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A DNA barcoding approach to assess coral species richness and biogeographic affinities of Hexa- and Octocorallia in Cabo Verde

UNIVERSIDADE DO ALGARVE

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A DNA barcoding approach to assess coral species richness and biogeographic affinities of Hexa- and Octocorallia in Cabo Verde

Declaro ser a autora deste trabalho, que é original e inédito. Autores e trabalhos consultados estão devidamente citados no texto e constam da listagem de referências incluída.

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ABSTRACT

Coral reefs are the most biodiverse marine ecosystems on earth. Often described as biodiversity hotspots, they cover less than 1% of the ocean floor but host more than 25% of all marine species. However, coral reefs are undergoing massive degradation around the world, prompting a need for further studies on global coral populations to support their protection. Tropical reefs in particular, are essential for biodiversity but are understudied in many parts of the world and therefore insufficiently understood. This is the case in Cabo Verde, currently listed as 8th among endangered biodiversity hotspots. With less than 1% of national waters protected, the archipelago lacks data and knowledge on its species diversity, a regional tendency for West Africa. Thus, this study aimed to assess shallow coral species richness (< 50m depth) and consolidate current species diversity knowledge within Cabo Verde, to reveal cryptic species before they might become threatened or disappear. While 21 species were morphologically identified, molecular methods were used to build the first DNA barcode library for Cabo Verde's hexacorals and octocorals. The use of complementary mitochondrial (COX1 and MutS) and nuclear (28S) DNA markers, field identification, and litterature-based species lists helped to successfully identify 27 samples to the species level and three others to the genus level, which previously had only been morphologically identified. *Balanopsammia wirtzi* constituted a new barcode for the region and the alien species *Carijoa riisei* was confirmed through barcoding of mitochondrial COI and nuclear 28S genes. Phylogenies confirmed biogeographic affinities of three out of the four dominating hermatypic species (*S. radians*, *P. porites*, *P. astreoides*) to be closely related to the Caribbean. The study also revealed noteworthy differences in species richness between Cabo Verde and the other Macaronesian archipelagos, sharing a few common species throughout the Scleractinia and Antipatharia order and only the species *Eunicella verrucosa* in the order Alcyonacea. None of the dominating four hermatypic species in Cabo Verde could be found in any other of the Macaronesia islands. This research represents one of the first attempts, and the most exhaustive one to date, to characterize the coral species composition of Cabo Verde using DNA barcoding, and produced a geographically referenced coral DNA catalog baseline that will inform further research, education and conservation initiatives.

Key words: *shallow corals, biogeography, Cabo Verde, DNA barcoding, Scleractinia, Antipatharia, Alcyonacea*

RESUMO

Os recifes de coral são os ecossistemas marinhos com maior biodiversidade do planeta. Muitas vezes descritos como hotspots de biodiversidade, cobrem menos de 1% do fundo do oceano, mas albergam mais de 25% de todas as espécies marinhas. No entanto, os recifes de coral estão a sofrer uma degradação maciça em todo o mundo, o que torna necessários mais estudos sobre as populações globais de coral para apoiar a sua proteção. Os recifes tropicais, em particular, são essenciais para a biodiversidade, mas são pouco estudados em muitas partes do mundo e, por conseguinte, insuficientemente compreendidos. É o caso de Cabo Verde, atualmente classificado em 8º lugar entre os hotspots de biodiversidade ameaçados. Com menos de 1% das águas nacionais protegidas, o arquipélago carece de dados e conhecimentos sobre a sua diversidade de espécies, uma tendência regional para a África Ocidental. É no contexto geográfico único de Cabo Verde e nas importantes distinções biogeográficas já estabelecidas em relação à região da Macaronésia que procuramos investigar se os conjuntos de corais são igualmente discursivos. Assim, o objetivo deste estudo é caraterizar a diversidade de espécies de corais moles e duros (< 50m de profundidade) e a comunidade de corais de Cabo Verde, bem como consolidar o conhecimento atual sobre a diversidade de espécies em Cabo Verde, para revelar espécies crípticas antes que estas se tornem ameaçadas ou desapareçam. Mais detalhadamente, pretendemos 1) criar uma biblioteca de códigos de barras de DNA baseada em COI, 28S e MutS, específica para os corais de Cabo Verde, a fim de confirmar e/ou corrigir a classificação taxonómica morfológica; 2) investigar a presença de espécies crípticas ou diversidade inexplorada; e 3) avaliar se as espécies de coral (Scleractinia, Alcyonacea) de Cabo Verde são geneticamente diferentes das espécies do mesmo género noutras regiões, particularmente na Macaronésia.

Foram recolhidas em Cabo Verde amostras de tecido de Hexacorallia e Octocorallia de vários espécimes (n = 62) (presumivelmente Scleractinia: 41, Antipatharia: 13, Alcyonacea: 8). Enquanto 21 espécies foram identificadas morfologicamente, foram utilizados métodos moleculares para construir a primeira biblioteca de códigos de barras de ADN para os hexacorais e octocorais de Cabo Verde. Embora se tenha antecipado a descoberta de espécies crípticas, a sua maioria pertencia à ordem Antipatharia, que acabou por ser excluída da análise molecular. Além disso, para garantir a credibilidade da base de dados de referência de sequências genéticas para Cabo Verde, compilámos uma lista de Hexacorallia e Octocorallia previamente registados ou suspeitos de estarem presentes. A utilização de marcadores complementares de ADN mitocondrial (COX1 e MutS) e nuclear (28S), a identificação no

terreno e as listas de espécies baseadas na literatura ajudaram a identificar com sucesso 27 amostras ao nível da espécie e três outras ao nível do género, que anteriormente só tinham sido identificadas morfologicamente. *Balanopsammia wirtzi* constituiu um novo código de barras para a região e a espécie exótica *Carijoa riisei* foi confirmada através do código de barras dos genes mitocondriais COI e nucleares 28S. Não obstante, a classificação taxonómica morfológica foi corrigida para certas espécies, como Oculina patagonica, e foi fornecido um novo código de barras para a espécie *Balanopsammia wirtzi*, mas seriam necessários primers especificamente concebidos e, mais importante, melhores bases de dados de referência, para as quais este estudo representa um grande contributo, para proporcionar uma melhor resolução genética.

O marcador 28S constituiu um desafio e não pôde ser utilizado para a análise filogenética, o que se deveu aos indels encontrados nesta região do ADN, uma limitação comum nos genes nucleares dos corais. A resolução genética do COI muitas vezes não permitiu distinguir entre espécies diferentes após BLAST. Para investigações futuras, aconselha-se a conceção de primers específicos para cada espécie e a utilização de primers complementares que funcionem melhor com este conjunto de dados.

As filogenias confirmaram as afinidades biogeográficas de três das quatro espécies hermatípicas dominantes (*S. radians*, *P. porites*, *P. astreoides*) como estando estreitamente relacionadas com as Caraíbas. Nenhuma das quatro espécies hermatípicas dominantes em Cabo Verde pode ser encontrada em qualquer outra das ilhas da Macaronésia. Embora a partir das listas de táxones da Macaronésia compiladas existentes, algumas espécies de Antipatharia pudessem ser encontradas em três das quatro ilhas da Macaronésia e em Cabo Verde, distribuídas esporadicamente, a semelhança estava mais relacionada com o nível do género, uma vez que muito poucas espécies estavam amplamente distribuídas. Antipathella wollastoni foi a única Antipatharia comum encontrada em todos os arquipélagos e em Cabo Verde. Algumas espécies comuns são partilhadas na ordem Scleractinia entre a Macaronésia e Cabo Verde do género *Madracis e Polycyathus* e dentro da ordem Alcyonacea, apenas *Eunicella verrucosa* era comum. Foi possível fazer uma distinção nas afinidades das espécies, enquanto certos taxa de Scleractinia, Alcyonacea e Antipatharia podem ser encontrados em todas as ilhas da Macaronésia e Cabo Verde, as composições de espécies das quatro ilhas comparadas (Açores, Madeira, Ilhas Canárias, Cabo Verde) foram muitas vezes diferentes, e Cabo Verde dominou as espécies de coral hermatípico parecem constituir comunidades distintas da Macaronésia e da África Ocidental.

Este estudo não fornece um código de barras de ADN completo de todas as espécies de Cabo Verde, mas é ainda o primeiro a fornecer sequências e dados filogenéticos sobre muitas das espécies presentes e a identificar com sucesso sete espécies do Arquipélago com base em dados genéticos, identificação morfológica e através de listas baseadas na literatura. Tanto quanto é do nosso conhecimento, esta investigação representa uma das primeiras tentativas, e a mais exaustiva até à data, de caraterizar a composição de espécies de coral de Cabo Verde usando código de barras de ADN, e produziu um catálogo de ADN de coral geograficamente referenciado que servirá de base a outras iniciativas de investigação, educação e conservação.

Em parceria significativa com esta região, o trabalho futuro precisa de continuar a identificar espécies dentro desta geografia única, utilizando um método não invasivo, como o eDNA, uma vez que é fundamental nesta região que a investigação não agrave ainda mais os impactos ambientais negativos sobre as espécies que procura conservar e proteger. Além disso, deve ser dada especial atenção aos projectos liderados por cidadãos, incluindo a Enseada do Coral e perto do Mindelo, uma vez que os esforços de conservação liderados por indígenas têm provado ser eficazes e respeitadores do ambiente natural.

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List of Abbreviations, Acronyms and Symbols

MPA	Marine Protected Area
GBR	Great Barrier Reef
ZEE	Exclusive Economic Zone
ICRI	International Coral Reef Initiative
CBD	Convention on Biological Diversity
NOAA	National Oceanic and Atmospheric Administration
ITCZ	Intertropical convergence zone
CC	Canary Current
MC	Mauritania Current
CVFZ	Cape Verde’s Frontal Zone
NECC	North Equatorial Counter Current
NEC	North Equatorial Current
WAHL	West African Heat Low
WAM	West African tropical Monsoon
USD	United Nation Dollar
GDP	Gross Domestic Income
WA	West Africa
CV	Cape Verde / Cabo Verde
nDNA	Nuclear DNA
MtDNA	Mitochondrial DNA
rDNA	nuclear rDNA (ribosomal proteins of the nucleus)
COX1/COI	Cytochrome c oxidase I (Mitochondrial gene)
28S	28S ribosomal DNA gene (Nuclear gene)

MUTS (MUTS-1)	Mutator S repair protein-coding gene (Mitochondrial gene only found in Octocorallia)

GENERAL INTRODUCTION

I. CORAL CONSERVATION

Habitat and Distribution

Coral reef ecosystems cover less than 1% of the ocean floor but harbor more than 25% of all marine species, representing the most diverse marine habitat per unit area. The ecological services and network that coral reefs provide are significant, complex, and misunderstood, benefitting greatly both marine species and humans alike (Timmers et al., 2021). In terms of diversity hotspots and complexity of inter-specie interactions, coral reefs are often compared to tropical rainforests, both complex ecosystems thriving in oligotrophic conditions (Swart, 2013). Coral species are therefore referred to as ‘ecosystem engineers’, as a key elements of sublittoral ecosystems in both tropical, cold, and temperate environments (Spalding et al., 2001, as cited in Rakka et al., 2020). Although corals can be found around the globe, key factors are limiting their growth and range expansion such as topography, depth, temperature, salinity, pH, oceanic currents and waves, tides, light penetration, turbidity, nutrient availability, and sediment transport (Freiwald et al., 2004; Roberts & Cairns, 2014).

Coral reefs are temperature and light dependent and thrive in highly oligotrophic (i.e., nutrient poor) conditions. These massive structures are therefore mainly confined to the photic zone, typically within the first 20 m of depth with water temperatures between 20 to 28^{o}C in tropical and subtropical oceanic zones (Forteath, 2001; Freiwald et al., 2004; Spalding et al., 2001; Swart, 2013). Coral communities are extremely complex and diverse, occupying a variety of marine realms, taking the form of colonies, gardens, or reefs (Roberts & Cairns, 2014).

Although coral reef communities of varying sizes can be found in over 100 countries, more than 50% of the surface area occupied by these reefs is found within 6 countries’ national waters: Australia, Fiji, Maldives, Indonesia, Philippines, and Papua New Guinea. The last three countries are part of what is widely known as the Coral Triangle, a marine area of high biodiversity for Anthozoa, sea turtles, and tropical fish. Coral communities organized as reefs are generally found in latitudes between 31^{o}40’ south and 32^{o}50’ north, being limited to minimal annual temperatures of around 18 ^{o}C (Hori, 1977, as cited in Yamano et al., 2001). Beyond those coordinates, as latitudes increase, overall reef-associated biodiversity and reef-building coral species richness decreases, to a point where, the latter becomes absent. Even so, this decrease in richness does not apply to cold or deep- water coral species (ahermatypic, occurring below 50 m), which comprise 65.6% of global coral species richness (Cairns, 2007). Thus, it is unsurprising Cordes et al. (2016) posited that cold-water corals, for the most part ahermatypic genera, can still thrive at high latitudes between 70 ° N and 60 ° S. Concomitantly, Freiwald et al. (2004) argued that species adapted to cold and deeper waters, pertaining mostly to Scleractinia or Antipatharia, can be found around the globe as solitary organisms or small colonies. Not only do corals have a wide geographic range (Figure I.I: Ahlenius, 2008), but they also occupy a wide bathymetric range throughout the euphotic (0-150m), mesophotic (30-150m) and aphotic or abyssal zones, settling on both sandy and rocky bottoms (Lesser et al., 2018).

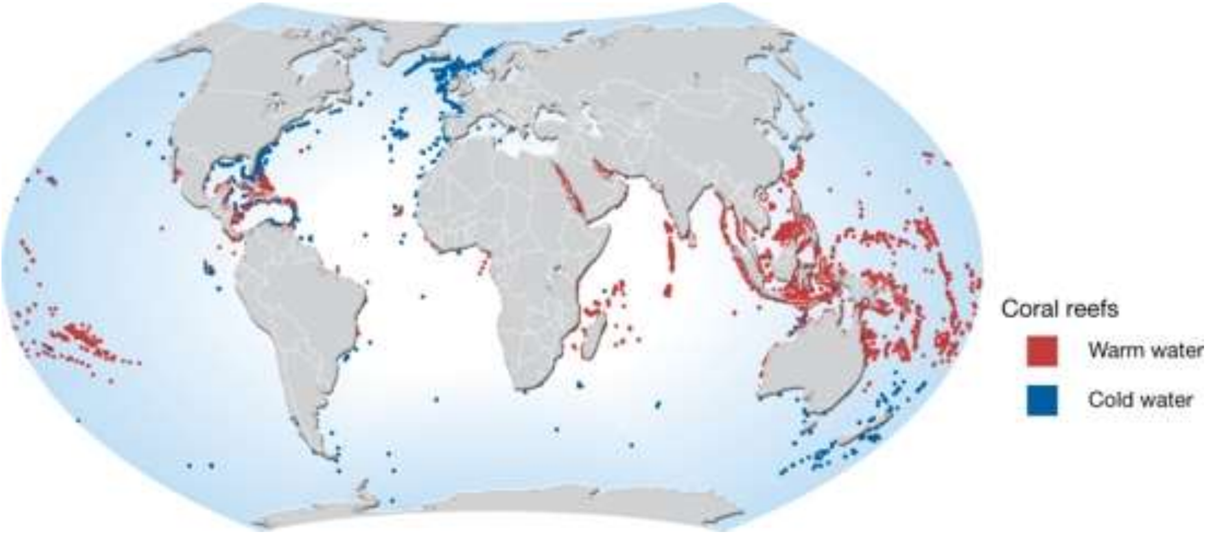

Figure I.I: Known global distribution of tropical (warm water) and cold water (deep) coral reefs.

Note: From *Distribution of cold water and tropical coral reefs,* by H. Ahlenius, February 2008, UNEP/GRID-Arendal Maps and Graphics Library (https://www.grida.no/resources/7197)

Shallow water and mesophotic reef-building species are referred to as hermatypic corals, represented by the order Scleractinia, the main reef-building organisms in the ocean, together with calcifying algae (Kleypas & Yates, 2009). Hermatypic species are generally found in warmer waters (Figure I.I) and are zooxanthellate, thriving in symbiosis mainly with the dinoflagellate algae *Symbiodinium*. Although generally zooxanthellate, shallow water corals can be either reef-building (almost all Scleractinia) or non-reef-building (octocorals). Comparatively, deep-sea corals are mostly ahermatypic and azooxanthellate, encompassing both octocorals and hexacorals, and relying on heterotrophy for energy intake, qualifying as suspension feeders. As ahermatypic corals have adapted to build reef-like frameworks, and have developed in more diverse environments, they can be found at deeper depths and are more widely distributed (Dipper, 2022). The latter deep-sea corals may at times be zooxanthellate, a characteristic also present in many Octocorallia, zoanthids, sea anemones, hydrozoans, and giant clams (Forteath, 2001).

