

Claudia Francesca Vaga

História evolutiva da ordem Scleractinia (Cnidaria,  
Anthozoa) e sua relação com mudanças climáticas  
globais

Evolutionary history of the order Scleractinia  
(Cnidaria, Anthozoa) and its relation to global climate  
change

São Paulo

Ano 2023

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Ai miei genitori  
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## ***Resumo***

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Os corais escleractíneos, também conhecidos como corais duros, são os principais engenheiros de recifes de águas rasas e profundas, os quais figuram dentre os ecossistemas marinhos mais complexos, produtivos e biodiversos. Apesar da importância ecológica e econômica, a história evolutiva da ordem Scleractinia permanece não resolvida em diferentes níveis, sendo que a aquisição/perda de características como fotossimbiose e colonialidade, em termos evolutivos, permanece em debate. Mais especificadamente, análises moleculares visando desvendar a história evolutiva da ordem têm sido historicamente prejudicadas pela omissão de espécies azooxanteladas e, conseqüentemente, desbalanço entre famílias. Neste contexto, e dentro do atual cenário de mudanças climáticas globais e seus impactos no futuro deste grupo animal, um melhor entendimento de suas relações filogenéticas é relevante e necessário. Para a presente tese, mais de 200 espécies de corais escleractíneos, principalmente azooxantelados, foram sequenciadas através de técnicas de enriquecimento ou de *skimming* do genoma, e as análises integradas com dados disponíveis de espécies de águas rasas/zooxanteladas. Para as espécies sequenciadas, elementos nucleares ultraconservados e genomas mitocondriais completos foram recuperados e usados para reconstruções filogenômicas da ordem ou de linhagens específicas. Novos clados que correspondem a novas famílias foram descobertos, e Turbinoliidae – uma das famílias mais diversas e composta apenas por espécies azooxanteladas – foi recuperada como polifilética pela primeira vez. As características macro e micromorfológicas dos novos clados foram analisadas visando uma (re) avaliação de características taxonomicamente informativas. Desta forma, integrando resultados moleculares e morfológicos, três novas famílias e um novo gênero são descritos nesta tese. Em adição, uma análise de relógio molecular foi aplicada à filogenia da ordem, sendo que taxas de diversificação entre diferentes linhagens e estados ancestrais de colonialidade, simbiose, relação com o substrato e faixas de profundidade foram calculadas. Os resultados foram utilizados para abordar como (i) mudanças globais na temperatura e concentração atmosférica de CO<sub>2</sub>, (ii) eventos anóxicos e (iii) eventos de extinção em massa conduziram a evolução e diversificação das linhagens de corais. Resultados sugerem que a origem da ordem Scleractinia ocorreu no Ordoviciano ca. 460 Ma, corroborando a ordem com os fósseis “escleractineomorfos”. Em adição, famílias coloniais e zooxanteladas surgiram em um

período de temperatura global e concentração de CO<sub>2</sub> estáveis, enquanto a maioria das linhagens azooxanteladas surgiram após eventos anóxicos e de acidificação do oceano durante o Mesozóico, os quais impactaram catastróficamente seus contrapartes de águas rasas. Assim, táxons solitários e de águas profundas provavelmente serviram como repositórios para a recolonização subsequente de águas rasas e reaparecimento de linhagens coloniais zooxanteladas. Em conclusão, esses resultados desvendam as relações de algumas linhagens de corais escleractíneos e melhoram nossa compreensão da história evolutiva da ordem, especificamente como diferentes linhagens resistiram a eventos ambientais adversos de magnitude global no passado.



## ***Abstract***

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Scleractinian corals, also known as stony corals, engineer entire shallow and deep-water reefs, which are among the most complex, productive, and biologically diverse marine ecosystems. Despite their ecological and economic importance, the evolutionary history of the order and the phylogeny of many scleractinian taxa remain unresolved at different levels and the maintenance of traits, such as photosymbiosis and coloniality, across evolutionary time scales remains in debate. Specifically, molecular analyses aiming at untangling the phylogeny of Scleractinia have been historically hampered by the omission of azooxanthellate species and, consequently, by an uneven species sampling between families. In this context, and within the current scenario of global climate change and its impacts on the future of this important animal group, a better understanding of their phylogenetic relationships is relevant and necessary. For the present thesis, more than 200 scleractinian species, mainly azooxanthellate, were sequenced through target enrichment or genome skimming methods, and results were integrated with available data of shallow-water species. Both nuclear-ultraconserved elements and complete mitochondrial genomes were retrieved and used for phylogenomic reconstructions of the entire order or specific lineages. Novel clades that do not correspond with any of the extant families were uncovered, and Turbinoliidae – one of the most speciose families composed exclusively of azooxanthellate species – was recovered as polyphyletic for the first time. Both macro and micromorphological characteristics of the aforementioned family and clades were analyzed to reassess the taxonomically informative features. Integrating molecular and morphological results, three new families and one new genus are described in this thesis. Moreover, molecular clock analyses, diversification rates among different lineages, and ancestral states regarding coloniality, symbiosis, relationship to the substrate, and depth ranges were calculated in the light of the phylogeny of the entire order. The results were used to address how past global (i) changes in temperature and atmospheric CO<sub>2</sub> concentration, (ii) anoxic events, and (iii) mass extinction events drove the evolution and diversification of scleractinian lineages. Molecular clock estimation pushed the Scleractinia origin to the Ordovician ca. 460 Ma, corroborating the linkage of the order with the “scleractiniamorph” fossils. Some colonial and zooxanthellate families arose firstly in a period of stable global temperature and CO<sub>2</sub> concentration, while the majority of azooxanthellate lineages arose after Mesozoic anoxic and acidification

