já os representantes da ordem iii. Sporolithales apresentam compartimentos calcificados isolados, conhecidos como câmara esporangial, com poros fechados por *plug* apical, onde são produzidos tetrasporângios cruciados (Le Gall *et al*., 2010, Nelson *et al*., 2015) (Figura 1.3).

Figura 1.3 – Caracteres delimitadores para a divisão das ordens Corallinales, Hapadiales e Sporolithales.



Fonte: Le Gall *et al*., 2010, Nelson *et al*., 2015 (adaptado).

Através de análises moleculares, os cientistas têm investigado as relações evolutivas entre as diferentes espécies e gêneros Corallinophycidae, pois antes do advento da sistemática molecular, as classificações se davam na maioria das vezes por distinção de caracteres vegetativos e reprodutivos (BAILEY e CHAPMAN, 1998; CABIOCH, 1972, JOHANSEN, 1972; LEBEDNIK, 1977). Entre os avanços a inclusão da ordem Rhodogorgonales foi recentemente sustentada por análises moleculares (PENHA *et al*. 2020). E é através do avanço nos estudos filogenéticos que se tem fornecido uma melhor compreensão da história dessas algas e sua relação com outros grupos de algas vermelhas (BROOM *et al*., 2008; RÖSLER et al., 2016; PENHA *et al*., 2020).

1.1 IMPORTÂNCIA DAS ALGAS CALCÁRIAS

As AC têm grande importância ecológica, desempenhando um papel fundamental na formação e manutenção de recifes de coral, fornecendo uma estrutura tridimensional e abrigo para uma grande variedade de organismos marinhos (LITTLER; LITTLER, 2013). Além disso, as crostas calcárias formadas pelas algas também contribuem para a consolidação do substrato, protegendo-o da erosão e fornecendo uma base sólida para o crescimento de outros organismos (GRAHAM *et al*., 2014).

A capacidade das algas calcárias crostosas de secretar carbonato de cálcio também as torna importantes na regulação do ciclo de carbono nos ecossistemas marinhos. Essas algas são capazes de absorver grandes quantidades de dióxido de carbono da água do mar durante a fotossíntese, contribuindo para a remoção desse gás de efeito estufa da atmosfera (KAMENOS *et al*., 2013).

As AC estão amplamente distribuídas em todo o mundo, incluindo as águas antárticas e subantárticas. No entanto, sua presença e diversidade nessas regiões são influenciadas pela interação complexa entre as correntes marinhas e as condições ambientais específicas (LEE *et al*., 2007). Esses ambientes são reconhecidos como ecossistemas únicos e extremos, caracterizados por condições climáticas severas e isolamento geográfico (GUTT, 2007). Nessas regiões, as algas detêm importância significativa, pois desempenham um papel fundamental na formação e manutenção dos ecossistemas (AMSLER *et al*., 2009; FRASER *et al*., 2013). Essas algas apresentam características únicas e adaptações especiais que lhes permitem sobreviver e prosperar em condições extremas de irradiância, temperatura, salinidade e disponibilidade de nutrientes (BROOM *et al*., 2017), e sua distribuição e abundância nesses ambientes estão intimamente relacionadas à influência das correntes marinhas, que atuam como importantes fatores determinantes da sua biogeografia (BARNES; SOUSTER, 2011; QUARTINO *et al*., 2007).

1.2 COMPREENDENDO AS RELAÇÕES EVOLUTIVAS E BIOGEOGRÁFICAS

Estimativas recentes apontam que nosso planeta conta com cerca de 7,8 milhões de espécies animais, 298 mil plantas, 611 mil fungos e 63.900 protistas (Wiens 2023). Entre estes últimos estão algas, como as algas calcárias. Estes números nos dão uma noção das dimensões que temos que enfretar para aprimorarmos a compreensão e de nossa biodiversidade. Dentre estes seres vivos encontraremos cerca de 72.500 espécies de algas (Guiry 2021), e entre elas os grupos historicamente menos conhecidos e valorizados, como as algas calcárias, apesar de suas supramencionadas importâncias. É nesse contexto que nos vemos diante de uma crise climática e ambiental sem prescedentes na história da humanidade, com a crescente necessidade de popularizarmos os conhecimentos sobre a biodiversidade do planeta, permitindo que um número crescente de pessoas possa compreender o funcionamento dos nossos ecossistemas hoje, interpretando os fatores que produziram grandes transformações na história evolutiva do planeta (Nanglu et al. 2023). Para isso é relevante popularizar grupos e ambientes que passaram e estão passando por grandes transformações. Ameaçados pelo aquecimento e acidificação do oceano as AC e os ambientes antárticos, representam fronteiras que nossa sociedade precisa conhecer do ponto de vista da composição da biodiversidade e de sua história evolutiva.

A revolução da genômica e os avanços nas técnicas de datação molecular e conjunto dos os crescentes bancos de dados, para gerar tempos de divergência entre populações e espécies de diferentes locais, nos permite hoje não só documentar as ocorrências como também testemunhar as grandes transformações ecológica-evolutivas pelas quais nossa biodiversidade passou. Dezenas de milhares de espécies tiveram sua história datada, e novas estimativas de tempo de divergência estão aparecendo em centenas de publicações a cada ano. Aproveitando esse cenário foram construídas sínteses globais que nos permitem detalhar processos que ocorreram no passado do nosso planeta. É esse entendimento da natureza multafatorial das variáveis que determinou os destinos da nossa biodiversidade, que vai nos permitir prever como as mutdaças produzidas pelos seres humanos nosso ambiente impactarão a distribuição e composição da biodiversidade no futuro (Hedges et al. 2015). Nesse sentido, bases de dados com ferramentas de análise, que sejam abertas ao público, como a TimeTree (https://timetree.org/) e o Paleobiology Database (https://paleobiodb.org/), são muito importantes para a popularização da história evolutiva de nossa biodiversidade. Entretanto, considerando eventuais fragilidades ou equívocos na identificação dos registros fósseis, análises podem ser recheadas de imprecisões que levem a intepretações inconsistentes sobre padrões e processos.

HIPÓTESE DE TRABALHO

Nesse sentido na presente dissertação partimos da hipótese de que a base de dados de ocorrência, paleontológicos e moleculares, de algas calcárias hoje disponível é suficiente para o entendimento de padrões e processos em todo o planeta considerando ferramentas disponíveis na web, como a *TimeTree* e *Paleobiology Database*.

OBJETIVO GERAL

Na presente dissertação buscamos contribuir com a discussão de ferramentas que podem ser utilizadas para popularizar o conhecimento da filogienia e biogeografia utilizando recursos web. Para isso, partimos da análise das algas calcárias crostosas, considerando seu potencial indicador de condições paleoecológicas, dos ambientes subantárticos e antárticos.

Assim pretendemos fornecer uma análise crítica sobre essas ferramentas que têm sido utilizadas para aprimorar nosso entendimento da história ecológica e evolutiva da biodiversidade de nosso planeta.

1.3 OBJETIVOS ESPECÍFICOS

- Identificar a distribuição das ACCs acompanhando a Deriva Continental, a partir de datação e relações evolutivas entre as espécies presentes no registro fóssil.

CAPÍTULO 1

RECONSTRUCTING THE EVOLUTIONARY HISTORY OF ANTARCTIC BIODIVERSITY FROM THE PHYLOGEOGRAPHY OF CRUSTOSE CALCAREOUS ALGAE

(manuscrito submetido no periódico *Frontiers in Marine Science*)

Formatação de acordo com a revista

2 CAPÍTULO: RECONSTRUCTING THE EVOLUTIONARY HISTORY OF ANTARCTIC BIODIVERSITY FROM THE PHYLOGEOGRAPHY OF CRUSTOSE CALCAREOUS ALGAE

Fernanda Maria Marques Soares[1,2*], Paulo Antunes Horta[2]

[1]Programa de Pós-Graduação em Oceanografia, Universidade Federal de Santa Catarina, 88040-400, Florianópolis, SC, Brazil.
[2]Laboratório de Ficologia, Departamento de Botânica, Universidade Federal de Santa Catarina, 88040-535, Florianópolis, SC, Brazil.

*Correspondence to: fernandamm.oceano@gmail.com

Keywords: calcareous algae, evolutionary history, phycology, phylogenetic, paleobiology.

ABSTRACT

This scientific article explores the evolutionary history and biogeographical relationship between crustose calcareous algae and ocean currents in Antarctic and subantarctic environments. It delves into the adaptations of these algae to extreme conditions, their role in ecosystem stability, and their phylogenetic development. The study employs phylogenetic trees and paleobiological databases to trace the diversification of these algae over geological time. The article highlights the importance of understanding these relationships for ecosystem conservation and adaptation to climate change, while acknowledging the challenges posed by limited fossil resources for constructing a comprehensive evolutionary timeline.

2.1 Introduction

Climatic and environmental colapse are approching fast (LENTON 2023), with the overcoming of important planetary tipping points, such as those represented by the unavoidable melting of West Antarctica (NAUGHTEN et al. 2023). This scenario raises an alert for the popularization of knowledge about the evolutionary history of environments and groups strategics to the understanding our past, raising general attention regarding the announced socioenvironmental crises (PÖRTNER et al. 2023) and needs on marine conservation (HORTA et al. 2020).

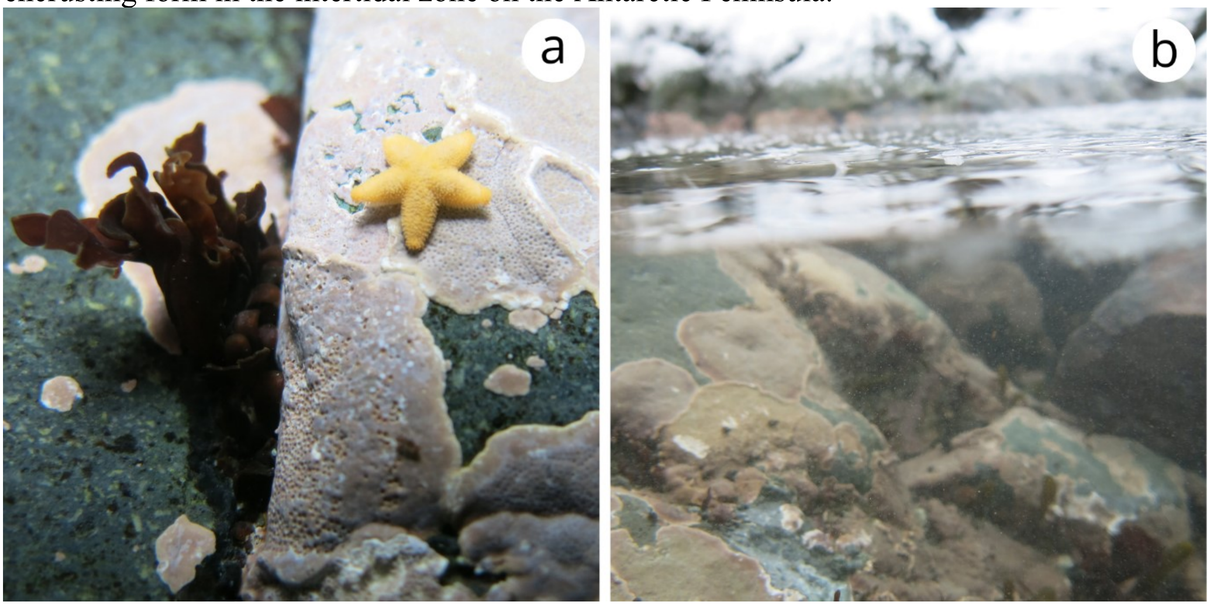
Along the history of life, environments that are now polar have undergone a variety of environmental conditions that are fundamental to the determination of distribution patterns observed in marine biodiversity today. Antarctica, a territory known for its extremes, experienced periods of warming, who left trace fossils of tropical forests closer to the South Pole in the Middle Cretaceous during the Turonian-Santonian era (92 - 83 Ma), in addition to other geographical configurations, considering the tectonic processes that govern our planet (KLAGES *et al*., 2020; ZUNDEL *et al*., 2019).