Inhabiting a great variety of environments, Scleractinians are more widely associated with shallow ecosystems; comparatively, Alcyonacea, including gorgonians, can be found in shallow and deep water; finally, black corals, although sometimes associated with shallow reefs, have been mostly studied in deep sea communities. Notwithstanding these general niches, deep sea Scleractinia do exist but mostly inhabit depths between 200 to 1000m, occupying the substrate as solitary polyps, within the Caryophylliidae family (Cairns, 2007). As for alcyonaceans, the maximum depth recorded is around 5850 m (Madsen, 1956, as cited in De Clippele et al., 2019); black corals may be found at depths over 8500 m, the deepest specimens of all coral orders (Yesson et al., 2017).

Coral reefs provide major cultural and economic services to humans such as fisheries (both commercial and recreational), tourism, cultural identity, scientific knowledge, and education. Other services include coastal protection and sediment generation in the global oceanic cycles (Woodhead et al, 2019; Ferrario et al., 2014). Coral reefs also play a significant part in biogeochemical and nutrient cycles, notably in carbon and nitrogen cycles through their fixation and recycling (Vanwonterghem & Webster, 2020). Further, coral communities contribute to other species as a feeding ground, nursery, habitat, critically facilitating ecological relationships and trophic networks across taxa. They also are greatly connected to adjacent habitats such as mangroves, seagrass meadows, or salt marshes, through dissipating tidal energy and providing nutrients (Woodhead et al, 2019).

The longevity of a coral community and its capacity to perform ecological services are reliant on certain biogeochemical conditions in the ocean. Seawater salinity levels globally are 35 ppt. Deep or shallow corals need very saline conditions but can tolerate salinity levels between 32 and 40 ppt (Henkel, 2010). Shallow water corals are light-dependent for their nutrient intake from their symbiotic photosynthetic algae, as 50% of the light is absorbed by the water within the first 10 m, such corals favor the euphotic zone, however, abundant reefs can still be found up to 30m deep if light penetration is still good and turbidity is low. Cold- and deep-sea corals, accustomed to waters between 4-13^{o}C, do not rely on sunlight as a main nutrient and energy source (Guinotte, 2005). The ocean's generic pH level is ranging between 8.0 to 8.5, with an actual average pH of 8.1 (Tanhua et al., 2015), but as corals are calcifying organisms, calcification is under optimal conditions at a pH level of 8.2 to 8.5 (Mollica et al., 2018). As previously mentioned, turbidity, as well as chlorophyll, are two other limiting factors that, if increased, can lead to a decrease in stony corals and phototrophic octocorals specifically (De'ath & Fabricius, 2010). Oceanic currents and waves, the main forcing mechanisms driving circulation, suspension and transport of sediment and nutrients in reefs communities, also have an important thermodynamic effect at different scales on the coral communities, where the seawater transport dictates temperature fluctuations and gradients in the water column (Rogers et al., 2016). On a biogeographical note, oceanic currents are also drivers of coral larval dispersion leading to new polyp or colony settlement. This phenomenon is enabled thanks to oceanic currents, winds, storms, and resulting rafting (Jokiel, 1984). In addition, tidal dynamics (low/high) and range will have a similar role to oceanic currents in cooling water temperature during the night or warming it up during the day in a tide-dominated reef ecosystem.

Challenges to Conservation

As coral-associated ecosystems play a considerable role for marine biodiversity and the ecological balance, the conservation of this complex and vulnerable marine realm is crucial. Threats of anthropogenic nature are increasingly affecting marine environments both directly and indirectly, whereby coral reefs and colonies continue to endure major losses in species diversity and surface area. Since 1994, humankind has acknowledged the existence of these threats, namely in the formation of the International Coral Reef Initiative (ICRI) during the First Conference of the Parties to the Convention on Biological Diversity (CBD). According to the National Oceanic and Atmospheric Administration (NOAA) (2016), all three global major threats to coral reefs are human-caused, including, land-based pollution and unsustainable fishing (direct), and Western-initiated global climate change (indirect).

Land-based pollution contributes to the degradation of marine ecosystems through runoff from urban and agricultural areas (non-point source) and direct pollutant discharge (point source), which encompasses industrial and sewage waste, agricultural pesticides and manure, pharmaceutical and chemical waste, or ballast water from ships and ports. These contaminants from a direct source (including sediments, chemicals, oils, debris) cause an increase in nutrient availability and alien compounds which can lead to a decrease in water quality, and an increase in eutrophication, harmful algal blooms, diseases, and disturbance of both the microbiome and internal system of the coral individual. Direct discharge of sewage waste into the ocean is usually the main source of pollution and coral reefs inhabiting areas close to river mouths or polluting point sources are particularly vulnerable, exposed to a continuous input of sediment and freshwater (Bryant et al., 1998). Such conditions promote algal growth and associated coral-competitor species. Furthermore, contaminated groundwater intrusion into the coastal waters slows the rates at which coral can calcify all the while, increasing the rates of coral bioerosion (Glynn & Morales, 1997)

Unsustainable fishing practices may physically destroy the reef's structure and deplete fish and other inhabitants of the reefs, threatening the ecological services and intrinsic balance of that ecosystem. Destructive fishing practices include using dynamite or cyanide (Polunin & Roberts, 1996, as cited in Roberts et al., 2002), a method deemed as cost-effective' in harvesting large amounts of live fish, often used to respond to high end culinary demands in food hubs like Hong Kong for example (Cesar, 2002). Illegal species poaching and trade for the aquarium market, mining coral and related sediments for construction materials, in addition to marine traffic or tourism, are other commonplace unsustainable practices (Cesar, 2002). Furthermore, intensive overfishing of herbivorous fish, and of apex predators such as sharks and groupers, have led to overgrowth of macroalgae on the reefs: preventing sunlight to reach the coral and their symbiont all the while consuming the oxygen needed for their respiration (Wilkinson, 2000), and to the development of new microorganisms, fungi, or bacteria, directly detrimental to the coral survival and increasing the competition for space. On the Caribbean reefs of Jamaica, Hughes (1994) noted that such algal encroachment over fragile coral communities, had stemmed from depletion of grazing fish from intense overfishing, exacerbated by hurricane episodes.

Moreover, an attendant rise in coastal and residential development, underwater mining, oil foraging and spills, also have caused massive coastal erosion, loss of reef coverage, destruction of deep-sea coral ecosystems and reduction of reproductive success in corals. Closely related to coral reefs, it is also other coastal habitats such as mangroves and seagrass meadows that suffer from near-coast development and erosion (Duarte & Cebrián, 1996). The coastal waters of Florida are a good concrete example of the interrelation of these three ecosystems and their fragile co-dependency in the face of the threat of coastal development. The removal of the mangroves for real estate and coastal construction contributed greatly to coastal erosion, decreasing shoreline sheltering from storm events all the while increasing the water turbidity and nutrient input from inland freshwater sources, endangering the coral reefs and the of seagrass beds in addition (De Freese, 1991). Concomitantly, all these extractive practices cause wholesale damage to reefs that can be permanent, and thwart the ecological resilience of this critical ecosystem.

Indirectly, the human-driven increase in greenhouse gases, notably carbon dioxide (CO2), released in the atmosphere has caused a higher presence of dissolved CO2 in the ocean, above its absorption capacity, leading to subsequent decrease of seawater pH and its acidification and an increase in seawater temperature. Further, as ocean temperature rises, so does destructive storm patterns, contributing to sea level rise and leading to more coral bleaching events (NOAA, 2016).

Natural threats also affect coral ecosystems such as storms, hurricanes, tides, weather patterns such as El Nino, extreme temperature variations, diseases, and predation (Wilkinson, 1999). Different organisms are known predators to coral species such as fishes, annelids, crustaceans, echinoderms, and mollusks. Such relation between prey-predator generally balances itself, but some cases of aggressive and damaging predatory behaviors have been documented such as with the crown-of-thorn starfish (*Acanthaster planci*) in the Great Barrier Reef (GBR). *A. planci* has therefore been considered an invasive species at worst, or an alien-specimen at best, Australia, and the Indo-Pacific region reef's second most significant cause of mortality due to the growing population of said specie (Rotjan & Lewis, 2008; De'Ath et al. 2012). Diseases have also increased intensely in recent times, more so in targeted regions such as the Caribbean Sea. The white pox disease striking mainly the staghorn corals (*Acropora palmata*) is an example of a virulent and well studies coral specific disease that brought about a loss of up to 88% of *A. palmata* in Floridian reefs ((Sutherland & Ritchie, 2004). The appearance of new diseases or predator proliferation are naturally occurring events, but their budding and accentuation can be attributable to anthropogenic activities (Wilkinson, 1999).

It is thus axiomatic why marine conservation remains a modern global priority. For instance, implementing Marine Protected Areas (MPAs), globally reducing industrial and transport related greenhouse gas emission, increasing research in coral biology, developing coral nursery and gardening, regulating fishing vessels and net sizes, implementing catch quotas, and pushing forward citizen-based projects represent a consortia of solutions currently used in marine protection and conservation. However, legislations are open to interpretation and quantitative regulations thresholds in fisheries or MPAs protection status and measures, are often too low (Christian et al., 2013; Schultz et al., 2022). Such conservation efforts have mainly targeted the biggest and more shallow reef ecosystems known, mainly in the Caribbean, Oceania, and south-east Asia to date, but mesophotic reefs (30 m +), which are usually the deeper extension of the reef, provision over two third of all coral species diversity. Deeper reefs may hence represent a genetic refuge for its counterpart as shallow reefs face more anthropogenic threats.

Conservation efforts would therefore need to be extended to adjacent reef areas and include MCEs (Mesophotic coral ecosystems) in global coral protection efforts as well as to other reef communities found in more neglected biodiverse regions (Lavericks et al., 2018).

II. <u>CABO VERDE</u>

Conservation efforts towards coral communities have been greatly focused on the largest coral reefs zones, principally in the Caribbean, Australia (Oceania), and South-east Asia since the beginning of the 21st century while other reef zones have been often overlooked and thus, understudied. These zones present high level of endemicity but also high economic dependency on fisheries resources, lacking in sufficient marine protected areas. One such zone is the insular country of Cabo Verde in the West African region, an important biodiversity hotspot which has been highly neglected in coral ecology and diversity research.

Geography, Climate, and Environmental Conditions

Cabo Verde is a country located in the eastern part of the Atlantic, about 450 km away from the coast of Senegal and the African continent. The country is located between 14°25′-17°75′ N and 21°50′-26°50′ W and is part of the West African region and Macaronesia geographical unit (Varela et al., 2022). The archipelago of Cabo Verde comprises 10 volcanic islands, and a few islets (15), totaling a surface area of 4.033 km^2 (Benchimol et al., 2009). The continental shelf covers a surface area of 5394 km^2 and the exclusive economic zone (ZEE), an area of 734 265 km^2. The country's ZEE's extensive distances, is spread between the islands, sharing maritime borders with two countries, Mauritania, and Senegal (Bravo de Laguna, 1985). According to a 2022 estimate (Central Intelligence Agency, s.d.), the population of Cabo Verde is close to 596 707, with a predominantly urban population (67.1%). Fisheries related activities (fish-processing, aquaculture), account for close to 80% of national exportations (International Trade Administration, 2022).

The archipelago is organized in two insular groups; the Windward Islands in the North: Santo Antão, São Vicente, Santa Luzia (which is uninhabited), São Nicolau, Sal, and Boa Vista, and the Leewards islands in the South: Maio, Santiago, Fogo, and Brava. The relief differs greatly between islands. The easternmost islands of Boavista, Sal and Maio are geomorphologically and topographically much more similar to each other, they are flatter, sandy, defined by wind patterns over a larger geological period. Most western islands (Santo Antão, São Nicolau, Santiago, Fogo, Brava) are very mountainous, rocky, and are geologically more recently formed (Bannerman et al., 2023).

Cabo Verde's climate is governed by several global atmospheric and oceanic systems dictating its two distinct seasons (dry season, rainy season), representative of the dry tropical and arid climate from the Sub-Saharan African zone. The four systems at play are the following: the subtropical Azores and Santa Helena anticyclones; the Intertropical convergence zone (ITCZ); the Canary Ocean current; the West African heat low (WAHL) (Lavaysse et al., 2016).

The archipelago is found at the front of three important oceanic and meteorological systems; it is found north of the ITCZ (Intertropical Convergence Zone), at the eastern boundary of the North Atlantic subtropical gyre and at the southern limit of the Canary Current. This Canary Current (CC) transports upwelled colder waters southwards along the African coast and deviates towards the west into the open Atlantic Ocean at approximately 20°- 25°N where it joins the North Equatorial Current (NEC), contributing to smoothen temperatures in Cabo Verde (Cropper, 2013; Fernandes et al., 2005). Other oceanic currents and systems are at play in the region such as the Guinea dome and the Mauritania current (MC). The Guinea current, the eastward continuation of the North Equatorial Counter current (NECC), is another driver for regional coastal upwelling and affects the guinea dome water dynamics (near-stationary circular current or cell) (Djakouré et al., 2017). The Guinea dome’s main drivers are the NECC, the NEC and the MC, produced by their associated cyclonic circulation (Lázaro et al., 2005). Forming at 10°N, south of Cabo Verde, it is very rich in chlorophyll A and nutrients, concentration peaking between September and November. The Mauritanian current, born from the NECC flowing towards the north of the west African coast, also carries warm oligotrophic equatorial water to the tropical eastern Atlantic (Lázaro et al., 2005).

One of the major upwelling regions in the world is the Northwestern African coastal zone (Karakaş et al., 2006). This upwelling exists from the Golf of Cadiz to Cape Blanc in Mauritania, reaching all the way to Cabo Verde’s frontal zone (CVFZ). The Canary upwelling and Mauritania upwelling are two zones under the same phenomenon with cold and richer deeper water reaching the surface due to north-easterly winds causing offshore flow of surface waters to be replaced by subsurface inflow via Ekman transport (Cropper, 2013). The upwelling phenomenon is affected by seasonality. Depending on its latitudinal position, upwelling zones between 20 to 25 ºC north occur year-round, while south and north of those latitude, the event occurs during winter (Northern hemisphere) (Fernandes et al., 2005). The

West African region is therefore exhibiting high primary productivity rates and important chlorophyll concentration (Karakaş et al., 2006). Such favorable conditions occur around the islands of Cabo Verde found closer to the CVFZ, most-affected, and fed by this north-eastern current (Benchimol et al., 2009).

Regarding the most important atmospheric systems at play, the ITCZ seasonal migration influencing the West African Monsoon, and the seasonality of the Azores high and equatorial low are co-interacting and affect Cabo Verde's climate (Cropper, 2013). Precipitation in Cabo Verde derives from the West African tropical Monsoon (WAM), which is dependent on the passage of the ITCZ north of the archipelago and its seasonal migrations. During the incursions of the ITCZ north (boreal summertime), southwest blowing winds (SW towards NE) bring with them tropical humid air masses and important rainfall episodes occur in Cabo Verde. Opposingly, northeast blowing winds (NE towards SW) occurring principally during the dry season (November-may) convey hot dry, sand-laden, air masses from the Sahara region, it is the Harmattan season (Neto et al., 2020). Around the same time of the year (December-June), the islands are under the influence of the eastern part of the Azorean high-pressure cell. This high-pressure cell is more defined and stronger during the winter all the while creating boreal trade winds (northeasterly winds) that weaken the Canary current and modify the intensity and paths of surrounding low-pressure systems, exerting a significant influence on Macaronesian precipitation (Neto et al., 2020; Cropper, 2013).

Understanding oceanographic patterns in relation to Cabo Verde's geography is crucial to comprehend distributional range of coral species and communities. Such parameters have often been explored to explain coral biogeographic affinities with other regions such as the Western Atlantic, the Mediterranean, Macaronesia, or mainland West African species (Nunes et al., 2011, Morri et al., 2000). It has also been said that the Canary current could be a limiting factor for coral communities' coverage increase (Lopes et al., 2014).