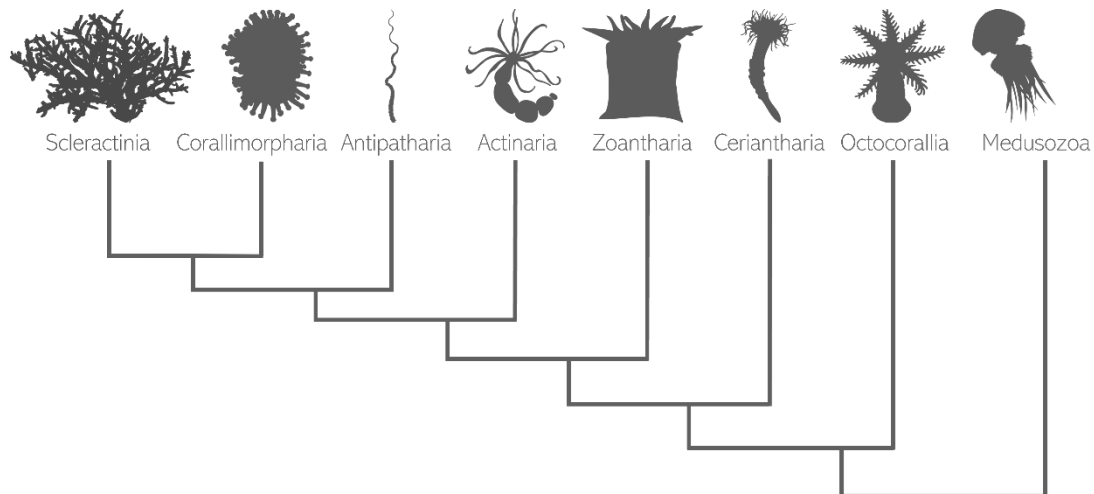
events that impacted catastrophically shallow-water counterparts. Thus, solitary and deep-water taxa possibly represented a repository for following the re-colonization of shallow waters, as well as the reappearance of colonial lineages. In conclusion, these results untangle the relationships of several scleractinian lineages and improve our understanding of the evolutionary history of the order in terms of how different coral lineages endured past global adverse events.

## ***General Introduction***

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The phylum Cnidaria, which is distributed worldwide, comprises remarkably diverse and ecologically significant taxa that early diverged within metazoan evolution (Park et al., 2011). Its members are united by the ability to synthesize the cnidae: organelle-like capsules with eversible tubules (Daly et al., 2007). The taxon, which include corals, hydroids, jellyfishes, sea anemones and sea fans, is composed of about 11,000 species, subdivided into six classes (Worms, 2023). Within Cnidaria, the class Anthozoa is composed of ~7,500 extant species that play crucial roles in a variety of marine regions and habitats (Daly et al., 2007). Members of this class live worldwide, and engineer or are part of shallow and deep-water reefs, which are among the most productive and biodiverse ecosystems (e.g., Reaka-Kudla, 1997; Rogers, 1999).

Within the class Anthozoa, members of the order Scleractinia are referred as stony corals once all members are able to secrete a solid and continuous calcareous – aragonitic (but see Stolarski et al., 1996; 2021) – skeleton (secreted by epidermal cells) that is external to the soft tissues, such a skeleton is unique inside the phylum (Daly et al., 2007). Within anthozoans, scleractinian corals are phylogenetically more closely related – i.e., sister group – to the order Corallimorpharia, and together they are sister to the black corals (order Antipatharia) (*Figure 1*). The order Scleractinia includes almost 1,700 extant species (Hoeksema & Cairns, 2023) that can be divided into three ecological groups (*Figure 2*). Members of one group – zooxanthellate corals – are mostly colonial, live in symbiosis with photosynthetic dinoflagellates – microalgae of the family Symbiodiniaceae which provide fixed carbon compounds to the coral host (e.g., Pearse & Muscatine, 1971) – and are, therefore, restricted to the photic zone (less than 200 m). Members of the second group – azooxanthellate corals – are mostly solitary, nonphotosymbiotic, and widely distributed bathymetrically (Cairns, 2007), with the deepest record being at 6,300 m for the genus *Fungiacyathus* (Keller, 1976). Members of the third group – facultative corals – present both zooxanthellate and azooxanthellate individuals and have the capacity to switch between states when environmental conditions become disadvantageous without negative impacts for the coral host (Dimon & Carrington, 2008). While the number of species belonging to the first two groups is currently almost even, facultative corals are rare and comprehends only 11 species known to date (Cairns et al., 1999).



**Figure 1.** Schematic view of the phylogenetic relationships of the main lineages within the class Anthozoa (with Medusozoa as outgroup).

In the past century, based on morphological observations, the order Scleractinia has been divided into up to thirteen suborders (Wells, 1956; Veron, 1995). Lately, however, molecular data pointed to only three main clades at suborder level (see *Figure 3*): (i) the early-divergent “*Basal*”, comprising only the families Gardineriidae and Micrabaciidae; (ii) “*Complex*”/*Refertina*; and (iii) “*Robust*”/*Vacatina*, these latter two embracing the vast majority of scleractinian families (Romano & Palumbi, 1996; Kitahara et al., 2010; Stolarski et al., 2011; Kitahara et al., 2014; Seiblitz et al., 2020; McFadden et al., 2021). But an exception to this division has been found by Quattrini et al. (2020) and Quek et al. (2023), in which the family Micrabaciidae was recovered as a sister group only of the “*Robust*”/*Vacatina* clade.