In these subantarctic and Antarctic marine environments, calcified algae are among the main primary producers with potential to tell us a bit more about the eco-evolutionary drivers responsable by the main shifts in marine life in the last 100 million years, once they have fossil representatives even older than that (Braga 2011; Peña et al. 2020). Currently they play an essential role in the formation of benthic communities and complex habitats in tropical and also in polar regions (KÜHL *et al*., 2015). Therefore their presence, regarding the morphology or taxonomical particularies, can help in the description of changes in sea-level (Adey 1983), sea temperatura (Kamenos et al. 2017), among other paleoenvironmental characteristics (Braga et al. 2012).

Southern polar areas are currentely characterized by low temperatures, variable salinities, and limited availability of nutrients and light, especially during the winter. Despite often inhospitable conditions, crustose calcified algae are conspicuous because they have developed physiological and morphological adaptations that allow them to survive under these extreme conditions (Schwars *et al*., 2006). For example, some species have photoprotective pigments that give them resistance to ultraviolet radiation, which is intense in these regions (PEREIRA *et al*., 2019; RIOSMENA-RODRÍGUEZ *et al*., 2014). They also can survive for long polar nights (Johnsen et al. 2020) or low irradiance (Hoffman et al. 2018). In addition, the calcareous structure of their cell walls provides mechanical strength and protection against the erosive action of icebergs, waves, and currents as well as efficient nutrient absorption and storage mechanisms, allowing them to cope with the low nutrient availability (PEREIRA *et al*., 2020; TEIXEIRA *et al*., 2016) (Figure 2.1).

In subantarctic environments, crustose calcified algae are widely distributed in the coastal regions of South America, New Zealand, Australia, Subantarctic Islands, and South Atlantic Islands. Studies have shown that the diversity of crustose calcified algae species increases in areas with greater availability of light and suitable substrate, such as rocky reefs (CATTANEO-VIETTI *et al*., 2000; HURD *et al*., 2014) where new taxa have been described (SCIUTO *et al*. 2021, TRENTIN *et al*. 2023).

Figure 2.1 – Encrusting form of red algae on rocks with associated fauna and flora; (b) encrusting form in the intertidal zone on the Antarctic Peninsula.



Author: Marina Sissini.

The Antarctic Peninsula and the South Shetland Islands are home to a rich diversity of crustose calcified algae. These algae are capable of colonizing hard substrates, such as rocks and mollusk shells, forming communities of extreme importance in the structuring of coastal marine ecosystems. They provide shelter and food for a variety of organisms, such as sea urchins, crabs, snails, and juvenile fish (BISCHOF *et al*., 1998; WIENCKE *et al*., 2007). Scientific studies have shown that the dispersal, colonization, and diversity of calcified algae in Antarctic and subantarctic environments are correlated with the direction and intensity of ocean currents in these regions (QUARTINO *et al*., 2007). These currents transport nutrients and particulate matter, as well as influence the temperature and salinity of the water, which are essential characteristics for the biogeography of calcified algae. These physical and chemical parameters directly affect the availability of essential resources for their growth and development (WIENCKE *et al*., 2017).

The Antarctic Circumpolar Current (ACC), a large-scale ocean current that encircles Antarctica, plays an important role in the dispersal and transport of marine organisms along the Antarctic and subantarctic coasts. This current influence the circulation of nutrients and the availability of sunlight, which are essential factors for the growth of calcified algae (HUOVINEN *et al*., 2018).

In subantarctic regions, ocean currents transport nutrients and organic matter, promoting a favorable environment for the growth of these algae. The ACC exerts a significant influence on the distribution of these algae, favoring their dispersal along continental coasts and adjacent islands (HAWES *et al*., 2020). Wind currents can also affect the distribution of these algae, creating upwelling conditions that bring nutrient-rich deep waters to the surface (BARTSCH *et al*., 2013; WIENCKE *et al*., 2019).

Ocean currents play a crucial role in the dispersal and transport of marine organisms, including algae (GÓMEZ *et al*., 2017). The dynamics of currents, such as direction and intensity, determine the spatial distribution of algae and their connectivity between different locations (HERNÁNDEZ-KANTÚN *et al*., 2017; SANTELICES *et al*., 2018). In subantarctic regions, the ACC exerts a significant influence on the distribution of these algae, favoring their dispersal along continental coasts and adjacent islands (HAWES *et al*., 2020). In Antarctica, marine circulation is essential for the transport of nutrients and the provision of suitable conditions for the development of crustose calcified algae. In Antarctica, the ACC, which flows west to east around the Antarctic continent, combined with the topography of the seabed, influences the formation of coastal currents and upwelling areas, creating favourable conditions for the development of crustose calcified algae (DUFFY *et al*., 2021). In addition, coastal currents and tides also influence the distribution of these algae, creating nutrient gradients and variations in the physical and chemical conditions of the water (AL-HANDAL *et al*., 2008; WIENCKE *et al*., 2019).

The biogeographical relationship between calcified algae and ocean currents goes beyond their geographic distribution. Phylogenetic studies have revealed the evolutionary history of these organisms, providing insights into their common ancestry and the speciation events that have occurred over time (GÓMEZ *et al*., 2009). Phylogenetic analysis helps to understand the phylogenetic relationships between calcified algae species and to identify patterns of diversification and dispersal related to ocean currents.

Understanding the biogeographical relationship between calcified algae in Antarctic and subantarctic environments with ocean currents is of paramount importance for the conservation and management of these unique ecosystems today ando n their eventual importance in the past (PECK; CLARKE, 2006). Knowledge about the influence of ocean currents on the distribution and diversity of these algae can help to predict the effects of climate change on these pristine and key ecosystems.

Understanding the relationship between crustose calcified algae and ocean currents, in addition to their phylogeny, is essential to understanding the dispersal and colonization of these species in subantarctic and Antarctic environments. Recent research has focused on the identification of species, their physiological and morphological characteristics, as well as their responses to environmental changes, such as rising temperatures and ocean acidification (MORROW *et al*., 2021).

2.1.1 **Geological History**

The origin and evolution of crustose calcified algae are still topics of study and research. It is believed that they evolved from filamentous ancestors, a diverse group of eukaryotic algae. During the evolutionary process, these algae developed biochemical and structural adaptations that allowed them to absorb dissolved calcium ions from the water and precipitate calcium carbonate to form the calcareous crusts (RINDI *et al*., 2011; STENECK *et al*., 2002).

These biochemical adaptations involve the production of enzymes and calcium transporters in the cells of crustose calcified algae. These mechanisms allow the selective uptake of calcium ions from the surrounding environment and their incorporation into the cells, where calcium carbonate synthesis occurs. It is believed that calcium carbonate synthesis occurs in special intracellular compartments called calcareous vacuoles, in which calcium carbonate precipitation occurs in a controlled manner (KAMENOS *et al*., 2013; RIES, 2011).

The formation of calcareous crusts provides several advantages for crustose calcified algae. They provide physical protection from predation and abrasion, as well as serving as anchoring to solid substrates. The crusts also provide a suitable surface for the colonization of other marine organisms, such as corals, sponges, bivalves, and other invertebrates. In this way, crustose calcified algae are important in the formation and stabilization of reefs and in the creation of diverse habitats in marine ecosystems (FOSTER; ADEY, 2004; JOHNSON; KÜBLER, 2010).

The evolution of crustose calcified algae is intrinsically linked to their interaction with the marine environment and with other organisms. Phylogenetic studies have revealed the existence of distinct lineages within this group, indicating the occurrence of speciation events over time (RINDI *et al*., 2011; STENECK *et al*., 2002). In addition, genetic analyses have provided insights into the molecular adaptations related to the synthesis and deposition of calcium carbonate in the cells of crustose calcified algae (RIES, 2011).

Crustose calcified algae have produced robust mechanisms for their existence and adaptation to the most diverse environments over time. Their history is fascinating, reflecting the climatic and environmental changes over geological time. These algae played an important role in the construction and stabilization of marine ecosystems (BOSENCE, 2005). During periods of great reef extension, such as the Devonian, Carboniferous, and Jurassic, these algae contributed to the formation of significant reef structures (KIESSLING *et al*., 2008; STANLEY, 2006). Fossils of crustose calcified algae from these periods, such as the genera Solenopora and Lithothamnion, are found in various parts of the world, evidencing their wide distribution and diversity (JAGT, 2000).

UNDERSTANDING EVOLUTIONARY AND BIOGEOGRAPHIC RELATIONSHIPS

Recent estimates indicate that our planet has around 7.8 million animal species, 298 thousand plants, 611 thousand fungi and 63,900 protists (Wiens 2023). Among the latter are algae, such as calcareous algae. These numbers give us an idea of the dimensions we have to face to improve our understanding of our biodiversity. Among these living beings we will find around 72,500 species of algae (Guiry 2021), and among them groups that are historically less known and valued, such as calcareous algae, despite their aforementioned importance. It is in this context that we find ourselves facing a climate and environmental crisis unprecedented in the history of humanity, with the growing need to popularize knowledge about the planet's biodiversity, allowing a growing number of people to understand the functioning of our ecosystems today, interpreting the factors that produced major transformations in the planet's evolutionary history (Nanglu et al. 2023). To achieve this, it is important to popularize groups and environments that have undergone and are undergoing major transformations. Threatened by the warming and acidification of the ocean, AC and Antarctic environments represent frontiers that our society needs to know from the point of view of the composition of biodiversity and their evolutionary history.

The genomics revolution and advances in molecular dating techniques and a set of growing databases, to generate times of divergence between populations and species from different locations, allow us today not only to document occurrences but also to witness major ecological transformations- evolutionary changes that our biodiversity has gone through. Tens of thousands of species have had their history dated, and new divergence time estimates are appearing in hundreds of publications each year. Taking advantage of this scenario, global syntheses were constructed that allow us to detail processes that occurred in our planet's past. It is this understanding of the multifactorial nature of the variables that determined the fate of our biodiversity, which will allow us to predict how human-produced changes to our environment will impact the distribution and composition of biodiversity in the future (Hedges et al. 2015). In this sense, databases with analysis tools, which are open to the public, such as TimeTree (https://timetree.org/) and the Paleobiology Database (https://paleobiodb.org/), are very important for popularization of the evolutionary history of our biodiversity. However, considering possible weaknesses or mistakes in the identification of fossil records, analyzes can be full of inaccuracies that lead to inconsistent interpretations about patterns, environmnetal drivers and processes.

Herein we evaluated web resources such as TimeTree and Paleobiology Database to reconstruct the evolutionary history of coralline red algae regarding their positive aspects and fragilities regarding the CA and Antarctica environmnet.