Threats to Cabo Verde's corals

Different environmental stressors threaten the world's ocean and terrestrial ecosystems globally. The insular country of Cabo Verde is no exception and shares many similar global and local environmental and anthropogenic threats, especially towards its coral habitats.

Fishing and tourism, while holding a significant economic importance in the country's development, also pose as major threats to its marine ecosystems and resources. Under estimation of fishing catches and uncontrollable foreign vessels activities, have led to overfishing and marine biodiversity and fisheries resources have declined in Cabo Verde, interlocking with a West African regional trend. As previously mentioned, destructive illegal fishing practices targeting corals have also taken places in various reef environments around the globe. Cabo Verdean reefs have not been an exception, this includes well-known habits such as the use of explosives and cyanide fishing (Almeida et al., 2014). Concerning tourism, urban development for touristic purposes is often done on environmentally sensitive areas, mostly in coastal areas, encroaching on shallow water environments to build marinas or other tourist attractions all the while not truly benefitting local communities. For example, the island of Boavista has seen an important increase in hotel development while being a major hotspot for marine biodiversity among all the islands of Cabo Verde (Benchimol et al., 2009).

The lack of marine protected areas, covering less than 1% of the coastal water poses a clear threat to fragile ecosystems such as reefs, stemming from a lack of funding and institutional infrastructure. Invasive species also pose a threat to Cabo Verde's marine diversity, specifically to corals. An invasive species, *Carijoa riseii* has already been identified, and while it is not yet known what consequences the presence of this specie will have on native ones, it has been found detrimental in coral reefs of the Pacific (Almeida et al., 2014). Uneven rainfall, discharge of polluted waters and damaged water systems infrastructures have led to important runoff and input of sediments or nutrients reducing the luminosity of coastal waters, the concentrations of nutrients, destabilizing the reefs and other sensitive environments. Signs of bleaching on *Siderastrea* pavements potentially related to such inputs in coastal waters near Baia das Gatas, Sao Vicente, have already been noted (Lopes et al., 2014). Solid waste also presents a challenge due to coastal development and port construction throughout Cabo Verde. An increase in marine traffic has also been observed in the last 20 years or so, leading to physical damage to coastal environment but also higher levels of polluted waters due to ballast water and other pollutant of chemical/toxic sources. For example, on the island of Sao Vicente, polluted waters have already seemingly increased the presence of algae in coralline communities (Lopes et al., 2014). Natural phenomenon such as droughts/flooding episodes are more and more frequent. The country is also vulnerable to hurricanes due to its geographical position in the Atlantic (Ministério da Agricultura e Ambiente, 2021, p. 37).

Biodiversity

Cabo Verde as a key hotspot for endemic species has been a known fact since the beginning of the 21st century. A study by Roberts et al. (2002), helped define 18 marine biodiversity hotspots for which conservation initiatives were urgently needed in order to prevent tropical reef species loss. Cabo Verde was ranked 11th out of 18th major biodiversity hotspot relatively to its richness of endemicity. The severity of threat towards these center of endemism was also assessed, and Cabo Verde was classified as 8th most vulnerable hotspot. The extensive dataset included 3285 species of corals, reef fish, snails, and lobsters (Roberts et al., 2002).

Cabo Verde boasts a considerable terrestrial and marine biodiversity. The archipelago harbors more than 20 species of cetaceans (12 species of whale and eight species of dolphin), five out of the seven existing sea turtle species, over 60 elasmobranchs' species (shark, rays, skates) and presents high endemicity of marine invertebrates (Benchimol et al., 2009; Hazevoet et al., 2010). Several factors are drivers of this diversity including atmospheric patterns and temperature gradients, topography, oceanic currents and processes, coastline distances, evolutionary patterns, and biogeography (Freitas, 2014).

➢ Cabo Verde communities and limitations

Although greatly underappreciated, coral species diversity and related habitats are well established in Cabo Verde. Indeed, Laborel (1974), indicated the presence of various coral communities in different countries of West Africa, this included Cabo Verde, São Tome, Senegal, Cameroon, Ivory Coast and Gabon. Especially in this region, coral species ecology and diversity's recent updated knowledge is lacking in scientific publications. As for Cabo Verde, its coral endemicity is poorly known but might be greater than anticipated. While a previous compilation by Spalding et al. (2001) found the presence of 15 coral species in the country, Wirtz (2022a, 2023) compiled a total of 26 species which included 8 Antipatharia and 18 Scleractinia species, also suspecting a greater biodiversity.

Coralline communities across the Cabo Verde islands are referred to as "reef islets", small agglomerations of different coral species (Lopes et al., 2014). While Monteiro et al. (2008), Spalding et al. (2001) and Lopes et al. (2014), advanced that no true coral reefs per se existed in Cabo Verde, they were referred to as mature coral communities, often occupying rocky reefs in patches. Other sources described the archipelago as having unique coral reefs compared to other archipelagos of Macaronesia, resulting from its tropicality (Spalding et al., 2007, as cited in Tuya & Haroun, 2009; Castro et al., 2022). Roberts et al. (2002) considered Cabo Verde to be an important hotspot of tropical reef biodiversity and a high priority zone for the global protection of reef habitats (Monteiro et al., 2008). Massive reef structures comparable to the Great Barrier Reef (GBR) or the Meso-American reef are usually associated to the definition of the term “reef”, nonetheless, small coral reefs or better yet, communities, are actually present in the coastal waters of Cabo Verde with some of them attaining the size of a football field (1 hectare) (Monteiro et al., 2008; Moses et al., 2003, as cited in Lopes et al., 2014).

Throughout the Cabo Verdean islands, these communities are reduced to sheltered bays where hydrodynamics is low (Almeida et al., 2014). Although the archipelago’s location in a tropical region would present a viable zone for a greater coral reef coverage, the exposure of the islands to strong wind systems throughout the year (Northeasterly Trade winds), to cold water currents (Canary current North), to the Equatorial Atlantic current South, in addition to the reduced insular shelf, prevent such growth (Lopes et al., 2014). Corals are also particularly sensitive to salinity, nutrients concentrations and temperature variations/conditions (Monteiro et al. 2008; Freiwald et al., 2004; Roberts & Cairns, 2014). As such, continental west coasts zones across the world are often dominated by upwelling zones which implies high nutrient input and cold-water temperatures, conditions which favor dense fisheries zones but limit coral habitat growth (Sheppard et al., 2017).

Regardless of their size, these coral communities thrive in a colder and more dynamic environment than most of the widely known barrier and fringing reefs found in Oceania, Asia, or the Caribbean, rendering their composition and structure quite unique. When comparing the Scleractinian group from Cabo Verde with that of the Caribbean, although smaller in specie composition (18 species identified to date VS. around 70 species in the Caribbean) (Wirtz, 2021, 2022a; Cortés & Reyes, 2017), certain species such as *S. radians* colony sizes were found to attain greater sizes of up to 10m (Moses et al., 2003) comparatively to their colony’s counterpart in the Caribbean coastal areas, with only reported sizes of up to 60 cm (Lewis, 1989).

➢ Cabo Verde coral species and endemism

Coralline communities observed across the archipelago are similar in specie structure, with an estimated richness of 18 species (Wirtz, 2021, 2022a) but mostly dominated by four main hermatypic corals from the genus *Porites, Siderastrea* and *Favia* (DGA, 2004, as cited in Lopes et al., 2014; Almeida et al., 2014). They thrive on three types of coral substrata, as described by Monteiro et al. (2008); sandy bottom substratum with bedrock patches (*Siderastrea radians* dominated), shallow rocky reef and platforms (Scleractinia-dominated with incursion of *Palythoa caribeorum*), and vertical or sub-vertical walls with rocky caves in coastal areas (Antipatharia-dominated, occasional Alcyonacea). The first two substratum mentioned, are confined mostly in the first 10 m of the water column, dominated by five species of Scleractinia; *Siderastrea radians*, *Porites porites*, *Porites astreoides*, *Favia fragum*, and a distant relative to corals, *Millepora alcicornis* (class: Hydrozoa) also mistakenly referred to as fire coral (Lopes et al., 2014). As for the third substratum, black corals (Antipatharia), and occasionally Alcyonacea could be found on vertical walls and caves between 10 and 20 m, varying in density according to location. While Scleractinia are usually confined to shallower rocky reefs or sandy bottoms, one specie can be found at various depths and substratum, identified as *Tubastraea*, suspected to be in fact *Atlantia caboverdiana* (Monteiro et al., 2008). Although coral species form very homogenous communities throughout the islands, some, dominated by pavements of *Siderastrea radians* of up to 2m, are deemed distinct at locations on Sal, Sao Vicente and Boavista islands (Lopes et al., 2014).

The exact degree of endemism regarding corals species is not known but at least five species of Scleractinia are presumably restricted to Cabo Verde: *Atlantia caboverdiana* (Capel et al., 2020), *Morabeza benitoi*, *Balanopsammia wirtzi* (Ocaña & Brito, 2013), *Thalamophyllia wirtzi*, *Leptogorgia capverdensis*. Of those, *A. caboverdiana* (2013), *B. wirtzi* (2015), *T. wirtzi* (2015), and *M. benitoi* (2019) were all described in the last 10 years, as well as *Euafricana wirtzi* (Ocaña & Brito, 2015; Wirtz, 2021; Wirtz, 2022a). More species are likely to be found around the islands (Wirtz, 2021). New specimens of black corals have already been singled out as potential new species according to Wirtz (2022b); one species of *Cirripathes*, two species of *Tanacetipathes*, and one new species of *Stichopathes* (Poliseno et al., 2017; Ocaña et al., 2015). Limited government resources and investments regarding scientific research, and restricted diving expeditions due to the absence of decompression chambers on national territory have hindered advancements in marine science. The scarce literature pertaining to Cabo Verdean corals is scattered inside literature concerning west Africa or Macaronesia and has proven hard to find. No centralized database can be found regarding corals in Cabo Verde and West Africa.

According to the available data on their distribution on the WORMS website, lack of literature on their presence in Macaronesia, and P. Wirtz (2020, 2022c, 2022d) Scleractinia pictorial catalogs from Azores and Madeira, the main four stony corals (*Siderastrea radians*, *Porites porites*, *Porites astreoides*, *Favia fragum*) found in Cabo Verde aren't found in the other Macaronesia islands and coral communities seem to be quite different between those archipelagos (Muhs et al., 2014). These four stony corals can be found in the Western Atlantic Ocean, in the Caribbeans and West Africa, while *F. fragum* and *S.radians* have also been found in the red sea near Saudi Arabia, and the latter, also in Fiji. *Schizoculina Africana*, a Guinean specie, is also found in Cabo Verde, typically growing on rocky bottom in areas of over 20 m deep.

To date, some of the Alcyonacea species are commonly found in Cabo Verde and West Africa but not in Macaronesia, including in Gabon (Friedlander et al., 2014), Gambia, Guinea, Sao Tome, and Principe or Senegal (Laborel, 1974). This commonality is often shared at the genus level encompassing: *Eunicella* (Grasshoff, 1992), *Leptogorgia* (Grasshoff, 1988) and *Carijoa* (Concepcion et al., 2010, as cited in Lopes et al., 2021; Lopes et al., 2021; Friedlander et al., 2014) as previously mentioned. Amongst Alcyonacea species found in Cabo Verde, *Carijoa riisei*, commonly known as the Snowflake Coral has been reported as an alien or even an invasive species in other key reef ecosystems. It is native to the Indo-West Pacific and can also be found in the Caribbean, the Western Atlantic (West Africa), the Gulf of Mexico and Hawaii, where this species has caused mortality in native Black Coral populations (Concepcion et al., 2008; Concepcion et al., 2010).

To date, coral communities have been observed and studied mainly in the following locations (Figure II.I):

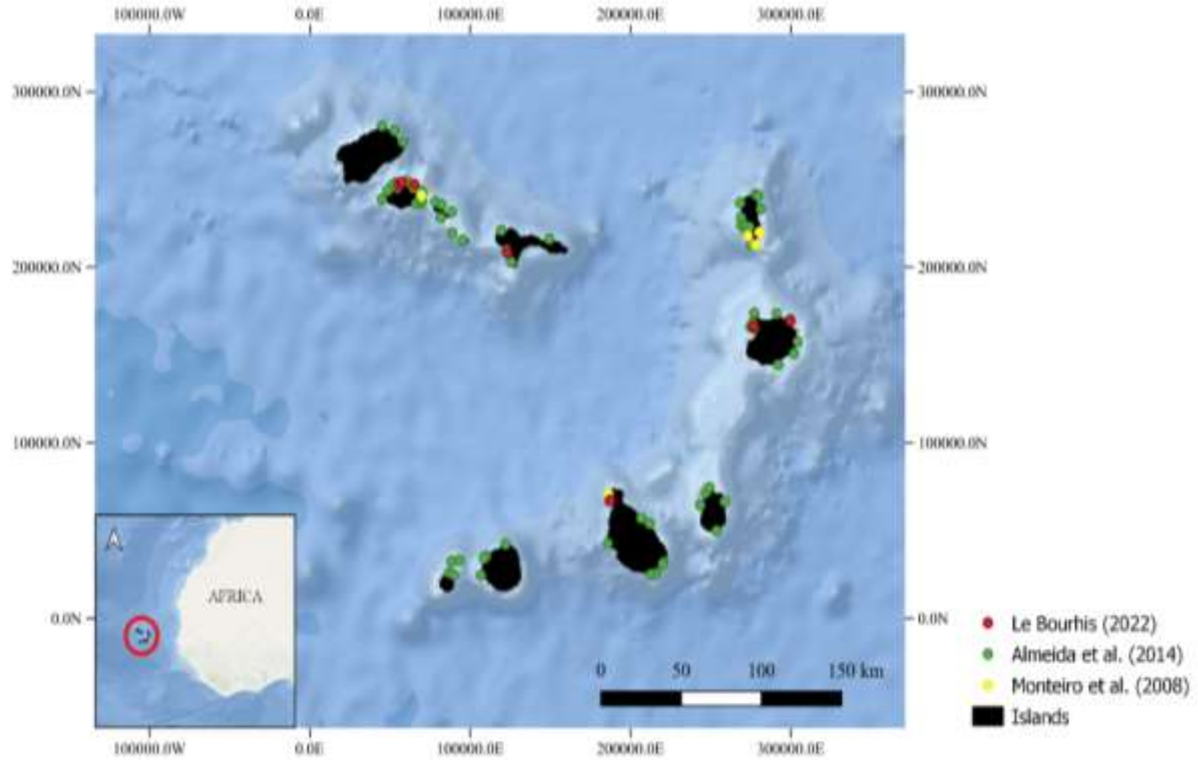

Figure II.I: Map of sampling locations for coral specimens in Cabo Verde (Cape Verde) from Almeida et al. (2014), Monteiro et al. (2008) and Le Bourhis et al. (2022)

Marine resources & Corals: Socio-economic Importance

Thus, although these coral communities are reduced in size, fragmented, and confined in specific locations, they hold not only a key ecological role, but also have a great socio-economic value for Cabo Verde. For this insular country, these reefs provide for a diversity of regulatory, supply, cultural, goods and services relating to the country's socio-economic growth (Lopes et al., 2014). Where coral communities can be found, human socio-economic activities were mainly commerce, tourism, and fishing. Reef associated species of fish, bivalves, crustaceans, accounts for the population's main protein intake source, thus alleviating food scarcity and malnutrition throughout the island's poorest communities. Ecotourism oriented towards the sea has also seen light in the last two decades with the recent establishment of dive-centers, international volunteering for turtle or bird conservation, whale and bird watching, etc. (Lopes et al., 2014).