**Figure 2.** The three ecological groups of scleractinian corals. From left to right: zooxanthellate, facultative, and azooxanthellate corals.

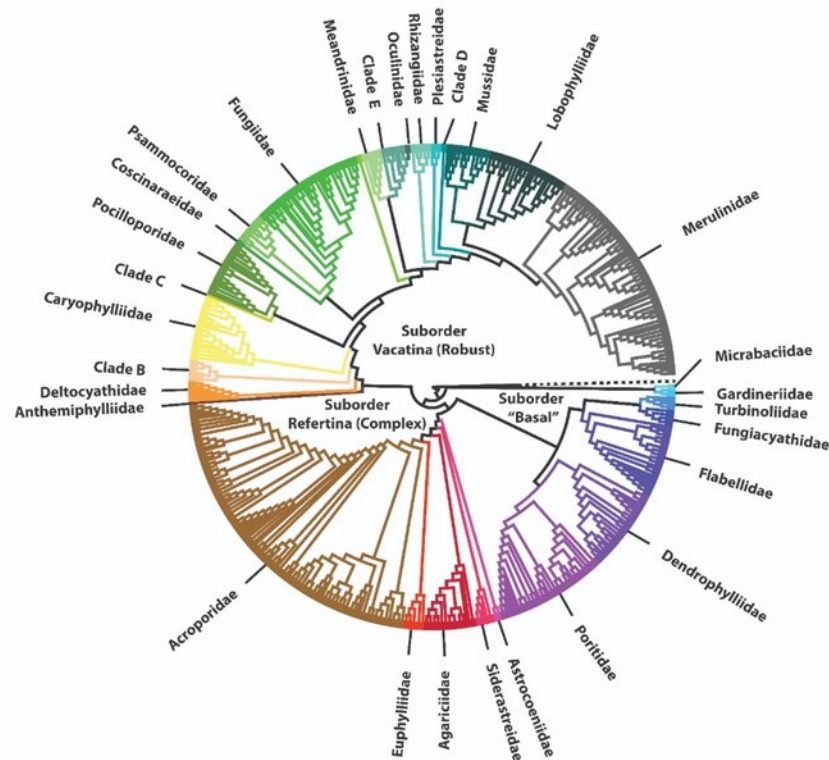
The very first genetic data for scleractinian corals were obtained in the early 1980s in studies conducted by Stoddart (1983, 1984) and Willis & Ayre (1985) using enzyme loci to examine the genetic diversity within *Pocillopora damicornis* and *Pavona cactus*. Over the following decades, different techniques and multiple

molecular markers were tested to untangle relationships within and between scleractinian taxa. Nevertheless, several recent works based on up to 12 DNA markers – both mitochondrial and nuclear –, showed that the phylogeny of many Scleractinia taxa remains unresolved at family, genus, and/or species levels (e.g., Fukami et al., 2008; Arrigoni et al., 2014; Huang et al., 2014; Kitahara et al., 2016). Moreover, in one of the newest and most comprehensive phylogenetic reconstruction, many families were recovered as para- or polyphyletic, with some examples of polyphyletic families that are still showing considerable uncertainties in their evolutionary history being Anthemiphylliidae, Caryophylliidae, Oculinidae, and Siderastreidae (e.g., Benzoni et al., 2007; Fukami et al., 2008; Kitahara et al., 2010, 2012). Even more surprising, some genera (comprising mainly azooxanthellate and deep-water species) unexpectedly grouped in novel clades that do not correspond with any of the extant families (*Figure 3*) (Kitahara et al., 2016), thus highlighting a necessity for a taxonomic and phylogenetic revision of many taxa and a re-definition of the synapomorphies applied to discern genera and families.

Such discrepancies between morphological and molecular results are most probably due to recognized challenges in stony corals morphological observations such as: (i) intraspecific phenotypic plasticity (see Todd, 2008), which can confound and overestimate the number of extant species; (ii) pervasive morphological convergence across various phylogenetically distant lineages (see an example in Chapter 1): i.e., species not closely related to each other that, for experiencing similar environmental conditions, developed resembling or identical morphological traits; and (iii) the low number of macromorphological characters used to describe and characterize taxa at various taxonomic levels.

Recently, the recognition that the deposition of the scleractinian skeleton is biologically controlled and not easily perturbed by environmental factors at the microstructural level (see Cuif et al., 2003; Janiszewska et al., 2011, 2013) has led to more detailed subcorallite observations (Budd et al., 2012; Kitahara et al., 2012, 2013; Huang et al., 2014; Janiszewska et al., 2015), and greater attention has been given to previously overlooked micromorphological and microstructural characters that helped to shed light on the taxonomy and evolutionary history of several scleractinian taxa (e.g., Stolarski et al., 2021; Seiblitiz et al., 2022). In the light of this recognition,

micromorphological observations have been lately frequently used combined with molecular results to describe new families through an integrative approach or to help untangle the systematic of several scleractinian lineages (e.g., Benzoni et al., 2012; Kitahara et al., 2012).