2.2 Materials and methods

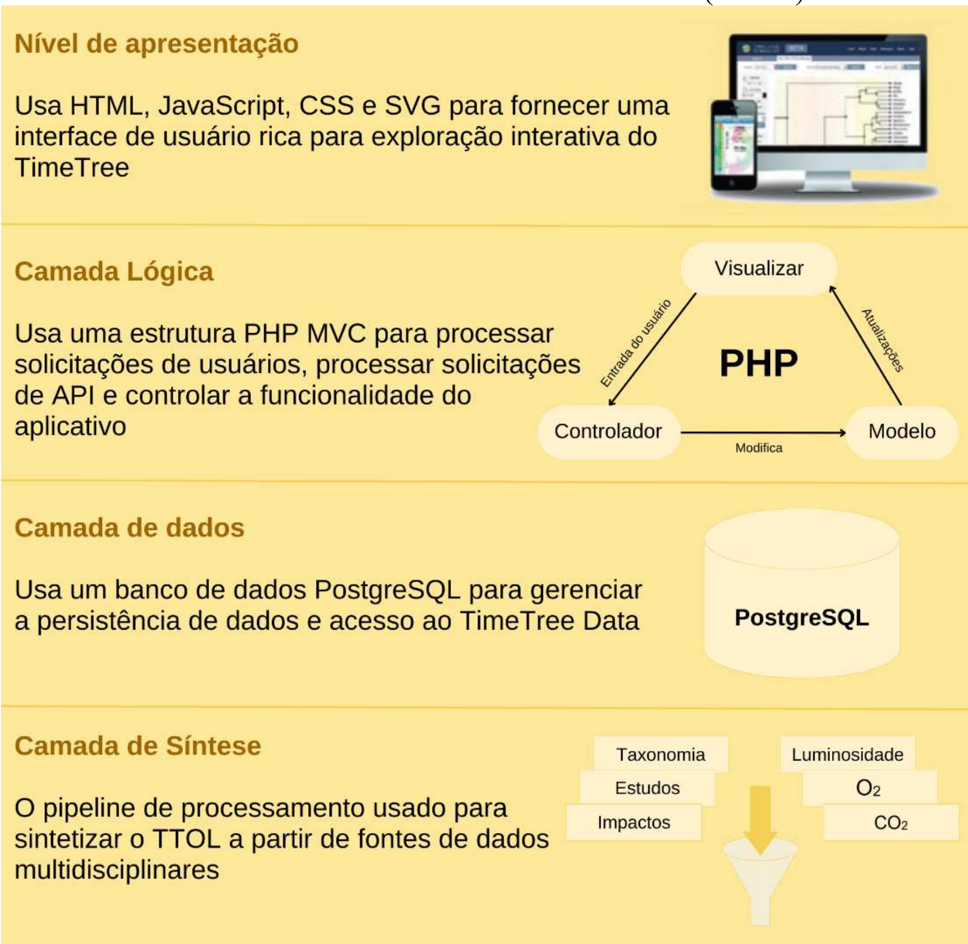
To visualize the diversification of crustose calcified algae over geological time and their distribution based on the theory of continental drift, the web resources TimeTree and Paleobiology Database were evaluated.

According to Kumar and collaborators (2017), the TimeTree resource has web-based multilayers (Figure 2.2) that includes a non-standardized computational database to store primary data in the form of phylogenetic trees scaled to the time required to compute and serve synthetic data with much greater information content. The new version of TimeTree has advanced significantly compared to the previous version released in Kumar and Hedges (2011).

To calculate divergence time, as described by the Timetree team, selecting two species or higher taxa are queried (e.g., Sporolithales and Corallinales) the TimeTree looks for these species in the TTOL to find their most recent common ancestor (MRCA). When one or both of the species are not present in TTOL, the NCBI taxonomy is scanned to find the closest relatives of the species or higher taxa requested by the user. Then, those taxa are used as proxies to find the MRCA for the given query. Finally, the divergence time for the MRCA is retrieved from the TimeTree database, where, in our case, the works of Aguirre et al. (2010) and Yang et al. (2016) were utilized.

Using the divergence time estimates for all taxa, stored in the TimeTree database, the evolutionary timeline shown was constructed by first locating the queried species (ie. Corallinales) or higher taxa in the TTOL and then traversing the tree toward the root, collecting divergence time estimates at each node in the tree.

Figure 2.2 – Schematization of the TimeTree. TimeTree of Life (TTOL).



Source: Translated and adapted (Kuma *et al*. 2017).

The Paleobiology Database (PBDB) is a public web-based database of paleontological data that provides information on the fossil record of life on Earth. The PBDB is a collaborative effort of scientists from around the world, and it contains information on over 1.5 million fossil specimens (Paleobiology Database, 2023).

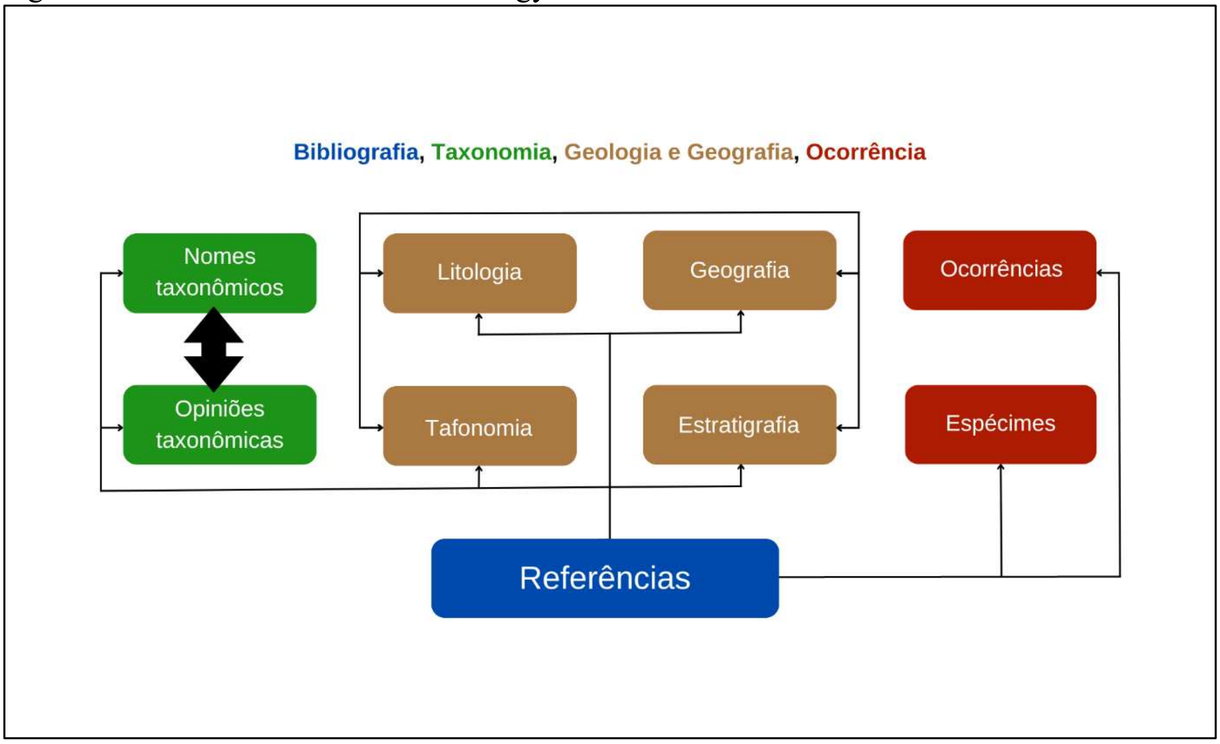
The main steps involved in the operation of the PBDB are as follows: Data is submitted to the PBDB by researchers. This data can include information on the taxonomy, morphology, and age of fossil specimens. The data is reviewed by a team of curators. These curators ensure that the data is accurate and meets the standards of the PBDB. The data is added to the PBDB database. The data is made available to the public through the PBDB website (Paleobiology Database, 2023).

The PBDB is a valuable resource for scientists studying the fossil record. The database provides a centralized location for information on fossil specimens, and it allows data to be shared and collaborated on for scientific research.

The flowchart (Figure 2.3) provides a simplified overview of the main steps involved in the operation of the PBDB. The specific steps involved in each of these stages may vary depending on the type of data submitted (Paleobiology Database, 2023). In addition to the steps presented in the flowchart, the PBDB also involves other activities, such as:

- Development of tools and resources to facilitate the use of the database;
- Promotion of the use of the database for educational and research purposes;
- Collection of new fossil data.

Figure 2.3 - Flowchart of the Paleobiology Database.



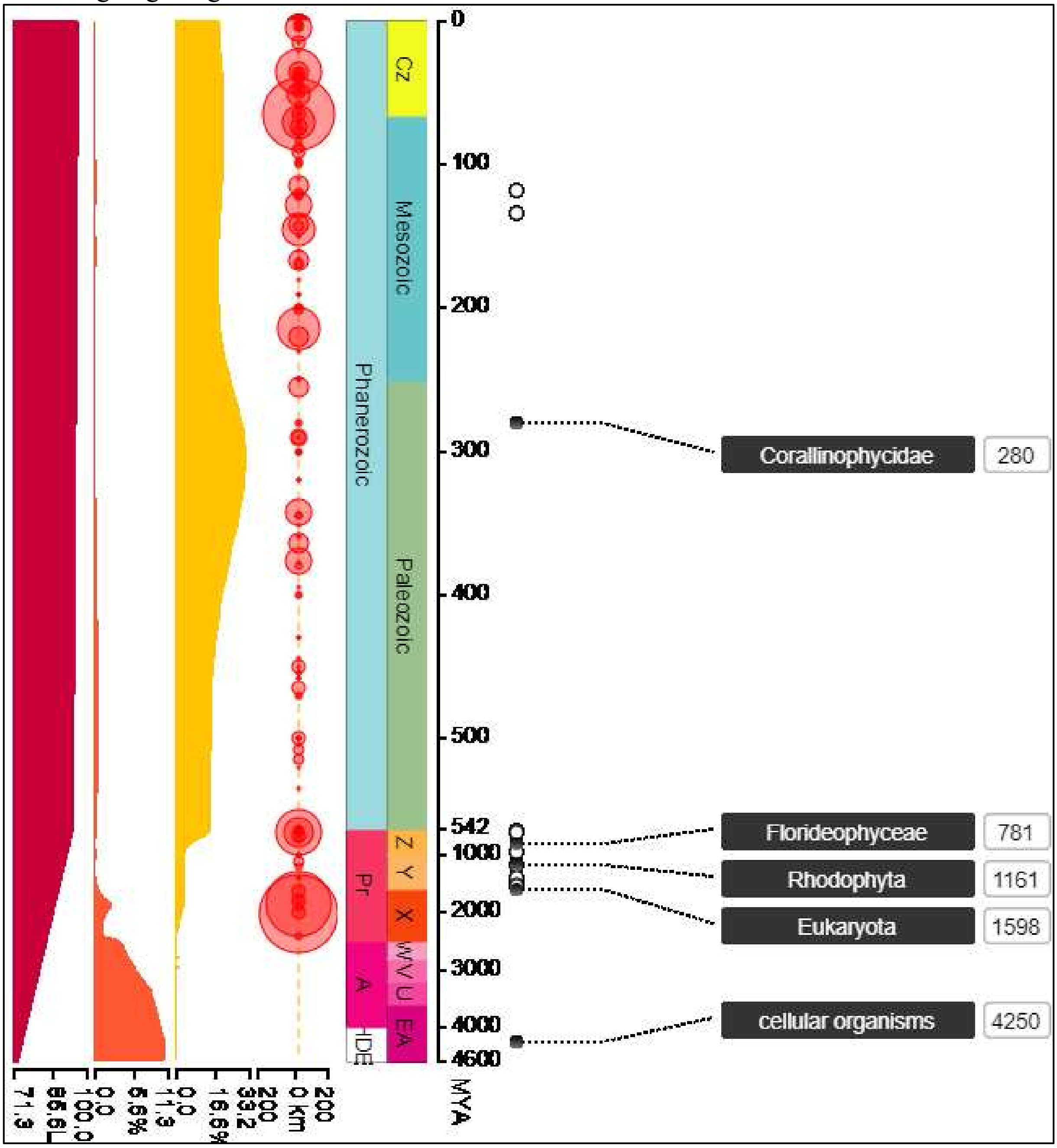
Source: Translated (Paleobiology Database, 2023).