Cabo Verde's main exportable resource is fish (mainly yellowfin, bigeye, skipjack tunas, as well as swordfish and blue shark), accounting for 85% of national exports. Fisheries directly or indirectly support the livelihoods of around 20% of Cabo Verde's population (FAO, 2008, as cited in Dancette, 2019; Sociedade de avaliaçao estratégica e risco SaeR 2015, as cited in Dancette, 2019). They account for 8.3% of the GDP (gross domestic product), an underestimated number, explained by partnership agreements with international fleets under-valuing fish quotas and the under-recording of a significant part of fisheries' economic activity. This data follows a regional trend, indeed West African fishing catches are deemed to be the most underestimated (by four times) in the world (Pauly and Zeller, 2016, as cited in Dancette, 2019; Benchimol et al., 2009). The country could be described as totally dependent on the ocean for transportation, trade, tourism, desalinized water, and its fish stock, for local consumption, market, and exports (Sociedade de avaliaçao estratégica e risco SaeR 2015, as cited in Dancette, 2019). Other than the ocean, sand and salt, no other resources can be exploited to increase Cabo Verde's economic development, lacking mineral resources compared to other similar-sized African countries.

Local coral communities harbor a large number of species of commercial interest, from demersal fishes, invertebrates, to other larger pelagic fish. The exact statistic of reef fish and other specie's contribution to national fisheries quotas is not known nor the economic value of the coral ecosystems for the country. Although artisanal fisheries mostly target species in coastal areas, many fish species are migratory, and therefore constitute a common target for larger foreign fishing fleets stationed at the 200 nautical mile EEZ borders, exacerbating unfair competition for the country's fisheries resources (Dancette, 2019). Demersal fish typically associated to coral and rocky reefs such as wrasses, damselfish, clownfish, parrotfish, moray eels are the main smaller-sized fish destined to local markets and consumption (100% of catch) caught by artisanal fishing methods (Lopes et al., 2014; Fortes, 2019). Yellowfin, bigeye, skipjack tunas, as well as swordfish and blue shark are coveted not only by large foreign and Cabo Verdean commercial vessels but also by artisanal fishing boats, increasing the competition for declining stocks (Dancette, 2019).

52.4% of the industrial fishing fleets in Cabo Verdean waters are foreign. EU countries such as France, Portugal and Spain monopolize commercial fishing rights (26.2%) followed by Japan and Senegal (8.9%) (Aquino, 2023). China also holds an important but complex role, often registering its fleets as national Cabo Verdean vessels. While remittances for fishing rights through foreign investments are low, but substantial, a majority of interested foreign parties devalue fishing stocks availability and catch quotas to pay less in terms of financial compensation (Aquino, 2023).

III. MARINE ECOREGION

Island biogeography and endemism

Biogeography is the science that studies the geographic patterns of distribution of marine and terrestrial species around the globe while examining the factors explaining those patterns. Its fundamental processes are dispersal, invasion, competition, adaptation, and extinction; complex concepts that have all greatly contributed to evolutionary biology (MacArthur & Wilson, 1963. To expand further on the theory of species' evolution, islands have been deemed an ideal ecological and discrete system to study, perceived as simplified microcosms of complex continental and oceanic systems. Islands, being numerous and diverse closed systems, thus pose as ideal natural replicates in which biogeography and insular biogeography theory can be tested and further developed (MacArthur & Wilson, 1963).

To background, Insular biogeography is the geographical analysis of the diversity of plants and animals' distribution on islands. Underlying island biogeography, there is a hypothesis that species diversity is positively correlated to the size of that island's landmass, but negatively related to the island's isolation from the mainland (Costanzi & Steifetten, 2019). In effect, larger, closer together islands can host more species then those smaller, and further apart. While a simplification of ecological conditions, an island's biota is deemed a result of a continuous interplay between immigration, extinction, and speciation processes that influence the species diversity on the island and its high rate of endemism (Whittaker et al., 2008). To elaborate, speciation is the splitting of a species of a single evolutionary lineage into many genetically-independent and reproductively-isolated lineages. Immigration refers to the arrival of new species to the island, while extinction refers to the loss of species from the island. It is therefore expected that larger islands or islands closer to the mainland will have a higher immigration rate and a lower extinction rate. Smaller and more isolated islands typically exhibit see a reverse tendency, with a low immigration rate and a high extinction rate (Costanzi & Steifetten, 2019). These rates are influenced by various abiotic variables including island isolation, island area, oceanographic conditions, habitat availability/diversity, geological history, climate, and biogeographic connections.

Species Connectivity: Regional Scale

- Macaronesia

Global geomorphological processes have led to two types of island formations: oceanic islands and continental islands. Oceanic islands such as Macaronesia's five archipelagos, were born from volcanic eruptions occurring on the ocean floor, are more recently formed than continental islands, and were never connected to the mainland continent. These archipelagos belong to two different European countries and one African country; for instance, Azores, Madeira, and the Savage islands are within Portugal, and the Canary Islands are owned by Spain, and Cabo Verde is an independent nation. Situated between 15° and 39°N in the North-Eastern Atlantic Ocean, Macaronesia's islands were historically classified as a biogeographically related group of islands (Sjögren, 2000, as cited in Freitas et al., 2019). Even so, this extended oceanic region has a diversity of climate associated with each archipelago, which contributes to it's a high habitat diversity, attendant with a broad range of latitudinal, altitudinal and island size variability (Florencio et al., 2021). This climatic gradient goes as follows: an oceanic temperate climate for the Azores, a Mediterranean climate in Madeira, the Selvagens and Canary Islands, and a warm arid climate in Cabo Verde (Fernández-Palacios, 2010, as cited in Florencio et al., 2021). Terrestrial habitats range from a desertic and semi-arid vegetation, which typify most of Cabo Verde, as well as the Selvagens' and Canary Islands' driest zones; additionally, habitats include humid green forests, dominated by laurel and juniper trees, which characterize the Azores, Madeira, and the mid-to high-altitudes of the Western and Central Canary Islands (del Arco-Aguilar et al., 2010, as cited in Florencio et al., 2021; Fernández-Palacios, 2010, as cited in Florencio et al., 2021). As well, each archipelago's geographical isolation from their adjacent continental mainland varies greatly. Flores (Azores) is 1500 km away from the Iberian Peninsula, while Fuerteventura (Canary Islands) is only 96 km off North Africa and Boavista (Cabo Verde), 450 km from Senegal (West Africa). Furthermore, geological age is extremely variable between the 31 islands, the most recently formed island being Pico (Azores) (0.27 Ma) and Selvagens as the oldest (29.5 Ma). Cabo Verde's islands are dated between 5.9 and 25.6 Ma with the eastern islands being older than the western ones due to the mid-Atlantic ridge divergent boundary (Cunha et al., 2017).

Across all their islands, the Macaronesia region is recognized as a significant center of biodiversity for both marine and terrestrial species, with high levels of endemicity and plant radiation for which comparison can be done with other insular hotspots like Hawaii or the Galápagos (Freitas et al., 2019; Madruga et al., 2016; Fernández-Palacios, 2010). Totaling a land area of 10 600 km^2, the region has over 5600 endemic species among the 23 000 terrestrial and marine species presently known (Madruga et al., 2016). Influential factors for this high endemism include the high distance from the mainland of these islands and the facts that they were never connected to the mainland, which under the theory of Island Biogeography, suggest high levels of speciation. While the degree of endemism seems higher for terrestrial plants than marine taxa, most biogeographers who have studied Macaronesia hypothesize that the colonization of these highly isolated oceanic islands can be mainly explained by long-distance oceanic dispersal, a process where oceanic currents and the distance to the mainland or the nearest island/shallow seamount is known to play an important role (Tuya & Haroun., 2009; Florencio et al., 2021; Freitas et al., 2019).

A recurring debate on Macaronesia's geographical and ecological classification has existed in the field of biological science for a long time. While early biogeographers grouped together these five archipelagos, terrestrial and marine organisms' distribution reveal the incoherence of Macaronesia as being a single biogeographical unit.

- Cabo Verde: Classification debate

Studies by Myers et al. (2000) and Mittermeier et al. (2004) from which the global biodiversity hotspot list of the IUCN was based, classifies the five archipelagos of Macaronesia in the Mediterranean basin hotspot. While the studied taxonomic groups were mostly terrestrial species, marine taxa were also included and criteria to qualify as a hotspot were; areas with exceptional concentrations of endemic species and experiencing exceptional loss of habitat (Freitas et al., 2019). Dansereau (1961, as cited in Freitas et al., 2019) was the first one to include Cabo Verde in the Macaronesia classification based on a study on cryptogamic plants throughout the Lusitanian province. The Macaronesia province as described by Spalding et al. (2007), falls in West Africa bioregion from the IUCN Bioregions (Kelleher et al., 1995, as cited in Castro et al., 2022).

Phytogeographical studies from the late 19th century pushed early on for an exclusion of Cabo Verde from Macaronesia based on its terrestrial flora, claiming its overall stronger flora specie affinity to that of adjoining Africa (Freitas et al., 2019). Some authors such as Lobin (1982, as cited in Freitas et al. 2019), went so far as to recommend that the term Macaronesia should be strictly employed in a geographical context and not to define a phytogeographical unit. A study by White (1983, as cited in Freitas et al., 2019) made a distinction between the lowland and mountain flora of Cabo Verde. It was found that the lowland flora of Cabo Verde was strongly Afrotropical. On the other hand, the endemic mountain flora of Cabo Verde was primarily related to species from Madeira and the Canary Islands. These species exhibited high levels of radiation, explained by an important recent colonization event (Kim et al., 2008; Romeiras et al., 2011; Mort et al., 2015, as cited in Freitas et al., 2019). A study focusing on the cryptogamic flora of Cabo Verde revealed that across all examined taxonomic groups, which included mosses, liverworts, and pteridophytes, the flora of Cabo Verde showed closer affinities with that of Tropical Africa rather than the cryptogamic flora found in the Azores, Madeira, and Canary Islands. As a result, this study rejected a broad definition of Macaronesia, which encompasses these neighboring Atlantic regions (Vanderpoorten, Rumsey & Carine, 2007, as cited in Freitas et al., 2019). In contradiction, in a recent biological study assessing terrestrial plants hotspots and related conservation strategies, Cabo Verde was yet again referred to as part of the Macaronesia region (Romeiras et al., 2016).

Cabo Verde’s native terrestrial fauna presents a more divided debate when it comes to its species taxa’s biogeographical patterns. The origin of the existing terrestrial bird population in Cabo Verde is primarily related to bird species found in the Palearctic region, which encompasses Europe, North Asia, and parts of Northern Africa, rather than the Sahel region, which is a transitional zone between the Sahara Desert and the West Sudanian Savanna (Hazevoet, 1995; as cited in Freitas et al., 2019). All native reptile's species from Cabo Verde are endemic and the archipelago has the highest number of endemic herpetofauna taxa in Macaronesia, within three genera: *Hemidactylus* (Gekkonidae), *Tarentola* (Phyllodactylidae) and *Chioninia* (Scincidae) (Vasconcelos et al., 2013). Phylogenetics reveal the endemic lizard genus *Chioninia* to be presumably originating from adjoining mainland Africa, and the *Tarentola* geckos, to be descendent of Canary Islands species (Miralles et al., 2011; Vasconselos et al., 2012; as cited in Freitas et al., 2019). In contrast, most arthropods taxa demonstrate strong affinities to the Afrotropical region. These phylogeographic patterns further emphasize the distinctiveness of Cabo Verde's fauna when compared to the other Macaronesian archipelagos (Borloti et al., 2020; Freitas et al., 2019).

Biogeographic research focused on the marine realm are scarcer than for the terrestrial realm in Macaronesia, but the region, encompassing a wide range of marine habitats due to its diverse climatic gradient, requires further investigation into marine biogeographical patterns and processes considering many known and cryptic species are yet to be identified and listed (Florencio et al., 2021; Ávila et al., 2018).

Compared to the terrestrial realm, Cabo Verde's marine biota's distinction from Macaronesia seems to be more unanimous all the while patterns of endemicity specific to each archipelago regarding marine flora and fauna taxa are not so evident (Florencio et al., 2021). Marine ecoregions of the World (MEOW) as a global classification system puts the Azores, Madeira, the Selvagens Islands and Canary Islands in the Lusitanian province (Temperate Northern Atlantic realm), while Cabo Verde, due to its tropicality, was categorized in the West African Transition province (Tropical Atlantic Realm). This province also included the Sahelian Upwelling ecoregion (Mauritania, Senegal, Gambia, Guinea-Bissau) (Spalding et al., 2007). The Lusitanian province, including four of the five archipelagos of the umbrella term Macaronesia's most northern islands, is dominated by rocky reefs. In comparison, Cabo Verde (West African Transition province), under the influence of a more tropical climate, is the only archipelago to harbor coral reefs, supporting, among others, hermatypic corals (Spalding et al., 2007, as cited in Tuya & Haroun, 2009; Castro et al., 2022).

In a phytogeographic analysis of the marine flora of the region, Tuya & Haroun (2009) also referred to Macaronesia as strictly the Lusitanian province. The latter, revealed a coherence for the distinction of Cabo Verde from the other archipelagos, stressing the divergence of brown, red and green algal species, and community composition, compared to the Lusitanian province. Regarding coastal fish species specifically, endemicity across the eastern Atlantic Macaronesia archipelagos differed. Cabo Verde had a higher degree of endemic coastal fish species while Madeira or Canary Islands had none. Azores was known to only have one endemic specie (Wirtz et al., 2013).

An ensemble of studies on gastropods, mollusks, echinoderms, macroalgae, brachyurans and marine ichthyofauna presented in a biogeographical review of Macaronesia from Freitas et al. (2019) also gathered that Cabo Verde's marine community structure and species diversity differed from the other archipelagos of the region. According to this multi taxa study echinoderms, (i.e., brittle stars, starfish, etc.), seemingly had no endemic species to the region or any specific archipelago. Only about 5.9% of the 152 species found in Macaronesia could be found in every archipelago, and Canary and Cabo Verde had the highest number of specie's diversity. The region had over 1312 species of gastropods, from which about 3.4% are observed in every archipelago. While the Canary Islands had the highest number of species (811), Cabo Verde had the highest number of endemic gastropods, 44.1% (268/608 total species). In addition, 177 species of shallow water brachyuran (crabs), existed in the region, and 17.5% of them could be found in every island groups. Compositionally, 8.5% of the Cabo Verde brachyuran species (117) were endemic and the total of species in Cabo Verde was similar to that of the Canary Islands (120). Endemicity for the other island groups was unknown. Bristle worms or polychaetes shared only a few species between the island groups (18 out of 683). Cabo Verde had the third most species (213) after the Canary Islands (465) and Madeira (300) but only 4.2% were endemic species. Concerning the seaweed species (macroalgae), the overall number of species for the region was the second highest for that taxonomic group, with 946 species. About 10% of the species could be found in every Macaronesia Island and endemism percentages specific to each island or the region were not known. In this taxonomic group, the Canary Islands showed again the greatest species diversity (689) while Cabo Verde (333) and Selvagens Islands (295), showed the lowest (Freitas et al., 2019).

Overall, the divergence in insular endemism for different marine taxa, is influenced by a confluence of multiple factors. For instance, Freitas et al. 2019 posit that endemism in Cabo Verde is driven by the concurrent effect of its tropicality and its biogeographical distance from the mainland Western African shores in addition to the presence of the Northwest African Upwelling (NWAU), which supports high amounts of bio productivity within this geography. On the whole, divergence and endemism in the Macaronesia Region may be affected by a suite of factors, including an islands distance from the continent, the islands age, oceanic currents, and nearby seamounts (as potential steppingstones). The diversity of factors continues to be broad, as, for instance, scholars have suggested legasodic glaciation effects may explain modern ecological community structures and the current diversity of the marine biota (Hawkins et al., 2000, as cited in Tuya & Haroun, 2009; Wirtz et al., 2013; Whittaker et al. 2008, as cited in Triantis et al., 2010).

CORAL TAXONOMY AND DIVERSITY – MOLECULAR TOOLS

Taxonomy of Corals

Coral reefs constitute one of the oldest and largest biological structures on Earth (Veron, 2008). Corals belong to the class Anthozoa within the phylum Cnidaria (Domain: Eukarya, Kingdom: Animalia), amongst the oldest phylum, thought to have originated around 740 Ma. The class Anthozoa consists of two monophyletic (i.e., sharing a common ancestor) subclasses: Hexacorallia (also known as Zoantharia or hexacorals) and Octocorallia (also known as Alcyonaria or octocorals)(Drake et al., 2020; Kayal, 2012; Park et al., 2012). The subclass Hexacorallia includes approximately 4300 species, comprising 6 orders: Actiniaria, Antipatharia, Ceriantharia, Corallimorpharia, Scleractinia, and Zoanthidea (Daly et al., 2007). Octocorallia contains around 3500 species, including soft corals, sea pens, blue corals, and gorgonians. They can be classified in the following three orders: Alcyonacea, Helioporacea, and Pennatulacea (Doumenc & van Praët, 1987, as cited in Daly et al., 2007; McFadden et al., 2010). Phylogenetic relationship between coral taxa is complex and through the use of molecular methods, their taxonomy has been consistently revised through time.