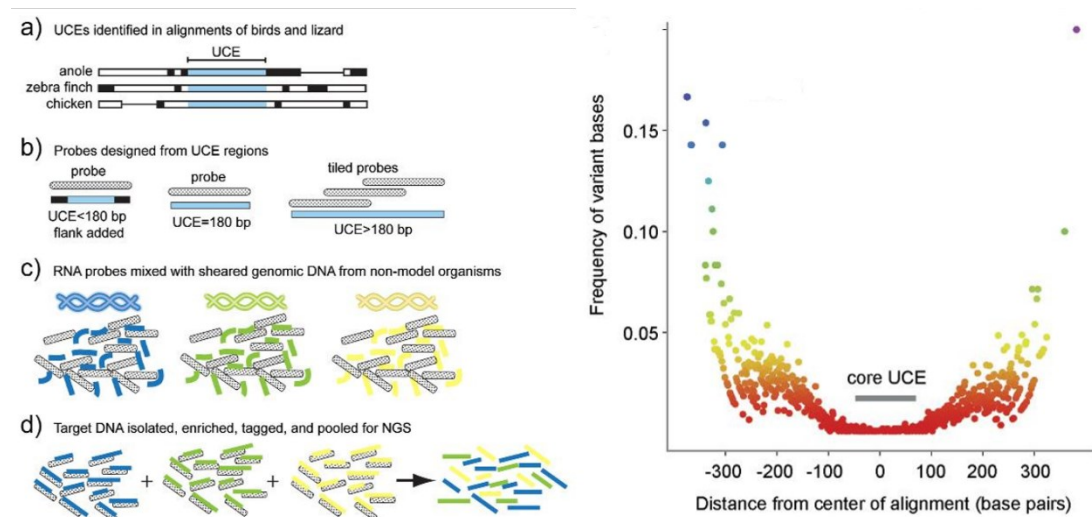
**Figure 3.** *Scleractinia* genus-level phylogeny based on 12 DNA markers. Clades without names (i.e., clades B, C, D, and E) are still in the process of morphological/molecular characterization. Branch colors indicate different families, and the dotted line indicates the outgroup (from Kitahara & Cairns 2021).

Besides problems with morphological observations, the goal of achieving reliable phylogenetic reconstructions of the order has long been hampered by a substantial underrepresentation of azooxanthellate and deep-water species, and a paucity of available molecular markers with a strong bias towards the use of mitochondrial and ribosomal loci (Stolarski et al., 2011; Kitahara et al., 2016). Shallow-water zooxanthellate corals have always received greater attention, due to the relative

ease with which they can be sampled and the concern about climate change threats that shallow-water coral reefs are facing (e.g., Pandolfi et al. 2011). On the other hand, studies on azooxanthellate and deep-water corals in many regions remain scarce and the species number underestimated (Cairns, 2007; Kitahara & Cairns, 2021). Nevertheless, it is well known that the acidification and deoxygenation of the oceans due to ongoing climate change are predicted to heavily impact deep-water environments with negative consequences for most calcifying species (Levin & Le Bris, 2015). Azooxanthellate and deep-water corals account nowadays for about half of the known scleractinian species (Hoeksema & Cairns, 2023), and include the engineers of complex deep-water reef-based ecosystems circumglobally (Roberts et al., 2009). Furthermore, several new azooxanthellate taxa have been recently described, and some of them, that are lacking molecular information, have been only tentatively placed inside a specific clade or family (Kitahara & Cairns, 2021).

Parallel to the aforementioned, in the last decade, high-throughput sequencing methods have been developed, enabling the access and handling of vast amounts of data in large-scale phylogenetic studies at relatively low cost (Goodwin et al., 2016; Kulkarni & Frommolt, 2017). These methods include amplicon sequencing, whole-genome sequencing, restriction site-associated DNA (RADseq), transcriptome sequencing, and target enrichment of genomic DNA (McCormack et al. 2013a). Specifically, the target enrichment of ultraconserved elements (UCEs) (Faircloth et al., 2012) has been proven robust in inferring phylogenies of a variety of different organisms (e.g., Crawford et al. 2012; Starrett et al. 2016) across both shallow and deep timescales (McCormack et al., 2013b; Smith et al., 2014; Manthey et al., 2016). UCEs are highly conserved regions that occur in high numbers throughout genomes across all taxa, including Cnidaria, but the flanking regions surrounding UCEs are more variable and phylogenetically informative (see *Figure 4*), making them easy to identify and align among divergent species (Faircloth et al., 2012; Ryu et al., 2012). Furthermore, other advantages include that they can be generated at a relatively low cost even from 100-year-old, formalin or ethanol preserved museum specimens and specimens with degraded DNA (McCormack et al., 2016; Ruane & Austin, 2017; Derkarabetian et al., 2019).

Target enrichment of UCEs has been already successfully used in several studies in the past few years to untangle the relationship between and within different cnidarians lineages (e.g., sub-phylum Anthozoa [Quattrini et al., 2018, 2020]; order Scleractinia [Quek et al., 2020; 2023]; family Acroporidae [Cowman et al., 2020]; class Octocorallia [McFadden et al., 2022]). Nevertheless, whole-genome shotgun sequencing method (also known as genome skimming or low-coverage sequencing) has also become lately more affordable and widely used to produce a vast amount of data that can be used for bioinformatically extract a wide range of molecular markers such as UCEs and exons loci, microbiome, as well as complete mitochondrial genomes (e.g., Golightly et al., 2022; Quattrini et al., 2023).



**Figure 4** Left image: Graphical representation of the workflow for using UCEs and target enrichment in phylogenomic studies. Right image: representation of genetic variability in the core and flanking regions of UCEs (modified from Faircloth et al. 2012).