2.3 Results and Dicussions

Combining the use of TimeTree and Paleobiology Data Base platforms, it was possible to obtain both phylogenetic trees and the distribution of Rhodophyta species in various geological periods and continent configuration, going futher the ingformations provided by the Timescale Creator Platform (Zehady et al. 2020). A timeline and a time tree each taxa are ilustrated by data regarding the geological timescale, impacts that the Earth has suffered over the years, solar luminosity, O_2 and CO_2 levels. However, despite the colorful layout, the absence of temperature information, paliocurrents and scarcity of fossil records from ancient periods represent the main limitations of these tools to interpret the environmental drivers that shaped the evolutiory history of coralline algae in the Antarctic region. Recent evidence points to strong correlations between the five mass extinction events and the global warming (Song et al. 2021), reinforcing the relevance of developing tools that facilitate the implementation of this eco-evolutionary driver (temperature) in relation to different regions and taxonomic groups.

Despite these limitations, it is importante to highlight the these tools make possible the observation of potential origin and diversification from phylum to orders through the time. The Rhodophyta node is estimated to be 1161.0 Ma old while Corallinophycidea, to be 280 Ma old. The graph produced identify suggest impacts of meteors occurred on Earth, such as the Santa Fe impact in New Mexico (1200 Ma) and the Amelia Creek impact in Australia (1120 Ma), which are approximately 13 and 20 km in diameter, respectively, that may have influenced evolution of life during that period. At these periods, O_2 levels are described as below 16% and CO_2 levels were between 0 and 5%, while solar irradiation was between 85 and 100 $L\odot$ (Figure 2.4). In the case of the class Florideophyceae, it is possible to observe that the node in the evolutionary tree is located at approximately 944 Ma, with a record of an impact on Earth of ~1000 Ma, the Isso-Naakkima impact, in Finland, with a diameter of 3.00 km.

Figure 2.4 – Graph created from the TimeTree resource of the estimated emergence of red algae according to geological time and terrestrial events.



As for the evolutionary tree, we can observe the division of the clades in order to differentiate the classes within the phylum, where the estimated time of the oldest organism of the class Florideophyceae is 944.8 Ma, still in the Proterozoic era. Oxygen levels were below 17% and carbon dioxide levels were declining, below 0.5%, and solar luminosity was between 90 and 95 $L \odot$ (Figure 2.5 and 2.6).

Figura 2.5 – TimeTree of the classes of the Rhodophyta phylum.

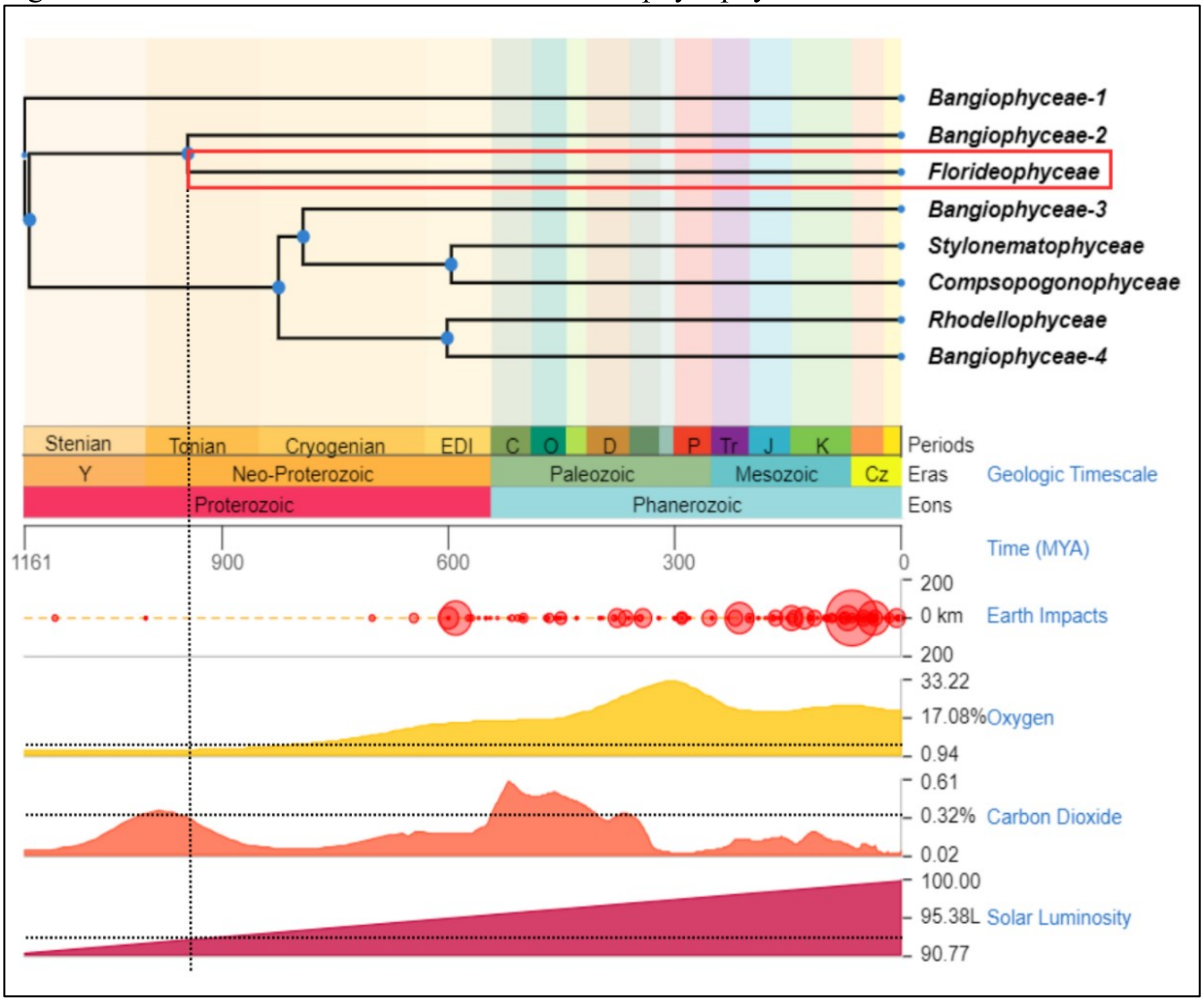
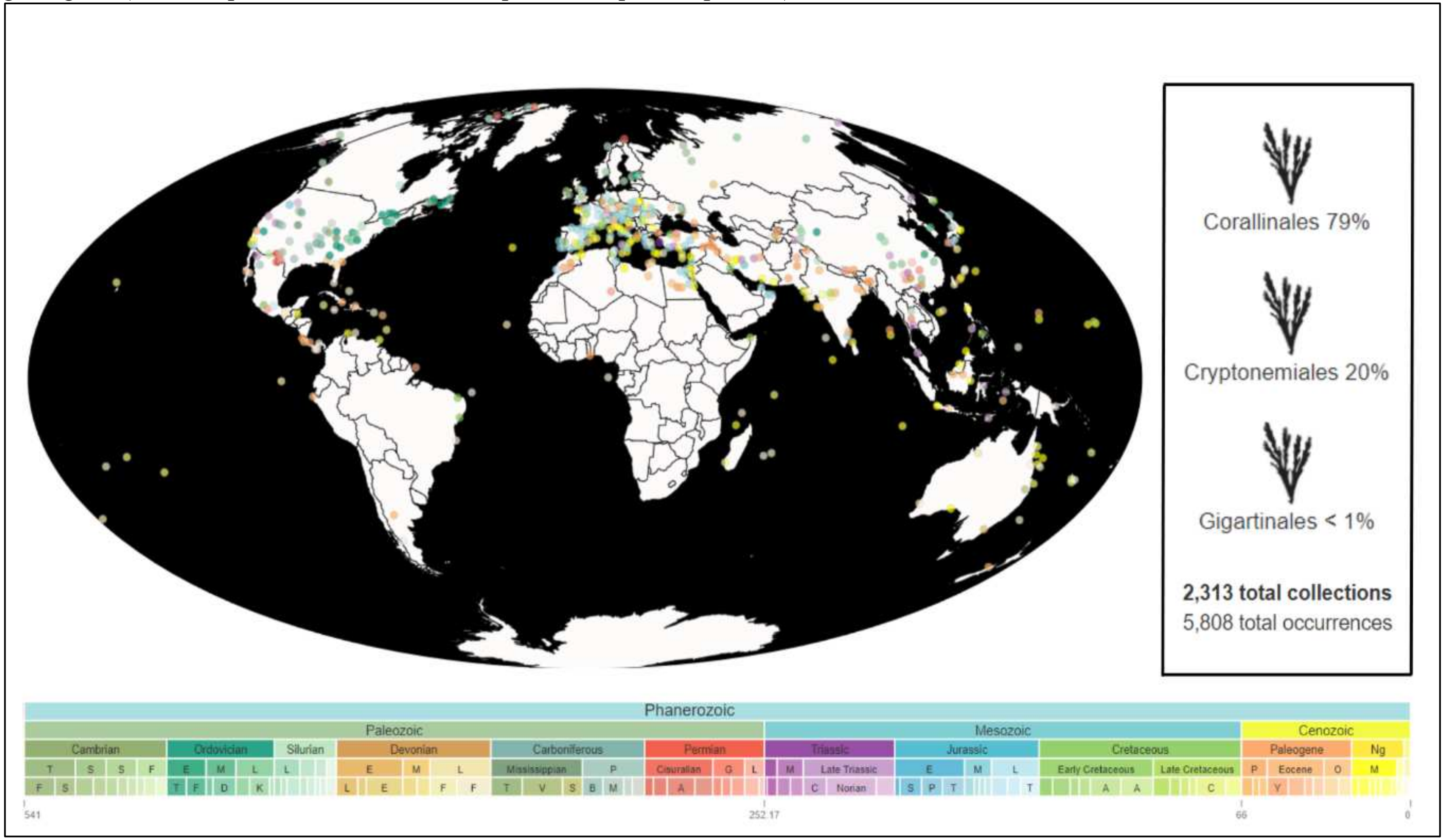
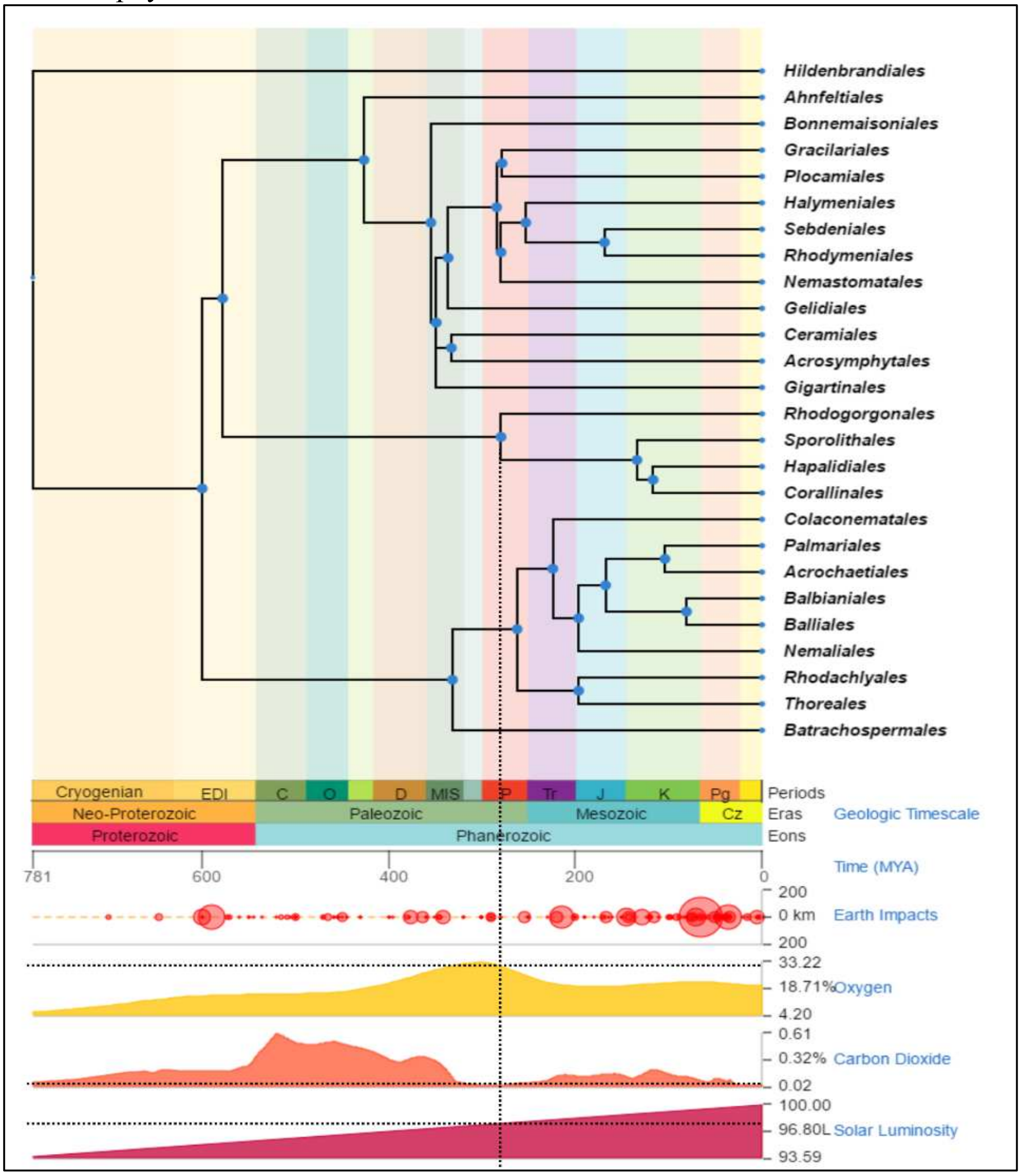