Overview of Molecular Tools

While the beginning of the molecular ecology field can be dated to the end of the 1800s, the invention of the Polymerase Chain Reaction (PCR) in 1983 represents the turning point in the application of advanced molecular techniques to answer different questions in ecology and phylogenetics (Monsen-Collar & Dolcemascolo, 2010). While morphological (i.e., the phenotypic characteristics of individual organisms) identification had been relied on the most in taxonomy, the advent of DNA-related methods such as DNA Barcoding through PCRs proved to be a cost-effective, accessible, systematic, and precise method to discriminate between cryptic species (Hebert & Gregory, 2005, as cited in Friedheim, 2016; Hebert & Gregory, 2005).

High extinction rates across all specie’s taxa have been driven by anthropogenic disturbances, posing as the greatest threat to biodiversity. Consequently, coral reefs, the most diverse marine ecosystems on earth, have suffered substantially, sparking the need to develop and implement new and more effective approaches to coral reef conservation (Neigel et al., 2007). Comprehensive bio inventories have thus been needed to rapidly assess new species and assign specimens to known species, and one of the most effective tools to do so has been DNA Barcoding (Neigel et al., 2007; Smith et al., 2005, as cited in Hebert & Gregory, 2005).

In such molecular research, coral phylogenetic relationships and identification have represented a challenge owing to; their phenotypic plasticity (mainly for Hexacorallia), potential gene rearrangements in some specific species, their mitochondrial genomes evolving relatively slowly compared to other animals and, low levels of interspecific divergence among distantly related taxa, especially in Scleractinia (Shearer et al., 2002, as cited in McFadden et al., 2011; Shearer & Coffroth, 2008).

In Metazoan animals, the mitochondrial genome comprises 37 genes organized as a circular molecule with 13 protein-coding subunits, two ribosomal (r)RNA subunits, 22 transfer (t)RNA genes, and one major noncoding control region (Boore 1999; as cited in Lin et al., 2011). The presence of those genes and their specificity is also consistent in Anthozoa but includes a variety of divergent characteristic throughout their mitogenomes. In Hexacorallia, fewer tRNA genes, necessary for mitochondrial translation, are present, and they include tRNA−met (Methionine) and tRNA−trp (Tryptophan) genes, exclusively (Barrett et al., 2020; Lin et al., 2011). In Scleractinia and Antipatharia (order), two group 1 introns could be found, one within the NADH dehydrogenase subunit 5 gene (ND5) and another one within the cytochrome c oxidase subunit I gene (COX 1) (Ramos et al., 2023; Celis et al., 2017, as cited in Barrett et al., 2020). Unique characteristics such as the existence of many noncoding regions between genes and the presence of complete stop codons in almost all protein-coding genes, were also found in Scleractinians (Van Oppen et al. 1999a b, as cited in Lin et al., 2011). As for the class Octocorallia, while the nuclear and mt genome are generally well conserved, an additional protein-coding gene, undescribed in any other metazoan mt genome, the MutS gene was found, holding a role in DNA mismatch repair (Brockman & McFadden, 2012, as cited in Ramos et al., 2023; Bilewitch & Degnan, 2011, as cited in Ramos et al., 2023).

DNA barcoding

DNA barcoding as a main tool to identify species and assess biodiversity has expended greatly in the search to systematically catalog species and demystify phylogenetic relationships across a wide taxonomic range. For Scleractinian identification, this method has presented clear advantages over morphological methods, as it has been utilized on any life stage (larva, juvenile or adult) and was not influenced by phenotypic plasticity (Shearer & Coffroth, 2008).

Similar to how Universal Product Codes (UPCs) distinguish commercial products at supermarkets, DNA barcoding utilizes a short and standardized region of the genome as a "barcode" to differentiate species. The process involves PCR amplification and sequencing of 400-800 base pair (bp) fragments or bigger, depending on the gene region, using “consensus” or “universal” primers, enabling the analysis of sequences variability within the DNA barcode region for precise identification and taxonomic classification (Hellberg et al., 2016; Hebert et al., 2003, as cited in Amaral et al., 2016). The use of thresholds to assess sequence divergence and its efficacy, principally when using the COI gene, has been controversial and widely debated, problematic for corals in general, and recommended to be specifically estimated for each taxonomic group (Neigel et al., 2007).

DNA barcoding can be done by targeting different genes in the mitochondrial DNA (MtDNA) or nuclear DNA (nDNA). While MtDNA genes generally present more advantages as barcodes in Metazoans because of their high copy number and rapid evolution, ensuing a higher yield of mitochondrial DNA, it is not the case for many species of Anthozoans (i.e., corals, sea fans and their kin) (Foran, 2006; Dawnay et al., 2007; Hellberg; 2006). It has been reported that their MtDNA evolves slower than for other marine species, and slower than their nDNA, their MtDNA holding less sequence variability than inside their nDNA (Hellberg, 2006). Thus, while the utility of a single barcoding gene region has been recognized, the use of an ensemble of mitochondrial and nuclear genes might be more useful to genetically identify species (Herrera & Shank, 2016; Vences et al. 2005, as cited in Shearer & Coffroth, 2008).

Among these genetic markers or primers, some have been used more often to discriminate between coral species in phylogenetical analysis such as, the mitochondrial 12S (rRNA), 16S(rRNA), MutS (in octocorals), the COX I and the Cyt B genes; or the nuclear genes 18S (nDNA), 28S (nDNA), ITS 1 and ITS 2 regions (nuclear rDNA) (Shinzato et al., 2021; Alexander et al., 2020; Korphage et al., 2022). In this study, the focus was put on some primers used conjunctly for specie discrimination purposes such as the “universal” mitochondrial primers for the COX I and MutS (for octocorals) genes, and on the nuclear primer for the 28S (large-subunit) ribosomal RNA gene, deemed successful in a comprehensive research that included Hexacorallia and Octocorallia species (McFadden et al., 2014; Korphage et al., 2022).

Genetic Markers in Coral Research

- Cytochrome C oxidase subunit I (COI or COXI)

Folmer et al. (1994), in an attempt to develop molecular techniques for phylogenetic studies of new deep-sea invertebrates, were the first ones to use the mitochondrial Cytochrome C oxidase subunit I (cox1 or COI) gene as a “universal” DNA primer. Since then, this mitochondrial gene has been used as a standardized genetic marker for members of the entire animal kingdom, including the phylum Cnidaria (Hebert et al., 2003a; Hebert et al., 2003b; Shearer & Coffroth, 2008;). Following its widespread success in species diagnosis, global reference libraries of DNA barcodes were developed from COI-5 sequences. A minimal 500-bp region of the cytochrome c oxidase I (COI) gene is necessary for data submission (Ratnasingham & Hebert, 2007). The responsible organization for all these global barcoding databases is the Consortium for the Barcode of Life (CBOL) (http:// www.barcoding.si.edu/). CBOL’s web based genetic database is called the Barcode of Life Data Systems (BOLD) (http://www.boldsystems.org), coordinating the data collection activities of worldwide barcoding projects and performing data analysis (Ratnasingham and Hebert 2007, as cited in Neigel et al., 2007). Other such repository exists like GenBank, a public genetic database of both nucleotide and protein sequences, including all submitted BOLD sequences (Hanner, 2005, as cited in Neigel et al., 2007). Both the BLAST search tool in GenBank and the BOLD identification engine, the main public repositories of DNA barcode sequences, have proven useful for taxonomic identifications (Meiklejohn et al., 2019).

Geller et al. (2013), using redesigned primers (degenerate positions and internal inosines) from the COI Folmer region (jgLCO1490 /jgHCO2198), obtained 9105 specimen’s sequences across multiple invertebrate phylum from San Francisco Bay (1419) and Moorea (7686). For the Moorea Biocode Project, specimens from the Scleractinia (133) and Alcyonacea (8) orders were included and successful amplification of 72.5% of all the sequences across taxa accurately occurred (70% for both Moorea and San Francisco Bay projects), where the Folmer primers (LCO1490/HCO2198) had failed (44%). These primers proved to amplify successfully but contrastingly, at the specie level.

Another study by Snell (1997), based on the COX I gene exposed that even between congeneric species, sequence divergence might be greater than for species of different genera (genus). Such rates, consistent with the concept of the Barcoding gap (Shearer & Coffroth, 2008) could be seen when comparing species such as *Diploria strigosa* and *Favia fragum* (both of scleractinian family Faviidae but two different genus), exhibiting very low divergence in COI nucleotide sequences (0.16%) while congeneric species *Montastraea cavernosa* and *Montastrea annularis*, had a sequence divergence of 2.4% (Shearer et al., 2002). When referring to said, "barcoding gap", the barcoding system based on COI implies that sequence divergence between most congeneric species is generally greater than 2% (Hebert et al. 2003b, as cited in Shearer & Coffroth, 2008), whereas intraspecific variation is under 1% (Avise 2000, as cited in Shearer & Coffroth, 2008). In the previous study, it was revealed that COI markers presented as problematic in determining an intraspecific variation threshold, mainly in scleractinians, where almost 40% of the congeneric Scleractinian species exhibited genetic distances of 0%.

COI as single barcoding sequence has its limitations. The reduced variability of this gene region and the lack of divergence in Anthozoan mitochondrial genome in general reduces the utility of this COI barcoding method in scleractinians and octocorals (McFadden et al., 2011; Neigel et al, 2007; Shearer & Coffroth., 2008). While degenerate primers from the COI gene show potential in specimen identification at the genus and specie level in general (Geller et al., 2013), the use of mitochondrial and nuclear genes, rather than a single gene, would be more efficient to genetically identify coral species (Vences et al., 2005, as cited by Shearer & Coffroth., 2008). In fact, it has been shown that amongst octocorals, multi locus barcodes could successfully distinguish up to 70 % of morphospecies (McFadden et al., 2014).

- MutS mitochondrial gene

Octocorallia mitogenome presents a unique protein-coding gene, MutS, which can only be found in this order's mitochondrial genome and in no other coral or Anthozoa taxa. Wolstenholme (1992, as cited in Pont-Kingdon et al., 1995) was one of the first to note that the Octocorallia MutS homolog was the only protein-coding gene other than the typical 13 energy-pathway protein gene present in in a taxa of Metazoa.

This gene has been widely used for species discrimination and often with the 28S nuclear (rDNA) and COXI mitochondrial genes (McFadden et al., 2011, 2014). This mtMutS gene has been favored in octoral molecular analysis for its reported high information content (Bilewitch

& Degnan, 2011), possessing the “highest level of systematically-informative variation amongst any protein-coding mitochondrial gene examined to date within octocorals” (McFadden et al., 2011, as cited in Bilewitch & Degnan, 2011). Furthermore, Van der Ham et al. (2009), found compelling evidence suggesting that the msh1 gene (i.e., MutS homologous genes in octocoral), unique to this particular cnidarian subclass, stands out as the most rapidly evolving protein-coding region in an otherwise slowly evolving mitogenome. Consequently, it emerges as the most promising candidate to serve as a mitochondrial barcode. Additionally, COI and MSH1 inter and intra specific genetic variations overlapped but pairwise comparisons among species of the same genus for MSH1’s genetic distances were generally 2 to 3 times greater than those for COI (McFadden et al., 2011). Using the MutS mitochondrial barcode, 81% (42/52) of species from the genus *Sinularia* (class: Octocorallia, Family: Alcyoniidae) were correctly identified while the success rate at identifying *Sinularia* species using a combination of mtMutS barcode and in situ colony morphology was 96 % (McFadden et al., 2014).

- <u>28S (large subunit) ribosomal DNA genes.</u>

The need to find a genetic marker better suited to identify hexa- and octocorals than COI has led researchers to delve into the use of other mitochondrial genes markers but also nuclear primers and using a combination of such primers. The 28S rDNA is a nuclear gene coding, with other ribosomal proteins, for the large ribosomal subunit called (28S rRNA) and has been increasingly used in recent phylogenetic analyses (Winnebeck et al., 2010). In a research on soft coral species from Palau (Octocorallia), species richness accuracy was generally higher when 28S was used, either alone or in combination with mitochondrial barcode (McFadden et al., 2014). Other contradicting studies have deemed the 28S rDNA to be more appropriate in resolving broad phylogenetic issues at the order relatedness level (Smith et al., 1992, as cited in Chen et al., 1995).

The suitability of the 28S rDNA marker, but also the MutS mtDNA marker, was further demonstrated by Mcfadden et al. (2017) for its genetic species discrimination success and reiterated in a recent phylogenetic study by Korphage et al. (2022). While using genetic methods and proteomics methods to identify corals species around Iceland, the use of a combination of two mitochondrial markers (MutS and COI) paired with two nuclear markers (ITS2 and 28S) allowed to distinguish 17 out of 18 presumed species, including both octocorals and hexacorals. The study also concluded that the markers mtMutS (ND42588F/MUT3458R, 870 bp) and 28S rDNA (28SFar/28SRar, 800 bp, or 28SFar/28SRab, 650 bp) were the most suitable barcodes. Such findings should prompt the need to build reference libraries based on the 28S sequences as well as the MutS sequences, lacking behind the already extensive reference libraries available for the COI barcode.

As a final consideration, the lack of concordance amid the various molecular markers used in coral phylogenies is not unusual, more so in recently separated clades broadly (Radice et al., 2016, as cited in Quattrini et al., 2019). Studies on octocorals show that mitochondrial and rDNA barcodes may be useful in species assessments for some taxa but not all. To achieve more reliable species delimitation, researchers recommend a) considering multiple markers, (comparing them for example), and other lines of evidence (McFadden et al., 2017, as cited in Quattrini et al., 2019) and b) complementing genetic information with morphological methods.

For the purpose of this study of octocorals and hexacorals in Cabo Verde, a multi marker analysis was prioritized, following findings from Herrera & Shank (2016) and Shearer & Coffroth (2008), as this study is the first to aim at bridging the molecular knowledge gap on coral species diversity in Cabo Verde. An emphasis will be put solely on three coral orders, Scleractinia (true corals), Antipatharia (black corals), and Alcyonacea (soft corals) as following previous findings in the region (Laborel, 1974; Morri & Bianchi, 1995; Morri et al., 2000; Spalding et al., 2001; Monteiro et al., 2008; Moses et al., 2003; Lopes et al., 2014; Almeida et al., 2014). Building this DNA barcode library is a novelty in the field concerning this region and through it, we hoped to increase biodiversity knowledge and discover cryptic species, anticipated to represent up to 38 species contrarily to previous compilations.

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A DNA barcoding approach to assess coral species richness and biogeographic affinities of Hexa- and Octocorallia in Cabo Verde

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ABSTRACT

Coral reefs are the most biodiverse marine ecosystems on earth. Often described as biodiversity hotspots, they cover less than 1% of the ocean floor but host more than 25% of all marine species. However, coral reefs are undergoing massive degradation around the world, prompting a need for further studies on global coral populations to support their protection. Tropical reefs in particular, are essential for biodiversity but are understudied in many parts of the world and therefore insufficiently understood. This is the case in Cabo Verde, currently listed as 8th among endangered biodiversity hotspots. With less than 1% of national waters protected, the archipelago lacks data and knowledge on its species diversity, a regional tendency for West Africa. Thus, this study aimed to assess shallow coral species richness (< 50m depth) and consolidate current species diversity knowledge within Cabo Verde, to reveal cryptic species before they might become threatened or disappear. While 21 species were morphologically identified, molecular methods were used to build the first DNA barcode library for Cabo Verde's hexacorals and octocorals. The use of complementary mitochondrial (COX1 and MutS) and nuclear (28S) DNA markers, field identification, and litterature-based species lists helped to successfully identify 27 samples to the species level and three others to the genus level, which previously had only been morphologically identified. *Balanopsammia wirtzi* constituted a new barcode for the region and the alien species *Carijoa riisei* was confirmed through barcoding of mitochondrial COI and nuclear 28S genes. Phylogenies confirmed biogeographic affinities of three out of the four dominating hermatypic species (*S. radians, P. porites, P. astreoides*) to be closely related to the Caribbean. The study also revealed noteworthy differences in species richness between Cabo Verde and the other Macaronesian archipelagos, sharing a few common species throughout the Scleractinia and Antipatharia order and only the species *Eunicella verrucosa* in the order Alcyonacea. None of the dominating four hermatypic species in Cabo Verde could be found in any other of the Macaronesia islands. This research represents one of the first attempts, and the most exhaustive one to date, to characterize the coral species composition of Cabo Verde using DNA barcoding, and produced a geographically referenced coral DNA catalog baseline that will inform further research, education and conservation initiatives.