Although mitochondrial sequences can be problematic for hexacorals phylogenetic reconstructions (Kayal et al., 2013; Kitahara et al., 2014) due to their slow rates of evolution (Shearer et al., 2002; Huang et al., 2008) and high level of substitution saturation (Pratlong et al., 2017), complete mitochondrial genome of anthozoan taxa has attracted recently particular attention (e.g., Seiblitiz et al., 2020, 2022; Quattrini et al., 2023). Nonetheless, it has been proved that some genes rearrangements (which include transpositions, inversions, and duplications) could be used as an additional taxonomic character/synapomorphy of specific lineages (Seiblitiz et al., 2022; Capel et



al., *submitted*) and, therefore, could help to resolve the evolutionary history of some non-monophyletic taxa.

Both shallow and deep coral reefs are facing increasing threats at local and global scales. Globally, increase in sea surface temperatures, ocean acidification, and the decrease in depth of the aragonite saturation horizon are leading to mass coral bleaching (and mortality) and reducing the ability of corals to build skeletons, due to a rapid buildup of CO<sup>2</sup> and other greenhouse gases in the atmosphere (e.g., Caldeira & Wickett., 2003; Marlon et al., 2008). Locally, threats like coastal development, sewage discharges, trawling fishing, and coral mining are reducing the resilience of corals to withstand global threats (Hoegh-Guldberg et al., 2007; Carpenter et al., 2008). Studies regarding direct effects of ocean acidification with qualification and quantification data are still scarce and, mainly, regarding zooxanthellate corals (e.g., Moya et al., 2012). Consequently, we still do not completely understand how lineages of this order are being impacted by the current climate changes, being a better understanding of their phylogenetic and adaptive relationships topical and necessary (Quattrini et al., 2020). In the Brazilian context, this knowledge is of direct importance, since the diversity of zooxanthellate endemics, as well as deep-water scleractinian corals reported to its coast is large (Kitahara, 2007; Pires, 2007; Nunes et al., 2008; Kitahara et al., 2020), and they are already facing pressures of anthropic origin (Kitahara, 2009).

Moreover, despite the ecological and economic importance of scleractinian corals, we understand remarkably little about the evolutionary origins of this group (Fukami et al., 2004, 2008; Huang et al., 2009; Kitahara et al., 2010; Huang et al., 2011). Likewise, the maintenance of morphological and ecological traits, such as photosymbiosis, coloniality, and depth range, across evolutionary time scales remains in debate (Barbeitos et al., 2010; Campoy et al., 2020; Gault et al., 2021). Fossils of scleractinian corals appeared abruptly in the Middle Triassic (ca. 240 Ma), but the already vast range of morphological diversity observed among these fossils (Roniewicz & Morycowa, 1993; Veron, 1995), in addition to molecular clock estimates (Stolarski et al., 2011; Arrigoni et al., 2017; Campoy et al., 2020), suggests an extensive Palaeozoic evolutionary history for Scleractinia. Based on the estimated origin of the order, Stolarski et al. (2011) linked the Ordovician “scleractinomorph” fossil – *Kilbuchophyllia* ca. 450 Ma – to the very early scleractinian lineages.

In this scenario, solving the existing phylogenetic uncertainties of specific scleractinian lineages through an integrative approach that combine morphological and molecular data is of paramount importance. Reliable phylogenetic reconstructions are the basis for better understanding of diversification processes and lineages endurance through geological times for every group of organisms. To fill the gaps in Scleractinia systematics and phylogeny, during the development of the present thesis, target enrichment, genome skimming, as well as morphological observation were used to (i) build the most comprehensive phylogeny (i.e., with an equal representation of azooxanthellate and zooxanthellate species from all the known families [with the exception of Guyniidae]) of scleractinian corals to date; (ii) identifying the new clades that needed to be described as new families; (iii) investigate the diversity of the complete mitochondrial genome across various lineages; and (iv) address how past global (1) changes in temperature and CO<sub>2</sub> concentration, (2) anoxic events, and (3) mass extinction events drove the evolution and diversification of scleractinian coral lineages. Specifically, we investigated potential traits and depth ranges that enabled these lineages to endure past adverse events to reduce uncertainties about stony corals' future in the light of ongoing climate changes.

More specifically I aim to:

**Chapter 1. Use an integrative approach to shed light on a case of morphological convergence between a species of Deltocyathidae and the family Turbinoliidae.**

The family Deltocyathidae was recently erected to accommodate all the species from the genus *Deltocyathus*, previously belonging to the family Caryophylliidae. However, one species, *Deltocyathus magnificus*, consistently clustered with species of the family Turbinoliidae. To solve the enigmatic position of this species, I used an integrative approach – which coupled nuclear and mitochondrial data, as well as micromorphological observations – to formally transfer *D. magnificus* to a new genus inside Turbinoliidae.

**Chapter 2. Describing of a new family of solitary azooxanthellate corals – Stephanocyathidae – using a genomic approach.**

The family Caryophylliidae has long been known to be polyphyletic. As part of the process of resolving the systematic and phylogeny of caryophylliid lineages, I used a

genomic approach – whole mitochondrial genome analysis coupled with a phylogenomic (including UCEs and exon data) reconstruction of part of the scleractinian species – to describe a new family, Stephanocyathidae, that comprehends solitary and azooxanthellate species.

**Chapter 3. Characterize the mitochondrial genome of two understudied deep-water solitary species to investigate their phylogenetic position.**

Species belonging to the “true” Caryophylliidae lineage – clade that comprehend the type genus of the family, *Caryophyllia* – have been found to show a specific rearrangement of the genes order in their mitochondrial genome from that of the “canonical” gene order present in the vast majority of scleractinian species. Nevertheless, to date only few caryophylliid genera have had their whole mitochondrial genome sequenced and annotated. In the attempt to fill in the gaps I have produced the complete mitochondrial genome of two species of the genus *Crispatotrochus*. I found that they present the same mitochondrial rearrangement of the “true” Caryophylliidae clade and, therefore, confirmed their phylogenetic position.