Figura 2.6 – Current coralline algae distribution (Florideophyceae, Rhodophyta) around the world and their fossil record according to each geological (Where: spots in different colors represent respective periods).



For the subclass Corallinophycedae and the diversification of orders of calcareous algae occurred around 133.8 Ma, of the class Florideophyceae, a phylogenetic tree with a geological time scale was obtained, where we can observe that its age is estimated at 280.2 Ma, with levels of approximately 33% O_2 and below 0.3% CO_2, and solar luminosity of ~97 $L\odot$ (Figure 2.7).

Figura 2.7 - TimeTree of the Rhodophyta orders, reinforcing the cluster of the Corallinophycedae.



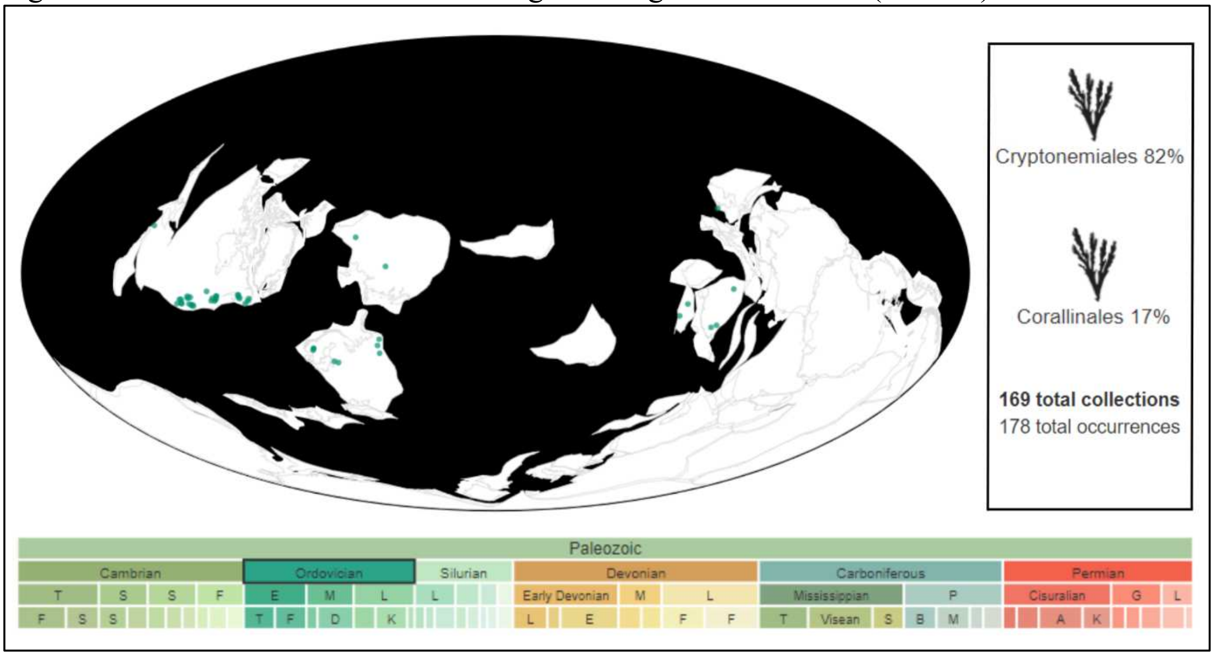
The results obtained by these web tools present a synthesis of the evolutionary and biographical process with moderate precision considering usual phylogenetic methods, taxa at different levels and results based on studies that used multiple molecular markers (PEÑA *et al*. 2020). The absence of significance of each node, as well as the potential variability of divergence time, simplifies the outline of the graph but impoverishes the presented scientific information (WILEY *et al*. 1991; BARIDO *et al*. 2020). Taking into consideration non-calcified records from the Precambrian as a stem group of coralline algae, Yang *et al*. (2016) estimated a much earlier divergence of the subclass Corallinophycidae around 579 Ma (95% HPD: 543–617) Ma. On the other hand, Aguirre et al. (2010) propose the divergence of this group 338 Maa ago, while Peña *et al*. (2020) estimate this process 179.88 Ma ago. However, all these studies agreed that the radiation of the taxon took place in the Lower Cretaceous, as observed in the Timetree analysis.

Although the phylogeny for the orders proposed by Timetree reinforces the monophyly of Corallinophycidae, reproducing the evolutionary relationships that have been observed in studies that focused on the aforementioned group (AGUIRRE *et al*. 2010; YANG *et al*. 2016; PEÑA *et al*. 2020), the phylogenetic analyzes considering the species showed divergences. Besides considering different taxa and an unnamed one (Corallinales sp. AC-2018d), this analysis presents the relationship of Rhodogorgonales with the monophyletic group represented by Sporolithales, Corallinales and Hapalidiales, as Yang *et al*. (2016), while Peña *et al*. (2020) suggest a monophyletic group composed of the orders Rhodogorgonales and Sporolitales, which would have diverged from the other Corallinophycidae 179 Ma ago. Taxonomic inconsistencies are observed, as is frequently illustrated in work dealing with this group, and the presence of the genus *Lithothamnion* in different groups can be cited as an example. These weaknesses may be related to the low knowledge of the taxonomy of the group, which has recently grown, revealing new genus (MIRANDA-COUTINHO *et al*. 2022; GABRIELSON *et al*. 2023) or even orders (JEONG *et al*. 2021), which were previously considered to represent the aforementioned taxon.

Regarding these tools as communication allies, from the graphs and phylogenetic trees obtained from web resources, it is possible to identify some events that occurred on Earth that contributed to mass extinctions, to adaptations and diversification of others. For Exemplo, During the Paleozoic era, from approximately 540 to 250 million years ago, calcareous algae were already present in the oceans (Figure 2.8). The Ordovician period was the period with the most marine changes, with the extension of epicontinental seas, flattened marine bottoms, and reduced land spaces, often represented by the formation of archipelagos, due to the high magmatic and tectonic activity that served as sources of clastic and carbonate sediments. The biogeographical changes that occurred during this period were decisive for speciation, mainly in the southern hemisphere, as they directly affected planktonic, nektonic, and benthic organisms, as well as climatic zoning (HARPER, 2006).

Fossils of crustose calcareous algae from this period are found in sedimentary deposits, revealing the presence of communities of crustose calcareous algae in ancient reefs. These reefs were composed primarily of sponges, corals, brachiopods, and other marine calcifying and non-calcifying organisms (STANLEY, 2016).

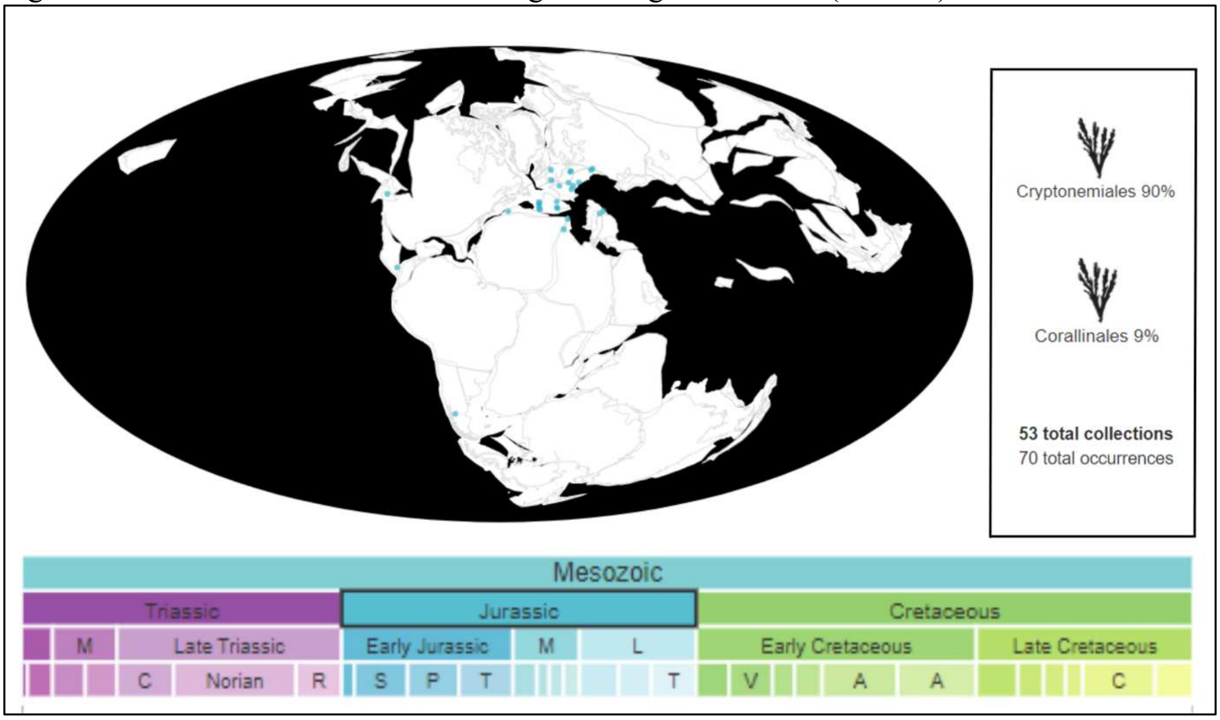
Figure 2.8 – Distribution of calcareous algae during the Ordovician (464 Ma).