1 INTRODUCTION

Oceans harbor fragile but crucial intertwined marine realms, that provide many ecosystem services (i.e., significant production of atmospheric oxygen) and host tremendous biodiversity.

Specifically, coral reefs across oceans are among the most biodiverse ecosystems on earth, said to provide a wide variety of ecosystem services for more than one million species, including humans (Environmental Protection Agency [EPA], n.d.). Often described as 'biodiversity hotspots', reefs cover less than 1% of the ocean floor but host more than 25% of all marine species (Fisher et al., 2015). As our current understanding of global biodiversity is limited, estimates for the number of marine species housed in coral reefs may be up to three times than is currently known (McFadden et al., 2014). However, this vast genetic and species diversity has the potential to be unrealized, as high rates of extinction affect all ecosystems, drastically accelerated due to Western-initiated anthropogenic disturbances. As the effects of climate change accelerate, Known and cryptic species are disappearing faster than they can be catalogued (Lees & Pimm, 2015), presenting a huge challenge among marine biodiversity studies. Specifically, global warming, severe storms, diseases, and predation, such as by crown-of-thorns starfish in the Great Barrier Reef, for example, all have naturally significantly affected coral reef ecosystems (De'ath et al., 2012, as cited in Shinzato et al., 2021). Overfishing, land-based pollution, coastal development, and tourism represent the main direct sources of anthropogenic threats and have disturbed reef and coral communities negatively at different scope depending on their location (Edinger et al., 1998), while sea water temperature change and CO2 concentrations shifts, causing coral bleaching and incapacitating structural calcification processes, represent the main indirect effects from human-induced activities.

Compounded with their slow growth, corals development is similarly being outpaced by their rapid degradation. The loss of reef coverage losses impacts marine communities in ways that are still often misunderstood and is especially concerning within older community assemblages where anthropogenic stressors may lead to irreversible changes within coral reefs (Hughes, 1994). Concomitant to globally high rates of coral reef coverage loss (more than 14% worldwide since 2009), and the attendant species loss, which is greater than what can be catalogued, coral ecosystems are among the most vulnerable biodiverse habitats on earth (International Coral Reef Initiative [ICRI] et al., 2021).

As corals are a key species in marine ecosystems, , damage to coral reefs has resounding ecological consequences to their associated ecological services. For instance, reefs play a significant part in biogeochemical and nutrient cycles, notably in carbon and nitrogen cycles through their fixation and recycling (Vanwonterghem & Webster, 2020). They contribute to other species as a feeding ground, nursery, and habitat, facilitating ecological relationships and trophic networks. They also are greatly connected to adjacent habitats such as mangroves, seagrass meadows, or salt marshes, through dissipating tidal energy and providing nutrients (Woodhead et al, 2019). Coral reefs are also an important economic and social system for humans. Fisheries, tourism, cultural identity, scientific knowledge, advances in medical science, sediment generation, carbon sequestration, and coastal protection are just some of the central ecological services rendered by these vital players (Woodhead et al, 2019; Ferrario et al., 2014; Cesar et al., 2003).

Corals are classified in the subclass Hexacorallia and Octocorallia and hold complex phylogenies and evolutionary divergence. Each subclass is further divided into orders, three of which are particularly emblematic, Scleractinia ("stony coral"), Antipatharia ("black corals") and Alcyonacea ("soft corals") (Fabricius & Alderslade, 2001). On top of harboring great communities of many different taxa, corals include more than 7000 species (Daly et al., 2007; Doumenc & van Praët, 1987, as cited in Daly et al., 2007), across a wide range of habitat. Coral reefs specifically, are built from hermatypic species, are confined to shallow euphotic (less than 20 m) warm waters between 20 to 28^{o}C (Spalding et al., 2001; Swart, 2013), occurring in tropical and sub-tropical zones. Therefore, corals are found to build reefs in warmer waters, while also forming biodiverse coralline communities or colonies in colder and deeper waters.

Western continental coasts across the world are often dominated by upwelling zones, conferring high nutrient inputs to support primary production, as well as cold-water temperatures, which favor dense fisheries zones but limit coral habitat growth (Sheppard et al., 2017). Conversely but not exclusively, Eastern continental coasts have been known to harbor great coral barriers and the main focus of conservation and scientific research, overshadowing upwelling dominated zones, overlooked in coral connected research and conservation initiatives. The Eastern Atlantic Ocean, along the coasts of West Africa, is an internationally important fishing grounds boasting great endemicity, threatened by an important regional underestimation of fisheries catches (the most underestimated in the world, by four times) (Pauly and Zeller, 2016, as cited in Dancette, 2019; Benchimol et al., 2009). In parallel, this poses a socio-economic problem, West Africans highly depending on these ocean resources, with a staggering 56% of the regional GDP derived from ocean services (The World Bank, 2017). It is estimated that over 6.7 million people depend on these fisheries for their food and livelihoods and that regional fisheries generate over 3.5 billion USD per year in landed value, dominating its GDP in terms of foreign trade (Belhabib et al., 2015). This trend can be even more important at a national level, with 85% of Cabo Verde archipelago's exportation being related to blue economy, for example (FAO 2008, as cited in Dancette, 2019; Sociedade de avaliaçao estratégica e risco SaeR 2015, as cited in Dancette, 2019).

Within these heavily used fishing regions, shallow and deep coral communities extend from Mauritania, Senegal, Gambia, Guinea, Cameroon, Ghana, Ivory Coast (Buhl-Mortensen et al., 2023), all the way to Gabon (Friedlander et al., 2014), and in the archipelagos of Sao Tome and Principe (Laborel, 1974) and Cabo Verde (Monteiro et al., 2008; Moses et al., 2003; Lopes et al., 2014; Almeida et al., 2014; Spalding et al., 2001). As coral reefs support fish communities directly in the provision of habitat and nurseries, among other ecosystem services, the importance of assuring their long-term viability should be axiomatic.

Beyond supporting economic prosperity within West Africa, these regions are also tremendously biodiverse. Coral specimens found in this region are mainly orders Scleractinia, Antipatharia, and Alcyonacea, which are linked to species identified and distributed in the Caribbean (Nunes et al., 2011), the Indo-pacific (Lopes et al., 2014; Concepcion et al., 2008; Concepcion et al., 2010), and the Mediterranean Sea (Buhl-Mortensen et al., 2023). In a study by Roberts et al. (2002), Cabo Verde is postulated as eleventh among eighteen of the richest centers of endemism in the world, and eighth in terms of facing imminent threats to habitat and species loss, thus highlighting it as a major biodiversity hotspot and an area of high conservation priority. Explanations for such patterns of diversity and endemicity were put forth by Freitas et al. (2019), including the archipelago's tropicality, biogeographical distance from the Western African mainland shores (~450km away from Senegal), in addition to the presence of the Northwest African Upwelling (NWAU) which supports high amounts of bio productivity within this area.

In studying Cabo Verde, comparisons for species range and distribution patterns are often drawn at a coarser scale within Macaronesia. Macaronesia includes Atlantic islands of Cabo Verde, the Canary Islands, Madeira, Azores, and the Selvagens islands. Cabo Verde's inclusion in this regional group has been mostly based on a geographic point of view, and biogeographic relationships for terrestrial and marine species have been often debated (Freitas et al., 2019; Florencio et al, 2021). Nevertheless, fish, echinoderms, gastropods, crustaceans, polychaeta, and macroalgae taxa have revealed important differences in species richness and distribution across the five archipelagos. While some species are commonly found across all of these insular territories of Macaronesia, endemicity indexes vary greatly with the more tropical islands of the Canary and Cabo Verde, having high values for restricted-range species (Freitas et al., 2019). Such a biogeographic review of Anthozoa (coral and anemone species) in the region is yet to be achieved.

Indeed, the uniqueness of Cabo Verde’s coral communities is a known fact amongst scientists studying Macaronesia and West Africa (Laborel, 1974; Spalding et al., 2001; Roberts et al., 2002; Monteiro et al., 2008; Lopes et al., 2014; Wirtz, 2022b; 2022c) and has been noted in government environmental reports (Almeida et al., 2014). However, molecular-based research on the taxonomic diversity of the Anthozoa group is lacking, as no official coral monitoring programs exist at either national or regional levels. This urgency is further emphasized by the lack of coastal protection in Cabo Verde, where only about 1% of national and coastal waters are under some level of marine protection, while the country registers a booming urban development (UNDP, 2009; Peters et al., 2016). About 18 species have been identified officially (Wirtz, 2021, 2022b, 2022c), studies argue upwards of 38 species could be present (Zibrowius, 1980; Ocaña & Brito, 2004; Molodtsova, 2006; Monteiro et al., 2008; Raddatz et al., 2011; Lopes et al., 2014; Ocaña et al., 2015; Zibrowius et al., 2017; Ocaña et al., 2019; Capel et al., 2020; Wirtz, 2023). Therefore, it is paramount to further coral species-specific diversity and abundance data to implement much needed effective conservation and management strategies.

In recent years, a multitude of tools have been developed to successfully monitor and protect coral communities, allowing for faster data collection at greater precision. Computerized methods such as real-time satellite imagery aided by AI technology or modelling have proven useful in global coral reef and long-term monitoring initiatives, while still being developed for smaller scale resolution application (Apprill et al., 2023). Underwater Visual Census (UVC) through scuba diving or snorkeling, video census, 3D photogrammetry mapping, are methods that have all been commonly used in reef monitoring, these approaches are time-, effort-, and resource-intensive (Apprill et al., 2023). Comparatively, molecular methods of eDNA metabarcoding and DNA barcoding support a deeper understanding of specific richness and diversity, as well as accurate taxonomic identification of cryptic species and those with important phenotypic plasticity (Shearer & Coffroth, 2008). Molecular methods have proven to be cost and time-effective, complementarily used with other monitoring techniques (Hebert & Gregory, 2005, as cited in Friedheim, 2016; Hebert & Gregory, 2005). Molecular analysis methods based on the barcoding of genetic sequences of species are built from different markers/primers which can be mitochondrial or nuclear DNA regions. It has been reported that corals and, in general, Anthozoa’s mtDNA, evolves slower than for other marine species, and slower than their nDNA, exhibiting less sequence variability than inside their nDNA (Hellberg, 2006). Even so, the most universally used barcode, from which global DNA repositories such as the Barcode of Life have been built, is the mitochondrial gene COX1 (COI). While degenerate primers from the COI gene show potential in specimen identification at the genus and specie level in general (Geller et al., 2013), the barcode gap solely based on such mitochondrial gene has revealed congeneric divergence to be most often than not, higher than between genera. The use of mitochondrial and nuclear genes, rather than a single gene, is therefore more efficient to genetically identify coral species (Vences et al., 2005, as cited by Shearer & Coffroth., 2008). In fact, it has been shown that amongst octocorals, multi locus barcodes can successfully distinguish up to 70 % of morphospecies (McFadden et al., 2014). Such a multi locus analysis was already conducted in Cabo Verde, and, using mitochondrial and nuclear markers (COI, an intragenic region between COI and trnM, a portion of the ITS1, 5.8S, ITS2 2 and a portion of 18S and 28S), a new genus, *Atlantia,* as well as a new species (*Atlantia caboverdiana*), were successfully delimited from their previously attributed genus *Tubastraea* (Capel et al., 2020).

It is on the unique geographical setting of Cabo Verde, and the important biogeographic distinctions already established from the Macaronesia region that we seek to investigate whether coral assemblages are likewise discursive. Thus, the objective of this study is to characterize the species diversity of soft and hard corals and the coral community assemblage of Cabo Verde. More thoroughly, we aim at 1) creating a DNA barcode library based on COI, 28S and MutS, specific to corals of Cabo Verde, in order to confirm and/or correct morphological taxonomic classification; 2) investigating the presence of cryptic species or unexplored diversity; and 3) assess if the coral species (Scleractinia, Alcyonacea) of Cabo Verde are genetically different from the species of the same genus in other regions, particularly in Macaronesia. This is a first attempt at creating a DNA barcode library specific to corals of the country, linking coral phylogenies with a biogeographical analysis of coral specie richness, endemicity, and affinities in a country from the West African region. Ideally, this research can support future efforts aimed to assess and monitor the diversity of coral communities in Cabo Verde, and support protection policies of this vulnerable ecosystem.

2 MATERIALS AND METHODS

2.1 CABO VERDE SPECIES LIST

To ensure the genetic sequence reference database's credibility for Cabo Verde, we compiled a list of Hexacorallia and Octocorallia previously recorded or suspected to be present (). These included coral ecology books (Freiwald & Roberts, 2005; Spalding et al., 2001), government and NGO reports (Almeida et al., 2014; Freiwald et al., 2004), records from online open-access databases, including World Register of Marine Species (WoRMS)), the Global Biodiversity Information Facility (GBIF, www.gbif.org), and the Ocean Biogeographic Information System (OBIS, www.obis.org). Peer reviewed literature was also included (Zibrowius, 1980; Boekschoten & Borel-Best., 1988; Morri et al. 2000, Moses et al., 2003; Ocaña & Brito, 2004; Molodtsova, 2006; Monteiro et al., 2008; Raddatz et al., 2011; Lopes et al., 2014; Ocaña et al., 2015; Zibrowius et al., 2017; Ocaña et al., 2019; Capel et al., 2020; Wirtz, 2023).

While all species found in Cabo Verde were included in this list, the objective of this record was primarily in order to document species whose habitat distribution was comprised between 0-50m depths, considering previous coral communities records from shallow areas across the archipelago (Morri et al. 2000; Monteiro et al., 2008; Lopes et al., 2014).

2.2 SAMPLING

Hexacorallia and Octocorallia tissue samples from various specimens (n = 62) (presumed Scleractinia: 41, Antipatharia: 13, Alcyonacea: 8) were collected in Cabo Verde between the 13th of march and the 26th of April 2022 by scuba diving and snorkeling at various depths and locations on the following four islands: Sao Vicente, Sao Nicolau, Boavista and Santiago. Samples were taken at nine different locations through these islands (**Erreur ! Source du renvoi introuvable.**).