**Chapter 4. Use morphological analysis to re-synonymize the two solitary genera *Deltocyathoides* with *Peponocyathus* (Scleractinia, Turbinoliidae).**

The taxonomy of Turbinoliidae has always been challenging due to their small dimensions and the difficulty of their sampling – mostly deep-water infauna species. Based on newly acquired data on the type of reproduction of two species, i.e., *Deltocyathoides orientalis* – type species of the genus – and *Deltocyathoides stimpsonii*, we synonymize the genus *Deltocyathoides* with *Peponocyathus*. This work is a step forward in our understanding of the taxonomy of the family.

**Chapter 5. Use an integrative approach to revise the family Turbinoliidae.**

The monophyly of the family has been historically based on the morphological feature of having the entire corallum invested with tissue, but until recently only four turbinoliid genera, which composed a monophyletic clade, had published sequences. Genomic data that I have generated increased the number of turbinoliid genera sequenced to nine and recovered them in a polyphyletic assemblage, specifically in three phylogenetically distant clades. Therefore, I performed morphological analysis to evaluate which clade corresponds to the characteristics of the type taxon of the family

– *Turbinolia* [fossil - no molecular data available] – and, therefore, retain the family name, and which clades represent new families.

**Chapter 6. Correlate how past climate change, extinction events, and anoxic events shaped the evolution and diversification of scleractinian coral lineages.**

To fill in the knowledge gaps in the scleractinian evolutionary history and phylogeny, I have generated genomic data for an extensive number of azooxanthellate species – either through target enrichment or genome skimming sequencing methods – and joined them with already available genomic data from zooxanthellate counterparts. With the resulting data I generated the most comprehensive phylogenetic reconstruction of the order Scleractinia to date. In addition, the phylogenetic reconstruction was also used to address how past global (i) changes in temperature and CO<sub>2</sub> concentration, (ii) anoxic events, and (iii) mass extinction events drove the evolution and diversification of scleractinian coral lineages. Specifically, we investigated potential traits and depth ranges that enabled these lineages to endure past adverse events to reduce uncertainties about stony corals' future in the light of ongoing climate changes.

## ***General Discussion and Future Directions***

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### *General Discussion*

The thesis presents the first phylogenomic reconstruction of the order Scleractinia with a comprehensive and even representation of zooxanthellate and azooxanthellate species. Together with the work of Quek et al. (2023) the here presented results prove that hexacoral/scleractinian specific UCEs and exon loci sets – recovered through either target enrichment or genome skimming technologies – are valuable and reliable tools to infer relationships with high support at deep nodes of the order. In parallel, other work (Cowman et al., 2020; Bridge et al., 2023) showed that the same tool can also be used to investigate relationships at the species and genus level (also corroborated herein). The final phylogenomic reconstruction (Chapter 6), while confirming the division of the order in only two main clades “Robust”/Vacatina and “Complex”/Refertina (as in Quattrini et al., 2020 and Quek et al., 2023), uncovered several incongruences between the taxonomically recognized scleractinian families and the lineages recovered (see Chapters 1, 2, and 5). Specifically, other than the family Caryophylliidae already known to be polyphyletic (e.g., Kitahara et al., 2010; Stolarski et al., 2011; Campoy et al., 2020; Seiblitiz et al., 2022), some mainly azooxanthellate families and genera, previously thought to be monophyletic, were recovered divided in phylogenetically distant lineages (e.g., genus *Trochocyathus*, genus *Oculina*, family Turbinoliidae, family Anthemiphylliidae [but also see Stolarski et al., 2011]). Moreover, some of these taxa were not recovered inside extant known families. Instead, they grouped in novel clades (e.g., Clade A and Clade B – Chapter 6) that do not correspond with any of the known scleractinian families, with some of these clades already shown in Kitahara et al. (2016). This result contrasts the previous hypothesis that most of the polyphyletic families were zooxanthellate while azooxanthellate families were mostly monophyletic (Kitahara et al., 2016; Quek et al., 2023). Results from the present work stress that the systematic of several scleractinian lineages is far from being understood. The problem being exacerbated by the fact that many species are still lacking any molecular information, therefore, their phylogenetic position is obscure and their assignment to a specific family only tentative (see Kitahara & Cairns, 2021). Therefore, results from this thesis, while solving some longstanding uncertainties about several scleractinian lineages, also uncovered many others that still need to be further addressed.