Source: Map of the distribution of calcareous algae during the Ordovician (464 Ma). 2023. Paleobiology Database, https://paleobiodb.org/.

During the Mesozoic era, between 250 and 65 million years ago, important climatic and geological changes occurred that affected calcareous crustose algae. During the Jurassic, for example, these algae contributed to the formation of reefs in shallow and tropical environments (Figure 2.9). Fossils of Jurassic calcareous crustose algae (173 Ma) are found in different regions of the world, including Europe, North America, and Asia (JAGT, 2000).

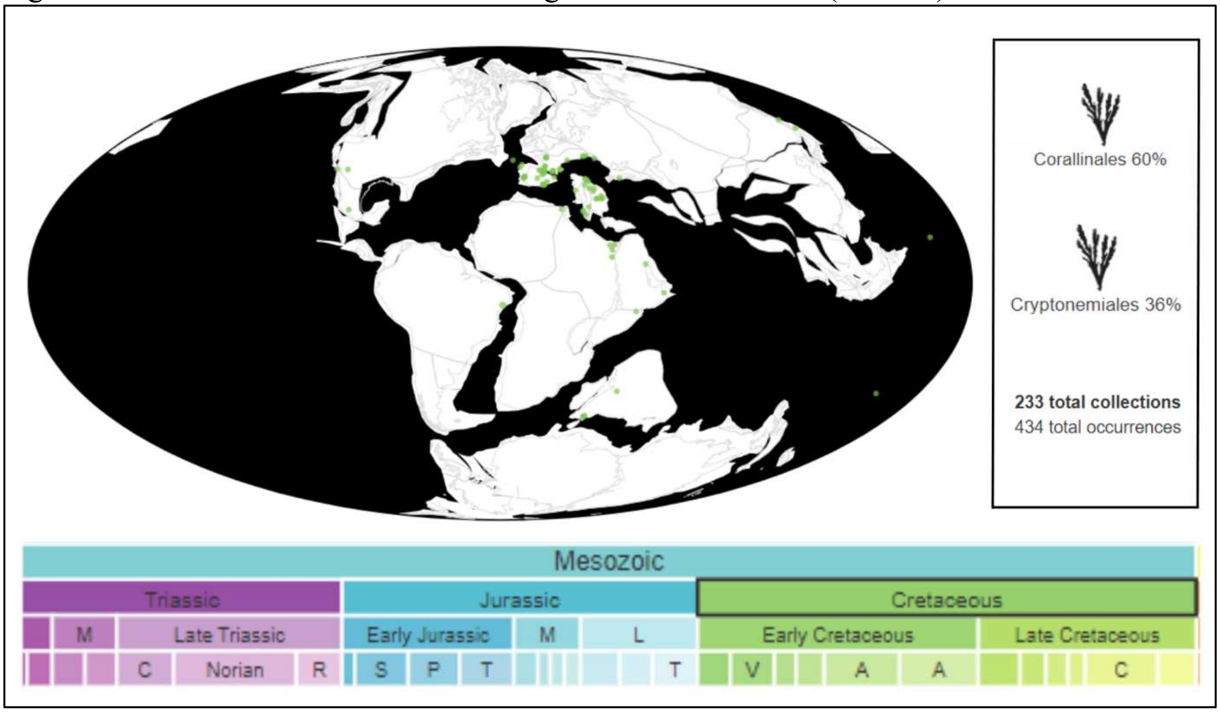
Figure 2.9 – Distribution of calcareous algae during the Jurassic (173 Ma).



Source: Map of the distribution of calcareous algae during the Jurassic (173 Ma) considering the available fossil record up to 2023. Paleobiology Database, https://paleobiodb.org/.

However, the Cretaceous period witnessed a significant change in oceanic conditions and marine ecosystems. During the Upper Cretaceous (122 Ma), elevated atmospheric carbon dioxide levels and ocean acidification negatively affected these algae, reducing their calcification ability and leading to a decrease in diversity and abundance (KAMENOS *et al*., 2008; STANLEY, 2016). Consequently, there was a decline in reef formation due to these changes in ocean chemistry, increased temperature, and mass extinction events (Figure 2.10). This decline allowed other reef builders, such as scleractinian corals, to assume a dominant role (JOHNSON; KÜBLER, 2010).

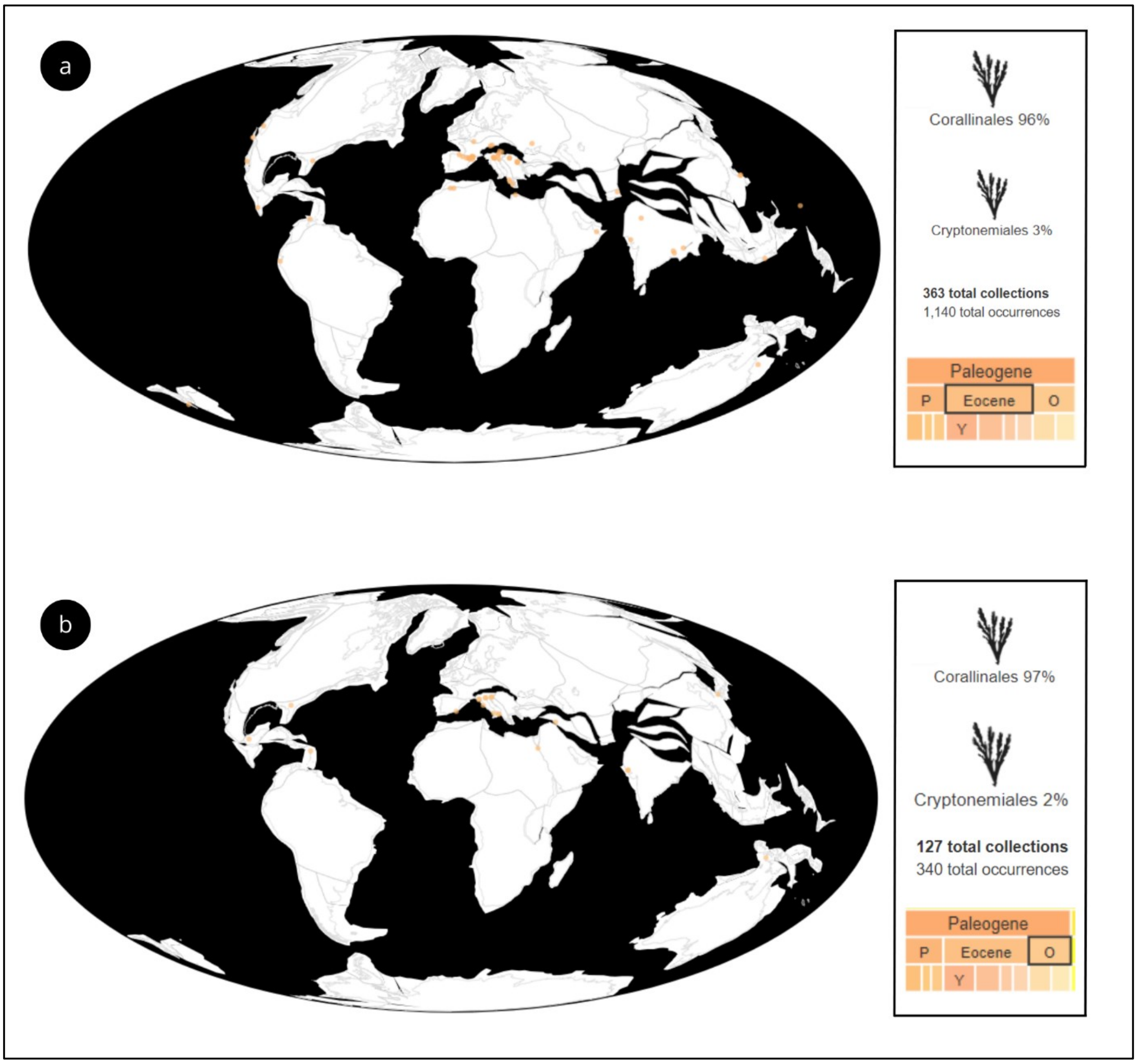
Figure 2.10 – Distribution of calcareous algae in the Cretaceous (105 Ma).



Source: Map of the distribution of calcareous algae in the Cretaceous (105 Ma). 2023. Paleobiology Database, https://paleobiodb.org/.

Throughout the Cenozoic, which spans the last 65 million years, significant changes have occurred in climate patterns and the distribution of marine ecosystems. For example, this period observed the formation of the embayment between the southern Atlantic and the coast of primitive Antarctica was observed. During the Eocene (44 Ma) and Oligocene (28 Ma), there was a resurgence of calcareous crustose algae communities in shallow-water environments (Figure 2.11). These calcareous crustose algae reefs coexisted with other reef builders, such as corals and molluscs (JOHNSON; KÜBLER, 2010). The presence of Corallinophycidea fossils in this region and period reinforces the importance of the group to help us in the interpretation of this period and processes.

Figura 2.11 – (a) Distribution of calcareous algae in the Eocene (44 Ma); (b) Distribution of calcareous algae in the Oligocene (28 Ma).



Source: Map of the distribution of calcareous algae in the Eocene (44 Ma) e Oligocene (28 Ma). 2023. Paleobiology Database, https://paleobiodb.org/.

However, during the Miocene and Pliocene, there was a gradual decline in calcareous crustose algae communities due to competition with other marine organisms and changes in environmental conditions, including sea level fluctuations and global cooling. The diversity and abundance of calcareous crustose algae were reduced, leading to a transition to communities dominated by corals and other life forms (KIESSLING *et al*., 2008).

Throughout the Pleistocene and up to the present day, they are experiencing a diversificiation process calcareous crustose algae are still present in a variety of marine habitats, although their di, colonizing diferente ecosytems and environmental conditions. However, marine pollution (Bjork et al. 1995), climate change and ocean acidification represent threats for these algae, as they can affect their calcifying ability and long-term survival (KAMENOS *et al*., 2013; 2017). Despite the evaluated tools limitations, to avoid the consolidation of the 6th extintion mass event (Davis 2023), to reduce green house emission and marine polution, as well as to develop more comprehensive protection actions to ensure conservation of CA and their environments are urgente (Costa et al. 2023).

2.4 Conclusion

The web resources used in this work, TimeTree and Paleobiology Database, are tools that can be used in phylogenetic research on various taxa, including crustose calcareous algae. During the work, these presented themselves as an alternative, since for many works and projects that involve phylogenetics, but which have low financial resources, it is often unfeasible to carry out field and laboratory work, which in turn involves from the travel to the study area of interest, collection of biotic data, up to DNA extraction, DNA sequencing and use of software for phylogenetic analysis.