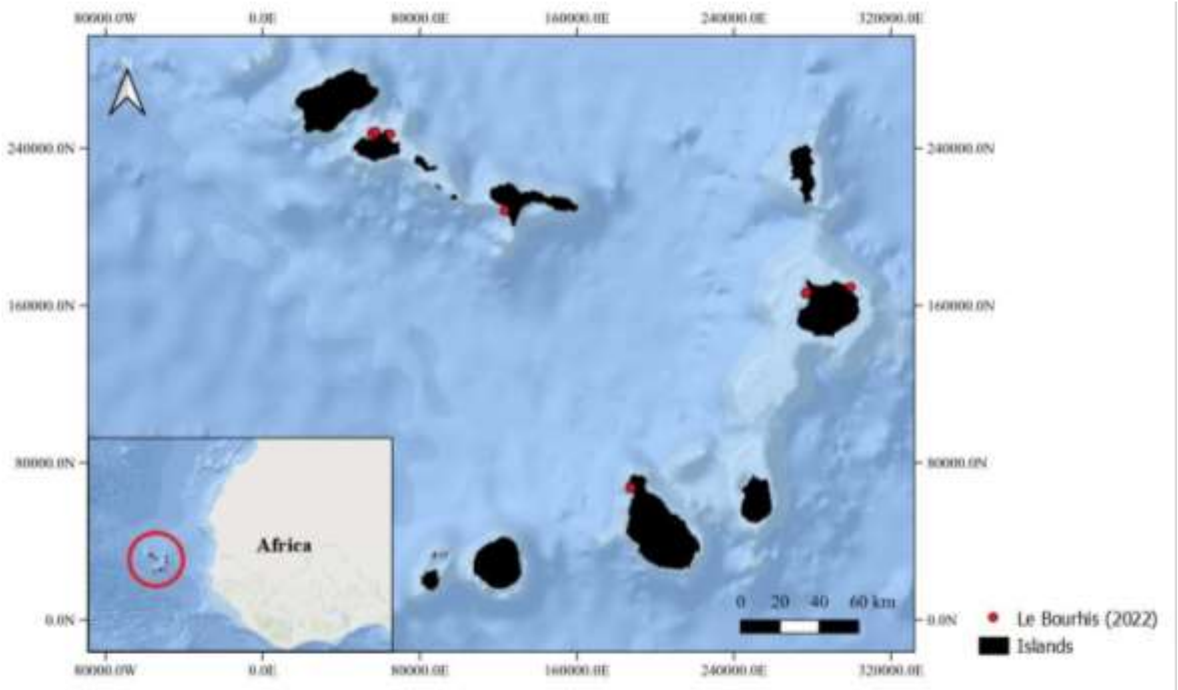

Figure 2.2.1: Map of the islands of Cabo Verde (Cabo Verde) where the samples for this research were taken

A depth interval of 20-50 m was selected, as to delimit the general shallow photic zone where hermatypic corals can be found (Cairns, 2007). Coral specimens' sightings for Cabo Verde were also often confined to that depth gradient and diving limitations in the archipelago would not allow to go deeper (Monteiro et al., 2008). Coral samples were retrieved by scuba diving at depths between 14-24 m by snorkeling between 0.5 to 3 m, some species were found at depth diverging from their theoretical distributional depth gradients. Although the distribution of coral species is seemingly heterogenous throughout the islands, as many species as possible were retrieved in order to build the most complete barcode library of coral species for Cabo Verde. Once taken out of the water, the samples were transferred to a sterilized container with 96% undenatured ethanol. The samples were processed within 24-48h of collection, kept frozen until use. In a sterilized laboratory, each sample was fragmented in smaller pieces (1/1.5 cm x 0.5/0.7 cm) and placed in 2 ml Eppendorf tubes containing 96% undenatured ethanol. Pincers and a knife were used to fragment the samples, sterilizing them with alcohol and bleach, between each sample treatment. The 96% undenatured ethanol was changed after 24h in each tube and all the samples were stored at -20°C or under coldest possible conditions. Each Eppendorf tube was labelled according to Island: location: morphological identification: specimen number, and vegetable parchment with the same sample label was placed inside the Eppendorf to prevent misidentification. All coral samples were stored at the Centro de Ciências do Mar (CCMAR), in Faro, Portugal.

2.3 DNA BARCODING

2.3.1 DNA Extraction

DNA extraction was carried out in the laboratories of the Center of Marine Sciences (CCMAR) with the use of a DNeasy Blood & Tissue Kit (QIAGEN, Valencia, CA, USA) per the manufacturer's instructions. Lab benches were disinfected with 60% bleach solution followed by 96% ethanol to avoid sample cross-contamination. All non-disposable material used in the protocol (e.g., pipettes, tweezers, and scissors) were cleaned with 60% bleach prior to each use, whereby tweezers and scalpels were disinfected with ethanol 96% after each sample fragmentation. The polyps were first removed by a sterile tweezer for DNA extraction. Up to 25 mg of tissue was ground in small pieces: once lysates were obtained, 180 μL of buffer ATL and 20 μL of Proteinase K were added and vortexed before incubating the samples at 56 ºC overnight. The completion of the extraction protocol was spread over a 48h period and the remaining steps after incubation followed the manufacturers protocol. Modifications to the recommended protocol include an extra centrifugation cycle at 10 000 g for 1 minute was added, whereby the supernatant was transferred into a new tube immediately after. Additionally, DNA was eluted into two batches, with two elutions of 50 μL of Buffer AE/each, performed in separate tubes. Incubation and centrifugation times were also increased to 2 minutes. DNA was stained with Gelred (Biotium, Inc) and was visualized with 0.8% agarose gel electrophoresis, for 29 samples out of 62.

As certain extraction seemed to yield diverging and poor DNA concentration according to the gel electrophoresis reads, some problematic samples were quantified in Nanodrop 1000 (ThermoFisher) to get an idea of the difference in their measure of concentration of DNA and purity.

2.3.2 DNA Amplification and sequencing

Polymerase chain reactions (PCRs) were conducted following initial and touch- up protocols as presented in Table 2.3.1, with the primer pairs in Table 2.3.2. General guidelines of the PCR protocol (PCR conditions and reagents) from GoTaq G2 Flexi DNA polymerase (Promega Corporation, Madison, WI, USA) were followed. Reagent volumes diverged according to two variables: primers and taxonomic level (subclass). Concentrations of each reagent did not change but volumes were modified according to the primer pair used during each PCRs. For PCRs using primers of the COI mitochondrial gene applied to Octocorallia, reactions were carried out with 6.2 μL of Milli Q (H_2O), 5 μL of Buffer 5x, 2 μL of $MgCl_2$, 1.3 μL of dNTPs (concentration of 8 mM: 2mM/dNTP), 2.5 μL/primer (forward and reverse), and 0.5 μL of Taq polymerase. Amplification reactions with mitochondrial gene COI and nuclear gene 28S primers for Hexacorallia were carried out with the same volumes and concentrations as for Octocorallia samples, except for the following reagents: 7.2 μL of volume for Milli Q (H_2O) and 2.5 μL of volume per primer (forward and reverse). Problematic Hexacorallia samples were amplified with a lower volume of primer: 8.2 μL for Milli Q (H_2O) and 1.5 μL per primer (forward and reverse) when reaction was carried out with Folmer region primer pair.

Table 2.3.1: PCR protocols used in this study

		Mitochondrial gene				**Nuclear gene**	
		MutS	COI	COI	COI	28s	28s
Initial PCR	Primer Forward	ND4L2475	jgLCO1490	COII8068F	LCO1490	28S Far	28s Far
	Primer reverse	MUT3458	jgHCO2198	COIOCTR	HCO2198	28S Rar	28s Rab
	Initial denaturation	4min / 94ºC	5min / 95 ºC	5min / 94ºC	**1min / 95 ºC**	2min / 94ºC	2min / 94ºC
	Denaturation	30s / 94ºC	30s / 95 ºC	30s / 94ºC	30s / 95 ºC	30s / 94ºC	30s / 94ºC
	Annealing	30s / 51 ºC	30s / 48 ºC	90s / 58 ºC	**30s / 45 ºC**	30s / 58 ºC	30s / 50–58 ºC
	Extension	60s / 72 ºC	45s / 72 ºC	60s / 72 ºC	90s / 72 ºC	**30s / 72 ºC**	40-90s / 72-75 ºC
	Final extension	5min / 72ºC	5min / 72ºC	10min / 72 ºC	10min / 72 ºC	5min / 72ºC	5min / 72ºC
	Cycles	30	35	40	35	35	35 (5)
Touch-up PCR	Initial denaturation	5min / 95 ºC	5min / 95 ºC	5min / 94ºC	5min / 95 ºC	2min / 95 ºC	5min / 95 ºC
	Denaturation	30s / 95 ºC	30s / 95 ºC	30s / 94ºC	30s / 95 ºC	30s / 95 ºC	30s / 95 ºC
	Annealing	30s / 51 ºC	30s / 46 ºC	90s / 60 ºC	30s / 47 ºC	30s / 60 ºC	30s / 60 ºC
	Extension	60s / 72 ºC	60s / 72 ºC	60s / 72 ºC	90s / 72 ºC	40s / 72 ºC	60s / 72 ºC
	Final Extension	10min / 72ºC	10min / 72ºC	10min / 72 ºC	10min / 72 ºC	5min / 72 ºC	5min / 72 ºC
	Cycles	30	35	40	40	35	35

Table 2.3.2: Primer pairs used for the amplification of the mitochondrial and nuclear genes in this study

primer	**gene**	**subclass**	**sequence (5'-3')**	**Expected fragment size (bp)**	**reference (primer)**	**reference (protocol)**
ND4L2475F	MutS	Octocorallia	TAGTTTTACTGGCCTCTAC	940	Brugler & France, 2008. (Seen in Pante et al., 2012)	McFadden et al., 2004

MUT3458R	MutS	Octocorallia	TSGAGCAAAAGCCACTCC	940	Sanchez et al., 2003. (Seen in Pante et al., 2012)	McFadden et al., 2004
jgLCO1490F	COI	Hexacorallia	TITCIACIAAYCAYAARGAYATTGG	709	Geller et al., 2013	Geller et al., 2013
jgHCO2198R	COI	Hexacorallia	TAIACYTCIGGRTGICCRAARAAYCA	709	Geller et al., 2013	Geller et al., 2013
COII8068F	COI	Octocorallia	CCATAACAGGACTAGCAGCATC	1100	McFadden et al., 2011 (primer design from: McFadden et al., 2004)	McFadden et al., 2004
COIOCTR	COI	Octocorallia	ATCATAGCATAGACCATACC	1100	France & Hoover, 2002	McFadden et al., 2004
LCO1490F	COI	Hexacorallia	GGTCAACAAATCATAAAGATATTGG	700-710	Folmer et al., 1994	Kitahara et al., 2010; Stolarski et al., 2011
HCO2198R	COI	Hexacorallia	TAAACTTCAGGGTGACCAAAAAATCA	700-710	Folmer et al., 1994	Kitahara et al., 2010; Stolarski et al., 2011
28S-Far F	28S	Hexa- and Octocorallia	CACGAGACCGATAGCGAACAAGTA	800 / 650	Korfhage et al., 2022	Korfhage et al., 2022
28S-Rar R	28S	Hexa- and Octocorallia	TCATTTCGACCCTAAGACCTC	800	Korfhage et al., 2022	Korfhage et al., 2022
28s-Rab R	28S	Hexa- and Octocorallia	TCGCTACGAGCTTCCACCAGTGTTT	650	Korfhage et al., 2022	Korfhage et al., 2022

Regarding the primers used in the present study, one mitochondrial (COI) and one nuclear gene segment (28S) were amplified for Hexacorallia species (Scleractinia and Antipatharia); two mitochondrial (MUTS, COI) and a nuclear gene segment (28S) were amplified for Octocorallia species. In total, 108 samples of hexacorals were amplified for both COI (54) and 28S (54) primers, and 24 samples for octocorals, which included 8 DNA amplicon for each three primers used (COI, 28S, MutS). The final dataset might be revised once results are obtained. For Hexacorallia, the mitochondrial gene segment for COI using the degenerate primer pair jgLCO1490-jgHCO2198 (Geller et al., 2013) amplified a fragment of ~709 bp and the universal “Folmer “ primers (LCO1490-HCO2198) (Folmer et al., 1994) amplified a region of ~700 to 710 bp. As the mitochondrial universal “Folmer” primer had reportedly failed to amplify COI segments in octocorals, subclass specific primers for Octocorallia (COII8068F-COIOCTR) were used to amplify a ~1100 bp fragment of the entire COI ‘Folmer region’ and an adjacent intergenic region (igr1) (McFadden et al., 2011). The mitochondrial and octocoral specific gene MutS (or Msh1) was amplified using primers ND4L2475 paired with MUT3458 and provided a final DNA fragment of ~940 bp. For both octocorals and hexacorals, the nuclear gene 28S was amplified using the forward primer 28S Far, subsequently paired with two distinct reverse primers, 28S Rar (~800 bp) and 28S Rab (~650 bp). The quality of all the amplification products was verified with a final gel electrophoresis step, using a 4 µL volume per each PCR product, running them on a 2.0 % agarose gel stained with GelRed™ dye, visualized on a UV light platform. Notwithstanding, all purified DNA amplicons sequencing was concluded at CCMAR's Sequencing Platform, with an Applied Biosystems 3130xl Genetic Analyzer, BigDye®Terminator v3.1 chemistry and POP7 polymer.

2.3.3 Sequence editing and taxonomic assignments

Once sequences were obtained, their status and quality were reviewed to see which ones could be used for further analysis. The samples with a high-quality length of read were kept, and all sequences ends were trimmed, reviewed for gaps or noise, and pair-wise alignments were completed, all through Geneious Prime® 7.1.9. For species sequenced with the reverse and forward primers, the consensus was kept as a final sequence, and all DNA sequences were searched against the GenBank (National Center for Biotechnology Information - NCBI) nucleotide database by using the BLASTn tool (Basic Local Alignment Search Tool), optimized with the Megablast algorithm. Sequences with similarity percentages of < 98% or sequences with no reference match were noted. Following methods from Korfhage et al. (2022), as species identified by BLAST varied with different markers and as matches could be multiple, choice of specie identification were based on the ones that were most likely to be found in the targeted geographic zone, as well as the reference sequence metadata. Available sample images, colony shape, preliminary taxonomic lists, and ones published by Wirtz (2021, 2022a), were reviewed.

2.4 BIOINFORMATICS AND PHYLOGENETIC ANALYSES

To build the desired phylogenetic trees, based on the specie’s genus found in Cabo Verde while including a geographic component to the analysis, different methods, and steps to extract and process molecular data through bioinformatics were used. First, an R script was created to get all the accession numbers from the NCBI Esearch utility for all the species included in the same genus as our sequenced samples. A filter was then entered for only COI, 28S and MutS primers nucleotide barcode. The output was a .csv file containing two items (genus, accession number). FASTA files (i.e. text-based file format containing nucleotide sequence) for each sequence were also needed and the previously created .csv files were added to the subsequent script as an input. One .csv file per genus per primer was previously generated, the FASTA file extraction step followed the same logic.

For the second section, the geographic information's were extracted manually for each genus and associated marker from GenBank. Individual search entry on NCBI included "genus" AND "gene". We downloaded a GenBank file containing metadata regarding all sequences for each genus for each primer, sorted by accession numbers. Using a script from the PERL 5.38.0 software version, geographic data was pulled out for each accession number. The input file from NCBI had a lot of information on the nucleotide sequence and was derived using the following code: < Get_country_info.pl >. Using the information from NCBI, we sorted the desired information from Genbank. Only accession number, organism name and country (when available) were used to create a new text file. A step to join all different file format together was also done through the following Perl script: < Join_AccN_country_GenusName_Marker.pl >, combining the first .csv file containing the accession numbers created from an R script and the text file containing the country information previously obtained. The output of this step was a text file as a simplified tabulated format with only letter and number symbols containing the Accession Number, species name and country information. An extra step to concatenate all the genus sequences with the different markers was done, including the latter in the first column. Sequence identifications were formatted in a shorter version to simplify any script that ran for the further steps. Finally, all the sequences extracted from GenBank properly formatted and the sequences from this research, were combined in one FASTA file.

Before beginning to process phylogenetic trees, an outgroup for each genus and each marker was determined through running a BLAST for one or more sequence samples for each of our genus. The nearest sequence(s) not belonging to that genus was then selected to be included. Inclusion of an outgroup is important in phylogenies as they determine the root of phylogenetic trees. Genus-specific outgroup species of the highest sequencing quality and proximity to the species' sequences under study is important to achieve high quality phylogenetic reconstruction (Schneider & Cannarozzi, 2009).

Thirdly, all GenBank and current research's samples were realigned for each genus and marker, using MUSCLE (MUltiple Sequence Comparison by Log-Expectation), permitting faster and more accurate large sequence group processing and re-optimization over other methods (Edgar, 2004) in MEGA X or Geneious Prime 7.1.9. Nucleotide sequences were also checked for the presence of pseudogenes by translating them into amino acids sequences, allowing to sharpen up phylogenetic information due to the reduced effect (noise) of residues, even in sequences with high presence of gaps, as proteins encompass 20 amino acids (Opperdoes, 2003). Specifically for the genus *Porites*, as too many sequences were available from GenBank, a step to group identical sequences into haplotypes was added, to reduce redundancy and computation time. For this purpose, the program ALTER (http://www.sing-group.org/ALTER/) was used. Furthermore, to get an overview of the haplotype groups, encompassing identical sequences within each genus, depending on the gene primer, the program DNASp, similar to ALTER, was employed to obtain the list of haplotypes for each dataset which calculated the number of sequences included in each haplotype per genera (**Erreur ! Source du renvoi introuvable.**). Only the phylogenetic trees of *Porites* (COX1) and *Leptogorgia* (MUTS) were based on the haplotype groups, as their final dataset included too many sequences, which rendered the trees difficult to comprehend.