Systematic classification based on morphological characters proved to be reliable for some groups of corals (e.g., *Fungiacyathiidae* and *Micrabaciidae* – families for which molecular data were available for very few species prior to this work and were still recovered as monophyletic even adding several new species into the phylogeny), while failed for many others as aforementioned. In the latter case, a different approach already known as “reverse taxonomy” used for different groups of animals (e.g., Kanzaki et al., 2012; Michaloudi et al., 2018) was applied in the present thesis: morphological characters of taxa formally belonging to different families but phylogenetically recovered in the same clade were reassessed in order to find common features that could be used as synapomorphy for describing the newly retrieved lineages. Indeed, in the majority of cases (but see Lawley et al., 2021) integrative approaches that couple morphological, ecological, and molecular data provide new taxa/lineages more robust description/diagnosis (e.g., Arrigoni et al., 2021; Juszkievicz et al., 2022), and are especially important for provide tools for their identification both in the field (or in museum collections) and through the use of molecular markers. At the same time, for species for which molecular data are not available or cannot be retrieved (e.g., lack of specimens properly preserved), particular attention needs to be given to morphological and/or ecological characteristics that could have been overlooked in the past (see Chapter 4). In general, the present phylogenomic reconstruction shows a pervasive recurrence of morphological convergence of many macromorphological characteristics previously used as synapomorphies to describe specific scleractinian lineages. Indeed, microstructural features of the scleractinian skeleton has been proved to be often more informative at higher taxonomic levels (e.g., Stolarski, 2000; Benzoni et al., 2012; Arrigoni et al., 2023), once again stressing the current need for integrative approaches for a better understanding of coral systematics. At the same time, some scleractinian taxa, especially those in early-diverging lineages, have been proved to show identical microstructural features to phylogenetically distant taxa (see Chapter 1), therefore, obscuring the taxonomic distinctiveness across lineages.

The complete mitochondrial genome (mitogenome) is an additional feature that has been lately explored for Scleractinia and Anthozoa systematics in general (see Quattrini et al., 2023). Phylogenetic reconstruction based solely on the mitogenome can be discordant from phylogenies based on a wide range of nuclear markers (Quattrini et al., 2023), leading to interpretations of the evolutionary history of Scleractinia that were

later refuted (Medina et al., 2006). However, mitochondrial-based phylogenies can be also informative, especially when used to prove the belonging of a species to a specific family/lineage (see Chapter 3). In the light of this, in previous works (e.g., Seiblitz et al., 2022) and two chapter of this thesis (Chapters 1 and 2) separated phylogenomic reconstructions based on both ultraconserved nuclear sequences and complete mitogenome sequences were built and mirrored. This approach allows to confer robustness to the results presented and further investigate possible discrepancies and/or congruencies between nuclear and mitochondrial based phylogenies.

The previous recognition that rearrangements and transpositions of the mitochondrial genes order from the “canonical” one (most commonly found in Scleractinia species) can have taxonomic relevance (see Seiblitz et al., 2022) incentivized its analyses for all the lineages examined in the present thesis. A novel rearrangement specific for the family Deltocyathidae was described (Chapter 1) and a transposition already known for the species *Paraconotrochus antarcticus* (Stolarski et al., 2021) was uncovered both for the newly proposed family Stephanocyathidae and one “turbinoliid” clade, herein named Pleotrochidae (Chapters 2 and 5). Moreover, the transposition described to be specific for the family Caryophylliidae (Seiblitz et al., 2022) was used to confirm the phylogenetic position of an understudied genus – *Crispatotrochus* (Chapter 3). Results presented in this thesis further confirmed that features of the mitogenome can be taxonomically informative and that mitogenome gene rearrangements/transpositions seem to occur more often in the “Robust”/Vacatina group rather than in the “Complex”/Refertina. Previous studies (e.g., Kitahara et al., 2014) had suggested a pattern of higher GC content for the mitogenome of “Complex”/Refertina taxa and the so called “Basal” group, lately – and in this thesis – recovered as sister group only of the “Robust”/Vacatina clade. Nevertheless, other lineages analyzed that are early-diverging inside the “Robust”/Vacatina clade showed similar higher GC content in contrast with the remaining vacatinian more derived lineages. Since Corallimorpharia, sister group of Scleractinia, also shows high GC content (see Lin et al., 2014) it is possible that this trait is ancestral in stony corals evolutionary history.

Stony corals are under threat as a result of the ongoing climate change (e.g., Pandolfi et al., 2011). Endeavoring to better understand the evolutionary history of the order Scleractinia and its correlation with past global adverse events, the time-

calibrated phylogeny, ancestral state reconstructions, and diversification rates were analyzed in the light of past marine acidification, anoxic, and extinction events in parallel to global changes in temperature and CO<sub>2</sub> concentration. The comprehensive time-calibrated phylogenomic reconstruction (~280 scleractinian species) pushed back the origin of the order in ~80 Ma from the only previous molecular clock performed using ultraconserved and exon loci (Quattrini et al., 2020), placing the most recent scleractinian common ancestor in the Middle Ordovician (460 Ma). The here presented divergence time also precede the one obtained by Campoy et al. (2020) – 415.8 Ma –, which performed a molecular clock analysis using a comprehensive phylogeny of the order based on two mitochondrial and two nuclear markers. The molecular clock analysis coupled with ancestral state reconstructions of several stony corals characters and depth ranges allowed to hypothesize that both some colonial/zooxanthellate and solitary/azooxanthellate lineages survived all past adverse global events that occurred after the rise of the order (see Chapter 6). At the same time, results also showed that the same adverse events drove the appearance and higher diversification of deep-water, solitary, and azooxanthellate taxa, probably responsible for a later re-colonization of shallow water habitats. How present rates of environmental changes compare to ancient one has been debated for decades, however, it has been showed that climate changes in the geological past could have happened as fast as the present ones and even with possible greater magnitude (Kemp et al., 2015), in contrast with common and previous hypothesis that the paces of geological climate changes have been slower (see Hardy, 2003). We are probably still far from reaching a deep understanding of past global climate changes but, if the former scenario holds true, while shallow-water communities will surely change if global and fast actions are not taken to diminish the release of anthropogenic CO<sub>2</sub> in the atmosphere, scleractinian corals as a lineage should survive as it did in the past 400 Ma.