However, during the use of these resources it was possible to identify some problems that require attention. One of them is that when building the phylogenetic tree, the TimeTree web resource does not present the percentage of consistency of the clades, this information being of great importance to develop the discussion of how close the taxa are or are not phylogenetically. Furthermore, the web resource Paleobiology Database presents deficiencies in its database, in the target group of this study, and this element needs to be considered on a case-by-case basis when selecting the tool for evaluating historical-evolutionary processes in specific locations. The absence of records of fossil species of crotate calcareous algae limited the analysis and discussions of the processes of climatic and environmental transformation, observed during the last geological periods, on the target group of the present study.

Therefore, it is possible to observe that these web resources are often not used in scientific research because they present these and other difficulties. But it is worth highlighting the importance of sharing scientific data in public databases, so that resources like these are more effective in their purpose of facilitating the understanding of the history of the evolution of life on the planet. These web resources need to be encouraged, as well as collaboration between researchers, making the database even richer and more reliable, enabling science, teaching and research to become increasingly accessible and socioeconomically fair.

3 CONCLUSÃO GERAL

Os avanços na ciência têm nos ajudado de inúmeras maneiras, incluindo a compreensão da nossa própria história e a evolução do planeta e da biodiversidade para que possamos melhorar nossa capacidade de previsão dos desafios que estão por vir. Conciliar a ciência e as tecnologias para isso é um ponto chave para aprender cada vez mais sobre como e quando ocorreram as grandes transformações do planeta elevando a atenção da sociedade para o desenvolvimento de arranjos necessários para termos maior resiliência socioambiental.

Os recursos web utilizados neste trabalho, *TimeTree* e *Paleobiology Database*, são ferramentas que podem ser utilizadas em pesquisas filogenéticas de diversos táxons, incluindo o das algas calcárias crostosas. Durante o trabalho estes apresentaram-se como uma alterantiva, visto que para muitos trabalhos e projetos que envolvam filogenética, mas que detém baixo recurso financeiro, fica muitas vezes inviável de desenvolver os trabalhos de campo e laboratório, o que por sua vez envolve desde o deslocamento a área de estudo de interesse, coleta dos dados bióticos, até a extração de DNA, sequenciamento do DNA e utilização de *softwares* para análises filogenéticas.

No entanto, durante a utilização destes recursos foi possível identificar alguns problemas que necessitam de atenção. Um deles é que ao construir a árvore filogenética o recurso web *TimeTree* não apresenta a porcentagem de consistência dos clados, sendo esta informação de grande importância para desenvolver a discussão do quão os táxons estão ou não próximos filogeneticamente. Além disso, o recurso web *Paleobiology Database* apresenta carências em seu banco de dados, do grupo alvo deste estudo, e este elemento precisa ser considerado caso a caso na seleção da ferramenta para avaliação e processos histórico-evolutivos em locais específicos. A ausência de registros de espécies fósseis de algas calcárias crotosas limitou a análise e as discussões dos processos de transformação climática e ambiental, observados durante os últimos períodos geológicos, sobre o grupo alvo do presente estudo.

Com isso, é possível observar que muitas vezes esses recursos web não são utilizados em pesquisas científicas por apresentarem essas e outras dificuldades. Mas vale ressaltar a importância do compartilhamento de dados científicos em bancos de dados públicos, para que recursos como estes sejam mais efetivos em seus propósitos de facilitar o entendimento da história da evolução da vida no planeta. Estes recursos web precisam ser fomentados assim como a colaboração entre pesquisadores e pesquisadoras, tornando os bancos de dados ainda mais ricos e confiáveis, e possibilitando que a ciência, o ensino e a pesquisa se tornem cada vez mais acessíveis.

REFERÊNCIAS

Adey, W. H., (1986). **Coralline algae as indicators of sea-level**. In Plassche, O. van de (ed.), Sea-Level Research: A Manual for the Collection and Evaluation of Data. Norwich: Geo Books, pp. 229−279.

Aguirre, J., Perfectti, F., & Braga, J. C. (2010). **Integrating phylogeny, molecular clocks, and the fossil record in the evolution of coralline algae (Corallinales and Sporolithales, Rhodophyta)**. Paleobiology, 36(4), 519-533.

Al-Handal, A. Y., Wulff, A., & Zainal, A. A. (2008). **Marine epiphytic diatoms from the shallow sublittoral zone in the Straits of Malacca**. In: The 10th International Marine Biological Workshop, The Marine Flora and Fauna of Hong Kong and Southern China. Hong Kong University Press, Hong Kong, 165-190.

Amancio, C. E. (2007). **Precipitação de CaCO3 em algas marinhas calcárias e balanço de CO2 atmosférico: os depósitos calcários marinhos podem atuar como reservas planetárias de carbono?** Instituto de Biociências, Universidade de São Paulo (USP). Dissertação de Mestrado.

Bartsch, I., Vogt, J., Pörtner, H. O., & Fredersdorf, J. (2013). **The potential of seaweeds as a source of antioxidants and other bioactive compounds for human nutrition**. Marine Drugs, 11(8), 2442-2471.

Basso, D., Boschian, G., Mietto, P., Russo, F., & Furia, S. (2015). **Coralline algae provide clues to shallow-water sedimentation dynamics: Evidence from the Triassic of the Dolomites (Italy)**. Geology, 43(4), 307-310.

Bellinger, Edward G., and David C. (2015). **Sigee. Freshwater algae: identification, enumeration and use as bioindicators**. John Wiley & Sons.

Bischof, K., Peralta, G., Kräbs, G., Van de Poll, W., & Pérez-Llorens, J. L. (1998). **Effects of solar ultraviolet radiation on canopy structure of Ulva communities from southern Spain**. Marine Ecology Progress Series, 162, 139-150.

Bjork, M., Mohammed, S. M., Bjorklund, M., & Semesi, A. (1995). **Coralline algae, important coral-reef builders threatened by pollution**. Ambio, 24(7-8), 502-505.

Bosence D.W. (1976). **Ecological studies on two unattached coralline algae from western Ireland**. Palaeontology, 19: 365-395.

Bosence, D. W. (2005). **A genetic classification of carbonate platforms based on their basinal and tectonic settings in the Cenozoic**. Sedimentary Geology, Volume 175, Issues 1–4, Pages 49-72, ISSN 0037-0738.

Braga, J. C. (2011). Fossil coralline algae. In Encyclopedia of Modern Coral Reefs: Structure, Form and Process (pp. 423-427). Springer.

Braga, J. C., Bassi, D., & Piller, W. E. (2012). Palaeoenvironmental significance of Oligocene–Miocene coralline red algae–a review. Carbonate Systems during the Oligocene–Miocene Climatic Transition, 165-182.

Brodie, J., Maggs, C. A., & John, D. M. (2007). **Green seaweeds of Britain and Ireland**. British Phycological Society.

Broom, J. E., Farr, T. J., & Nelson, W. A. (2017). **Algal Systematics in the 21st Century**. University of Adelaide Press.

Broom, J. E., Hart, D. R., Farr, T. J., Nelson, W. A., Neill, K. F., Harvey, A. S., & Woelkerling, W. J. (2008). **Utility of psbA and nSSU for phylogenetic reconstruction in the Corallinales based on New Zealand taxa**. Molecular phylogenetics and evolution, 46(3), 958-973.

Costa, D. D. A., Dolbeth, M., Christoffersen, M. L., Zúñiga-Upegui, P. T., Venâncio, M., & de Lucena, R. F. P. (2023). **An Overview of Rhodoliths: Ecological Importance and Conservation Emergency**. Life, 13(7), 1556.

Cattaneo-Vietti, R., Chiantore, M., & Gambi, M. C. (2000). **The influence of subtidal habitat complexity on the structure of a marine epibenthic community**. Marine Ecology Progress Series, 198, 149-159.

Davis, W. J. (2023). **Mass extinctions and their relationship with atmospheric carbon dioxide concentration: Implications for Earth's future**. Earth's Future, 11(6), e2022EF003336.

Duffy, G. A., Smale, D. A., & Hamon, K. G. (2021). **Surface currents and eddies around the sub-Antarctic islands: a review of observations and implications for ecology**. Marine Biology, 168(2), 1-20.

Falkowski, P. G., Lin, H., & Gorbunov, M. Y. (2019). **What limits photosynthetic energy conversion efficiency in nature? Lessons from the oceans**. Philosophical Transactions of the Royal Society B: Biological Sciences, 374(1781), 20160372.

Foster, M. S., & Adey, W. H. (2004). **The role of calcium carbonate in the physiology of coralline algae and other marine calcifiers**. In Calcium carbonate in algae and terrestrial plants (pp. 1-46). Springer, Dordrecht.

Geraldino, P. J., Yang, E. C., Boo, S. M., Le Gall, L., & Fredericq, S. (2019). **Barcoding analysis of selected Gigartinales (Rhodophyta) in the Philippines reveals high diversity and complex evolutionary history**. Phycologia, 58(6), 617-629.

Gómez, I., Huovinen, P., & Karsten, U. (2017). **Seaweeds of the Southern Ocean**. Springer.

Graham L. E., Graham J. M., and Wilcox, L. W. (2009). **Algae, 2nd edn**. San Francisco: Pearson Benjamin Cummings.

Guiry, M. D. (2012). **How many species of algae are there?.** Journal of phycology, 48(5), 1057-1063.
Hawes, I., Wood, S. A., Jungblut, A. D., Ellis-Evans, J. C., Edwards, R., Obryk, M. K., ... & Villasante, S. (2020). **Antarctic freshwater ecosystems: extreme in conditions, not biodiversity**. Polar Biology, 43(8), 1095-1112.

Hernández-Kantún, J. J., Riosmena-Rodríguez, R., & Adey, W. H. (2017**). Effects of oceanographic processes and environment on the distribution of rhodolith-forming species in the Gulf of California, Mexico**. Journal of Phycology, 53(4), 790-800.

Hurd, C. L., Harrison, P. J., Bischof, K., Lobban, C. S., & Raven, J. A. (2014). **Seaweed Ecology and Physiology**. Cambridge University Press.

Hofmann, L. C., Schoenrock, K., & De Beer, D. (2018). Arctic coralline algae elevate surface pH and carbonate in the dark. Frontiers in plant science, 9, 1416.

Horta, P., Pinho, P. F., Gouvêa, L., Grimaldi, G., Destri, G., Mueller, C. M., ... & Cotrim da Cunha, L. (2020). Climate Change and Brazil's coastal zone: socio-environmental vulnerabilities and action strategies. Sustainability in Debate/Sustentabilidade em Debate, (3).

Jagt, J. W. (2000). **Late Jurassic and Early Cretaceous calcareous algae from south-eastern Limburg** (Maastricht).

Johnsen, G., Leu, E., & Gradinger, R. (2020). **Marine micro-and macroalgae in the polar night**. Polar night marine ecology: life and light in the dead of night, 67-112.

Johnson, L. E., & Kübler, J. E. (2010). **Patterns and processes of population fragmentation in subtidal marine algae**. In Marine hard bottom communities (pp. 269-302). Springer, Berlin, Heidelberg.

Kamenos, N. A., Burdett, H. L., & Darrenougue, N. (2017). **Coralline algae as recorders of past climatic and environmental conditions**. Rhodolith/Maërl Beds: A Global Perspective, 27-53.

Kamenos, N. A., Burdett, H. L., Aloisio, E., Findlay, H. S., Martin, S., Longbone, C., ... & Calosi, P. (2013). **Coralline algal structure is more sensitive to rate, rather than the magnitude, of ocean acidification.** Global Change Biology, 19(12), 3621-3628.

Kangwe, J.W. (2005). **Calcareous Algae of a Tropical Lagoon: Primary Productivity, Calcification and Carbonate Production**.