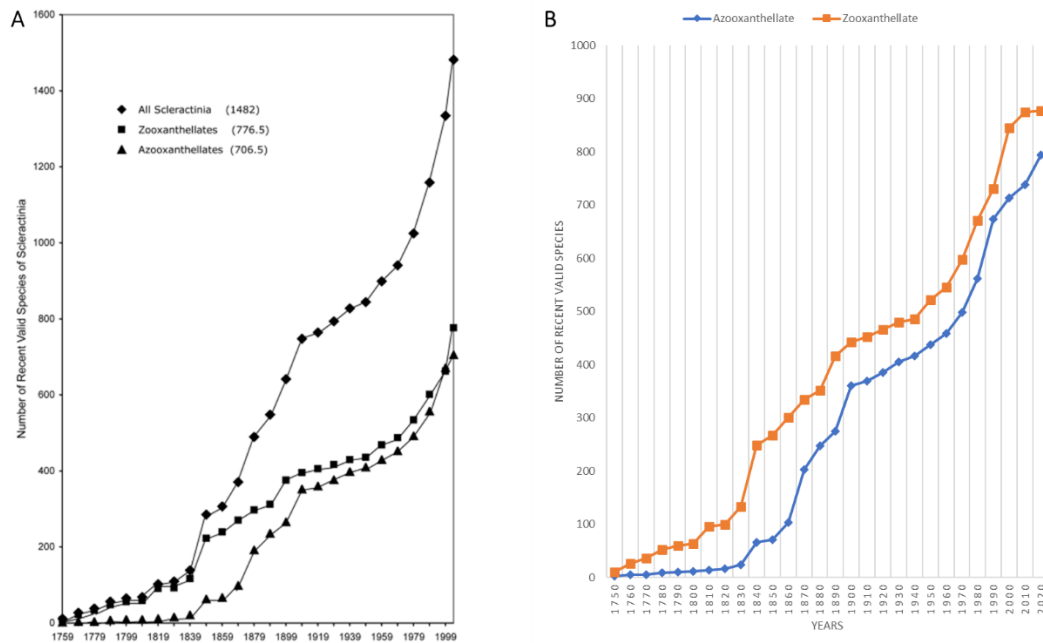
### *Future Directions*

The present thesis described new stony corals families and untangled the systematic relationships of several scleractinian lineages, but many more discrepancies between the “traditional” systematic classification and the phylogenetic reconstruction were uncovered but could not to be addressed in the present thesis. While zooxanthellate and shallow-water lineages have been extensively studied and their systematic evaluated – although many taxa still need more attention especially at the species level (e.g.,



*Pocillopora* – Oury et al. 2023; *Acropora* – Bridge et al. 2023) – this thesis show that many azooxanthellate taxa are yet in need of a systematic revision, a problem exacerbated by the lack of any molecular data for many solitary and deep-water species. In parallel to the forthcoming systematic revision (Chapters of these thesis that will be submitted soon) of the lineages included in the herein presented phylogeny, the future sequencing of additional deep-water taxa coupled with the re-evaluation of the morphological characteristics (as seen in Chapters 1 and 5) will be of paramount importance for a better understanding of the evolutionary history of the order.

This work, together with previous ones (Quattrini et al. 2018, 2020; Cowman et al. 2020; Erickson et al. 2020; Quek et al. 2023), showed how high-throughput sequencing methods – e.g., target enrichment, genome skimming – improved greatly the resolution and robustness of phylogenetic analyses, thus, solving the longstanding problem of the paucity of molecular markers available for inferring scleractinian relationships. At the same time, whole genome assemblies with reliable annotation are currently available for very few scleractinian and only one deep-water species (i.e., *Desmophyllum pertusum* [Herrera & Cordes, 2023]), hampering analyses that relies on an unequivocal knowledge of the coding and non-coding region of the DNA. The recent long read sequencing technologies (e.g., Nanopore, PacBio) – often coupled with short reads one (e.g., Illumina), so called “hybrid sequencing” – will aid in filling this knowledge gap and provide data for reliable reference genomes. Moreover, the genome skimming method has been proved valuable for retrieving the complete mitochondrial genome for a wide range of anthozoan taxa (e.g., Quattrini et al., 2023). Several transpositions and rearrangement of the mitochondrial gene order have been uncovered in scleractinian taxa and some of these have been suggested to be taxonomically informative (e.g., Seiblitiz et al. 2022; Capel et al. *submitted*; Chapter 1 and Chapter 2). However, this information is still lacking for many stony corals’ lineages; thus, advantage should be taken of high-throughput methods to provide this additional and potentially important information.



**Figure 1.** Cumulative curves of described species of Scleractinia across time from the work of Carl Linnaeus to (A) the end of the 20<sup>th</sup> century (from Cairns, 2007) and to (B) the present decade.

In parallel to the above, it is important to highlight that many (or the majority) of deep-water regions have not been explored yet. At this moment, the number of extant scleractinian species is somewhat evenly split between zooxanthellate and azooxanthellate species. However, the number of azooxanthellates is probably an underestimate due to their difficult sampling, as also suggested by the rapid increase in the number of recently described deep-water species (Fig. 1). It is of paramount importance that future research expeditions in deep-sea regions also focus attention on these group of animals to continuously improved our knowledge about their diversity and roles they play in the order evolutionary history.

These efforts as a whole will hopefully be fundamentals to fill in gaps in the knowledge of these charismatic animals, especially aiding in understanding their diversity, lineages relationships, and evolutionary history (as seen in Chapter 6) for the final goal of subsidizing future decisions and actions for their conservation in the light of ongoing global climate changes.

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