Kiessling, W., Flügel, E., e& Golonka, J. (2008). **Patterns of Phanerozoic reef crises. In Phanerozoic reef patterns** (pp. 709-755). SEPM Society for Sedimentary Geology.

Kühl, M., Holzinger, A., Lütz, C., & Karsten, U. (2015). **Ecophysiology, secondary pigments and ultrastructure of Chondrus crispus from arctic, temperate and tropical waters**. Botanica Marina, 58(2), 121-130.

Kumar, S., Suleski, M., Craig, J.E., Kasprowicz, A.E., Sanderford, M., Li, M., Stecher, G. e Hedges, S.B. (2022). **TimeTree 5: An Expanded Resource for Species Divergence Times**. Molecular Biology and Evolution, DOI: 10.1093/molbev/msac174.

Le Gall, L., and Saunders, G.W. (2007). **A nuclear phylogeny of the Florideophyceae (Rhodophyta) inferred from combined EF2, small subunit and large subunit ribosomal DNA: establishing the new red subalgal class Corallinophycidae**. Mol. Phylogenet. Evol., 43, pp. 118-1130, 10.1016/j.ympev.2006.11.012.

Le Gall, L., Saunders, G. W., & Maggs, C. A. (2015). Assigning morphological variants of Fucus (Fucales, Phaeophyceae) in the British Isles to recognized species using DNA barcoding and phenetic analysis. Journal of Phycology, 51(2), 313-332.

Leliaert, F., Tronholm, A., Lemieux, C., Turmel, M., DePriest, M. S., Bhattacharya, D., & Karol, K. G. (2016). Chloroplast phylogenomic analyses reveal the deepest-branching lineage of the Chlorophyta, Palmophyllophyceae class. nov. Scientific Reports, 6(1), 1-13.

Lenton, T. M. (2023). **Climate change and tipping points in historical collapse.** In How Worlds Collapse (pp. 261-281). Routledge.

Lin, S. M., Fredericq, S., & Hommersand, M. H. (2011). Molecular phylogeny and developmental studies of Apoglossum and Pseudoblastodinium (Corallinales, Rhodophyta) with a description of Apoglossum bhimasankarami sp. nov. from the Andaman Sea. Journal of Phycology, 47(6), 1399-1415.

Lin, S. M., Fredericq, S., & Hommersand, M. H. (2015). A phylogenetic reassessment of family Dumontiaceae (Gigartinales) based on psbA sequences and morphological evidence. Journal of Phycology, 51(2), 265-277.

Lin, S. M., Rodriguez-Prieto, C., Huisman, J. M., & Guiry, M. D. (2017). Proposal to reject the name Cryptonemiales (Rhodophyta). Taxon, 66(2), 468-470.

Lin, S. M., Rodriguez-Prieto, C., Huisman, J. M., & Guiry, M. D. (2017). Proposal to reject the name Cryptonemiales (Rhodophyta). Taxon, 66(2), 468-470.

Morrow, C., Jackson, C., Macaya, E., Le Gall, L., & Miller, K. A. (2021). Antarctic marine macroalgae: an ecophysiological overview. In Polar Marine Macroalgae (pp. 15-42). Springer.

Nagao, R. T., Trench, R. K., & Bird, C. J. (2009). Localization of the host-plant's (Porphyra yezoensis) 18S rDNA gene in cystocarpic and vegetative plants of the red algal parasite, Pythium porphyrae, by in situ hybridization. Journal of Applied Phycology, 21(5), 617-624.

Nanglu, K., de Carle, D., Cullen, T. M., Anderson, E. B., Arif, S., Castañeda, R. A., ... & Astudillo-Clavijo, V. (2023). **The nature of science: The fundamental role of natural history in ecology, evolution, conservation, and education**. Ecology and Evolution, 13(10), e10621.

Oliver, M. J., González-Rizzo, S., Fernández, C., Martín-García, R., & Viejo, R. M. (2018). Assessing the ecological role of kelp rafting communities in the planktonic realm: a perspective view for future research. Estuarine, Coastal and Shelf Science, 201, 215-225.

Paleobiology Database (2023). The Paleobiology Database. Checklist dataset https://doi.org/10.15468/zzoyxi accessed via GBIF.org on 2023-09-26.

Peña, V.; Bárbara, I. (2008a). Maerl community in the north-western Iberian peninsula: a review of floristic studies and long-term changes. Aquat Conserv Mar Freshw Ecosyst 18:339–366.

Peña, V., Vieira, C., Braga, J. C., Aguirre, J., Rösler, A., Baele, G., ... & Le Gall, L. (2020). Radiation of the coralline red algae (Corallinophycidae, Rhodophyta) crown group as inferred from a multilocus time-calibrated phylogeny. Molecular phylogenetics and evolution, 150, 106845.

Pereira, L., Carvalho, C., Bárbara, I., Cruces, E., & Gulbransen, D. (2020). The Role of Red Algae in Ocean Acidification Studies: Perspectives and Potential Solutions. In Oceanography and Marine Biology: An Annual Review (Vol. 58, pp. 159-187). CRC Press.

Pereira, L., Guilherme, A., Carvalho, C., & Domingues, V. (2019). Macroalgae from Antarctica: A comprehensive review on their ecological attributes and potential biotechnological applications. Marine Environmental Research, 147, 59-75.

Pörtner, H. O., Scholes, R. J., Arneth, A., Barnes, D. K. A., Burrows, M. T., Diamond, S. E., & Val, A. L. (2023). Overcoming the coupled climate and biodiversity crises and their societal impacts. Science, 380(6642), eabl4881.

Ries, J. B. (2011). A physicochemical framework for interpreting the biological calcification response to CO2-induced ocean acidification. Geochimica et Cosmochimica Acta, 75(14), 4053-4064.

Rindi, F., Guiry, M. D., & Cinelli, F. (2011). Molecular biodiversity, ecology, and evolution of marine macroalgae. In Evolutionary biology—concepts, biodiversity, macroevolution and genome evolution (pp. 235-266). Springer, Berlin, Heidelberg.

Riosmena-Rodríguez, R., Woo, J. H., & Boo, S. M. (2014). Ecological and physiological differences between two sublittoral Chondrus species (Gigartinales, Rhodophyta) from the northern Pacific. Phycologia, 53(5), 473-480.

Santelices, B., Ramírez, M. E., & Stierhof, H. (2018). Tides, winds and propagule availability as drivers of the distribution of seaweeds on the coasts of Chile. Diversity and Distributions, 24(9), 1229-1244.

Saunders, G. W., & McDevit, D. C. (2012). Methods for DNA barcoding photosynthetic protists emphasizing the macroalgae and diatoms. In Molecular methods for the study of marine biodiversity (pp. 207-222). Springer.

Saunders, G. W., Millar, K. R., & McDevit, D. C. (2019). DNA barcoding of Canadian Ahnfeltiales (Rhodophyta) reveals a new species—Ahfeldtia borealis sp. nov. Botany, 97(6), 391-406.

Sherwood, A. R., Kurihara, A., & Conklin, K. Y. (2008). A molecular method for identification of the morphologically plastic invasive algal genera Eucheuma and Kappaphycus (Rhodophyta, Gigartinales) in Hawaii. Journal of Applied Phycology, 20(6), 713-719.

Stamatakis, A. (2014) RAxML Version 8: A tool for Phylogenetic Analysis and Post-Analysis of Large Phylogenies. Bioinformatics 10.1093/bioinformatics/btu033 http://bioinformatics.oxfordjournals.org/content/early/2014/01/21/bioinformatics.btu033.abstract

Stanley, G. D. (2006). Introduction to the evolution of Paleozoic and Mesozoic reef ecosystems. Paleontological Society Papers, 12, 3-9.

Steneck, R. S., Dethier, M. N., & Vavrinec, J. (2002). A functional group approach to the structure of algal-dominated communities. Oikos, 97(3), 386-397.

Teixeira, V. L., Cassano, E. N., & Pereira, C. M. (2016). Algal communities from the South Shetland Islands, Antarctica: biomass and species composition. Botanica Marina, 59(1), 21-33.

Van Den Hoek, C., Mann, D. G., Jahns, H. M. (1995). Algae. An Introduction to phycology. University Press, Cambridge 1995. ISBN 0-521-31687-1. 623 PP., GBP 24.95.

Verbruggen, H., Maggs, C. A., Saunders, G. W., Le Gall, L., & Yoon, H. S. (2009). Data mining approach identifies research priorities and data requirements for resolving the red algal tree of life. BMC Evolutionary Biology, 9(1), 105.

Verbruggen, H., Maggs, C. A., Saunders, G. W., Le Gall, L., & Yoon, H. S. (2010). Redefining the major clades of Ceramiales (Rhodophyta) based on phylogenetic analyses of nuclear ribosomal DNA sequences. Journal of Phycology, 46(6), 1272-1284.

W.A. Nelson, J.E. Sutherland, T.J. Farr, D.R. Hart, K.F. Neill, H.J. Kim, H.S. Yoon. (2015). Multigene phylogenetic analyses of New Zealand coralline algae: Corallinapetra novaezelandiae gen. et sp. nov. and recognition of the Hapalidiales ord. nov J. Phycol., 51, pp. 454-468, 10.1111/jpy.12288

Wang, W., Sun, X., Li, J., Xu, J., Rong, J., & Liao, L. (2020). Transcriptome analysis reveals the adaptive responses of Pyropia haitanensis to high temperature stress. BMC Genomics, 21(1), 1-14.

Wiencke, C., Amsler, C. D., Clayton, M. N., & Schloss, I. R. (2019). The biology of polar benthic algae. In: The Biology of Polar Regions (pp. 187-218). Oxford University Press.

Wiencke, C., Clayton, M. N., & Gómez, I. (2007). Life strategies, ecophysiology, and photosynthetic performance of Antarctic macroalgae. In: Seaweed Biology (pp. 289-328). Springer.

Wiens, J. J. (2023). **How many species are there on Earth? Progress and problems.** PLoS biology, 21(11), e3002388.

Woelkerling, Wm. J. (1993). Type collections of Corallinales (Rhodophyta) in the Foslie Herbarium (TRH). Curweria 67, 1-289.

Wray, J. L. (1977). Chapter 2: Skeletal Calcareous Algae. Developments in Palaeontotoly and Stratigraph, volume 4 Pág. 13-31.

Wray, J. L. (1977). Chapter 2: Skeletal Calcareous Algae. Developments in Palaeontotoly and Stratigraph, volume 4 Pág. 13-31.

Wynne, M. J. (2011). A checklist of benthic marine algae of the tropical and subtropical western Atlantic: third revision. Nova Hedwigia Beih 140: 1-166.

Yang, E. C., Boo, S. M., Bhattacharya, D., Saunders, G. W., Knoll, A. H., Fredericq, S., ... & Yoon, H. S. (2016). Divergence time estimates and the evolution of major lineages in the florideophyte red algae. Scientific reports, 6(1), 21361.

Yoon, H. S., Hackett, J. D., Ciniglia, C., Pinto, G., & Bhattacharya, D. (2016). A molecular timeline for the origin of photosynthetic eukaryotes. Molecular Biology and Evolution, 33(12), 3085-3094.

Zuccarello, G. C., Price, N., Verbruggen, H., Leliaert, F., & Anderson, R. J. (2010). Phylogenetic position, morphology, and reproduction of Acrosymphyton purpuriferum (Halymeniaceae, Rhodophyta) from the Houtman Abrolhos Islands, Western Australia. Phycologia, 49(5), 457-466.