Table 2.4.1: List of the total of sequences and haplotypes (in parenthesis) per genus per marker obtained from DNASp and ALTER used to help build the phylogenetic trees

	Genus	**COI**	**28S**	**MutS**
1	Atlantia	19 (4)	-----------	N/A
2	Tubastraea	42 (14)	-----------	N/A
3	Porites	185 (25)	-----------	N/A
4	Siderastrea	22 (10)	-----------	N/A
5	Favia	115 (26)	-----------	N/A
6	Cladocora/Oculina	47 (9)	-----------	N/A
7	Carijoa	19 (6)	-----------	N/A
8	Leptogorgia	79 (20)	-----------	131 (45)
9	Eunicella	35 (14)	-----------	38 (6)

We selected a nucleotide substitution model in PartitionFinder 2.1.1, which allowed to use data partitions by codon (specific to codon 1 + 2 + 3), specifically for the mitochondrial COI gene, to minimize the saturation effects of codon positions on phylogenetic reconstructions, and to account for different rates of evolution for each one (Table 2.4.2).

Table 2.4.2: Nucleotide substitution model determined for each Genus and Marker, from data partition by codon through PartitionFinder 2.1.1

	Genus	**COI**	**28S**	**MutS**
1	Atlantia	F81(1+3), HKY (2)	------------------	----------------------
2	Tubastraea	HKY+I (1+3), GTR (2)	------------------	----------------------
3	Porites	HKY (1+2), HKY +G (3)	------------------	----------------------
4	Siderastrea	HKY (1+ 2), GTR (3)	------------------	----------------------
5	Favia	HKY +G (1+2), KHY (3)	------------------	----------------------
6	Cladocora/Oculina	HKY (1+2), GTR (3)	------------------	----------------------
7	Carijoa	HKY (1), F81(2), HKY + G (3)	------------------	----------------------
8	Leptogorgia	HKY + I (1), F81(2), GTR + G (3)	------------------	HKY +G (1+2 + 3)
9	Eunicella	HKY (1), KHY +I (2), F81(3)	------------------	HKY (1), HKY + G (1 + 2)

Phylogenetic tree reconstructions were performed using two model-based methods of phylogenetic inference: maximum likelihood (ML) in RAxML v8 (https://cme.h-its.org/exelixis/web/software/raxml/) and Bayesian inference (BI) in MrBayes v3.2.6 (https://pubmed.ncbi.nlm.nih.gov/22357727/). Using both ML and BI methods allows for a better supported organization of a tree’s clades, as Bayesian posterior probability provides more generous estimates of subtree sections reliability compared to nonparametric bootstrap through ML inference (Mar et al., 2005). For either two phylogenetic inference methods (ML or BI), two or more nucleotide substitution models, depending on genus (Table 2.4.2), were applied. Robustness of the Maximum Likelihood results was tested by bootstrap analyses with the standard 1000 replicates. For the Bayesian Inference analysis, four Markov chain Monte Carlo (MCMC) chains were run twice in parallel for 2 × 107 generations, sampling trees, and parameters every 1000 generations, with the heating parameter set to 0.25. Convergence of the analyses was considered to be reached when the average standard deviation of split frequencies was less than 0.01. The majority-rule consensus tree was estimated by combining results from duplicated analyses, after discarding 25% of samples as burn-in. Trees were visualized and rooted using FigTree v1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/) and later edited with Inkscape v1.1 software (https://www.inkscape.org).

Genetic distance similarity values (p-distance using Pairwise gap deletion) were obtained for haplotype groups and within and between species and subspecies for each genus and marker and were saved as excel files (Supplementary material Table S4-14).

3 RESULTS

3.1 SPECIE IDENTIFICATION AND DNA BARCODING

In this study, a total of 62 samples were collected. From this dataset, 21 species were initially identified based on morphological features and corroborated from the litterature (). After a thorough literature review, an estimated total of 38 deep and shallow species could be found in the archipelago (Table 3.1.1). 28 other species are said to be theoretically (T) present through relevant literature but many of these sightings are outdated or were misidentified. Most of the species classified as theoretical (T) are Antipatharia, found at deeper depths and species labeled with the most unreliable identities (in red), were sampled, and morphologically identified over 100 years ago.

Field identification of species was mainly done by Dr. Peter Wirtz, an expert in taxonomy specific to species of the Eastern Atlantic and Macaronesia, environmentalist Guilherme Mascarenhas, the steward of the “Enseada de Coral da Laginha” in Mindelo, and me. PCR for all Antipatharia corals (13 samples), failed for both the COX1 and 28S genes and so were not further analyzed. PCRs for 49 samples were processed (41 Scleractinia, eight Alcyonacea) for both COX1 and 28S, and eight samples, for MUTS (Alcyonacea). Some amplicons were further set aside from the dataset as after sequencing, quality for some of them was too low. Therefore, the dataset from the BLAST step was reduced to 39 samples of hexacorals and octocorals for COX1 and 28S. All samples were blasted for both groups for COX1 (6 octocorals, 33 hexacorals) and for 28S sequences (8 octocorals, 31 octocorals) and five samples out of the initial eight octocorals samples for MUTS (Table 3.1.2). The table with the best results from BLAST was determined based mainly on identity percentages (%), query coverage (%), and accession length based on the primer fragment size (Table S1-S3). Especially for 28S, the longer fragment size associated to the 28S FAR-RAB primer pair (800 bp.) enabled higher identity and query coverage percentages (Supplementary material Table S3).

In total, this table presents seven endemic species for Cabo Verde as opposed to the five previously identified species, including two cryptic species of Antipatharia.

Table 3.1.1: Scleractinia, Antipatharia (Hexacorallia) and Alcyonacea (Octocorallia) list of species diversity in Cabo Verde (Theoretical=T, Potential=P, Sampled=S) based on different factors related to references reliability (year of the reference, age of the last sample, morphological or molecular identification, number of sightings and samples, theoretical distribution region, specie occurrence/distribution based on WORMS, GBIF,OBIS maps/data). Purple species are endemic to Cabo Verde, reliability of ID graded from most reliable (Green) to least reliable (Red).

depth range (m)	order	*specie*	Superseded/unaccepted names	T	P	S	reliability of ID	References
0-19	Scleractinia	***Atlantia caboverdiana***	*Tubastrea caboverdiana*		✓	✓	🟩	Ocaña et al., 2015; Ocaña et al., 2019; Capel et al., 2020; Wirtz, 2021
0-50	Scleractinia	*Porites porites*			✓	✓	🟩	Boekschoten & Borel-Best, 1988; Morri et al., 2000; Moses et al., 2003; Lopes et al., 2014; Almeida et al., 2014; Wirtz, 2021
0-25	Scleractinia	*Siderastrea radians*			✓	✓	🟩	Boekschoten & Borel-Best, 1988; Morri et al., 2000; Moses et al., 2003; Lopes et al., 2014; Almeida et al., 2014; Wirtz, 2021
0-70	Scleractinia	*Siderastrea siderea*		✓		✓	🟧	Gravier, 1920
1-50	Scleractinia	*Porites astreoides*			✓	✓	🟩	Boekschoten & Borel-Best, 1988; Morri et al., 2000; Moses et al., 2003; Lopes et al., 2014; Almeida et al., 2014; Wirtz, 2021
n/d	Scleractinia	*Madracis sp.*			✓	✓	🟩	Lopes et al., 2014
0-10	Scleractinia	***Balanopsammia wirtzi***			✓	✓	🟩	Ocaña & Brito, 2013; Ocaña et al., 2015; Wirtz, 2021
0.5-20	Scleractinia	*Favia fragum*			✓	✓	🟩	Boekschoten & Borel-Best, 1988; Morri et al., 2000; Moses et al., 2003; Lopes et al., 2014; Almeida et al., 2014; Wirtz, 2021
6-333	Scleractinia	*Madracis pharensis*			✓	✓	🟩	Boekschoten & Borel-Best, 1988; Laborel, 1974; Wirtz, 2021
n/d	Antipatharia	*Stichopathes luetkeni*	*Stichopathes lutkeni*		✓		🟩	Morri et al., 2000
n/d	Antipatharia	*Tanacetipathes spinescens*	*Antipathes spinescens*		✓	✓	🟩	Morri & Bianchi, 1995; Morri et al., 2000; Wirtz, 2001; Wirtz, 2022b; Wirtz, 2023
20-1425	Antipatharia	*Antipathella wollastoni*			✓	✓	🟩	Morri et al., 2000; Molodtsova et al., 2006; Ocaña et al., 2006; Wirtz, 2022b; Wirtz, 2023
0-60	Alcyonacea	***Leptogorgia capverdensis***			✓	✓	🟩	Morri et al., 2000; Monteiro et al., 2008; Lopes et al., 2014
n/d	Alcyonacea	*Leptogorgia gaini*			✓	✓	🟩	Morri et al., 2000; Lopes et al., 2014
n/d	Alcyonacea	*Eunicella papillifera*			✓	✓	🟩	Morri et al., 2000

n/d	Alcyonacea	*Eunicella granulata*			✓	✓	🟩	Morri et al., 2000
n/d	Alcyonacea	*Carijoa riisei*			✓	✓	🟩	Lopes et al., 2021
n/d	Antipatharia	***tanacetipathes sp. 1***			✓	✓	🟩	Wirtz, 2022b;Wirtz, 2023
n/d	Antipatharia	***tanacetipathes sp. 2***			✓	✓	🟩	Wirtz, 2023
1-35	Scleractinia	*Schizoculina fissipara*			✓		🟨	Nunes et al., 2011
1-35	Scleractinia	*Schizoculina africana*			✓		🟩	Boekschoten & Borel-Best, 1988; Almeida et al., 2014; Wirtz., 2021
0-30	Antipatharia	*Tanacetipathes wirtzi*			✓		🟩	Monteiro et al., 2008; Wirtz, 2022b; Wirtz, 2023
n/d	Antipatharia	*Stichopathes sp.*			✓	✓	🟩	Almeida et al., 2014; Monteiro et al., 2008; Wirtz, 2022b;Wirtz, 2023
n/d	Alcyonacea	*Leptogorgia sp.*			✓		🟨	Almeida et al., 2014; Monteiro et al., 2008
3-19	Scleractinia	*Tubastraea aurea*	*Australopsammia aurea, Tubastrea aurea*		✓	✓	🟨	Morri et al., 2000, as cited in Lopes et al., 2014
12-150	Scleractinia	*Polycyathus senegalensis*			✓	✓	🟩	Zibrowius, 1980; Ocaña & Brito, 2004; Ocaña et al., 2015; Wirtz, 2021, 2022a
10-800	Alcyonacea	*Corallium rubrum*		✓			🟧	Grasshoff, 1992; Lopes et al., 2014
100-960	Alcyonacea	*Anthothela grandiflora*		✓			🟧	Lopes et al., 2014
1000-4000	Scleractinia	*Caryophyllia (Caryophyllia) seguenzae*		✓			🟧	Zibrowius, 1980; Lopes et al., 2014
n/d	Scleractinia	*Tubastraea sp.*		✓			🟩	Monteiro et al., 2013; Lopes et al., 2014
n/d	Alcyonacea	*Dendrophyllia sp.*			✓		🟩	Monteiro et al., 2013; Lopes et al., 2014
2-80	Scleractinia	*Phyllangia americana mouchezii*	*Phyllangia mouchezii, Coenocyathus mouchezi*		✓		🟩	Zibrowius, 1980; Boekschoten & Borel-Best, 1988; Bianchi et al., 2000; Ocaña & Brito, 2004; Ocaña et al., 2015; Wirtz, 2021
20-40	Scleractinia	***Thalamophyllia wirtzi***			✓		🟩	Ocaña et al., 2015; Wirtz, 2021
0-10	Scleractinia	*Euafricana wirtzi*	*Africana wirtzi, Africania wirtzi*		✓		🟩	Ocaña et al., 2015; Wirtz, 2021
n/d	Scleractinia	***Morabeza benitoi***			✓		🟩	Zibrowius, 1980; Ocaña et al., 2019; Wirtz, 2021
70 - 366	Scleractinia	*Cladopsammia manuelensis*	*Rhizopsammia manuelensis*		✓		🟨	Cairns, 1979; Zibrowius, 1980; Ocaña et al., 2019
n/d	Alcyonacea	*Keratoisis sp.*			✓		🟨	Raddatz et al., 2011
40-150	Alcyonacea	*Dendrophyllia ramea*		✓			🟧	Moseley, 1876; Zibrowius, 1980
50 +	Antipatharia	*Stichopathes occidentalis*		✓			🟧	van der Land, 2008
n/d	Scleractinia	*Siderastrea stellata*		✓			🟧	Nunes et al., 2011; Wirtz, 2021

1-50	Scleractinia	*Porites gabonensis*	*Porites bernardi*	✓			🟧	Laborel, 1974; Nunes et al., 2011
n/d	Scleractinia	*Porites branneri*		✓			🟧	Rathbun, 1888 (recently mentionned by Wirtz, 2022a); Wirtz, 2021
0-130	Scleractinia	*Tubastraea coccinea*		✓			🟧	Boekschoten & Borel-Best, 1988; Laborel (1974), as cited in Precht et al., 2014
1-43	Scleractinia	*Tubastraea tagusensis*		✓			🟧	Nunes et al., 2011
0-311	Scleractinia	*Madracis asperula*			✓		🟨	Moseley, 1881; Laborel, 1974; Zibrowius, 1980; Boekschoten & Borel-Best, 1988; Wirtz, 2021
0-98	Scleractinia	*Madracis decactis*		✓			🟧	Nunes et al., 2011
112-327	Scleractinia	*Madracis profunda*		✓			🟧	Zibrowius, 1980
39-2775	Scleractinia	*Desmophyllum pertusum*	*Lophelia pertusa*	✓			🟧	Gravier, 1920; Marenzeller, 1904; Rogers, 1999
55-1950	Scleractinia	*Madrepora oculata*		✓			🟧	Marenzeller, 1904; Gravier, 1920; Zibrowius, 1980;
0-400	Scleractinia	*Pourtalosmilia anthophyllites*			✓		🟨	Wirtz, 2021
0-51	Scleractinia	*Astrangia solitaria*	*Astrangia poculata*		✓		🟨	Boekschoten & Borel-Best, 1988; Wirtz, 2022a
4-50	Alcyonacea	*Eunicella verrucosa*			✓		🟨	Grasshoff, 1992 (p.15-17)
n/d	Antipatharia	*Stichopathes setacea*			✓		🟨	Ocaña & Brito, 2004; Wirtz, 2023
62-500	Antipatharia	*Antipathella subpinnata*	*Antipathes subpinnata*	✓			🟧	Ellis & Solander, 1786; Morri & Bianchi, 1995; Wirtz 2001
n/d	Scleractinia	*Balanophyllia sp*			✓		🟨	Morri et al., 2000; Ocaña et al., 2015
0-1150	Scleractinia	*Balanophyllia “italica"*		✓			🟥	Morri & Bianchi, 1995, Ocaña & Brito, 2013 recognize that the specie was misidentified with balanopsammia wirtzi, this balanophyllia is only found in the mediterannean
110-600	Scleractinia	*Dasmosmilia variegata*		✓			🟧	Zibrowius, 1980; Cairns, 1979
1430-6328	Scleractinia	*Fungiacyathus (Bathyactis) marenzelleri*	*Fungiacyathus marenzelleri*	✓			🟥	Zibrowius, 1980
183-1000	Scleractinia	*Deltocyathus eccentricus*		✓			🟥	Zibrowius, 1980
300-1530	Antipatharia	*Parantipathes hirondelle*		✓			🟧	Roule, 1905, as cited in Molodtsova, 2006

1311	Antipatharia	*Stauropathes punctata*		✓			🟥	Roule, 1905, as cited in Molodtsova, 2006
1400-2165	Antipatharia	*Stichopathes flagellum*		✓			🟥	Roule, 1905, as cited in Molodtsova, 2006
1694	Antipatharia	*Aphanostichopathes euoplos*	*Stichopathes euoplos*	✓			🟥	Schultze, 1902, as cited in Molodtsova, 2006
528-1384	Antipatharia	*Antipathes virgata*		✓			🟥	Esper, 1798, as cited in Molodtsova, 2006
50-1642	Antipatharia	*Tanacetipathes squamosa*	*Antipathes squamosa* *Aphanipathes squamosa*	✓			🟥	Von Koch 1886, as cited in Molodtsova, 2006
n/d	Scleractinia	*Polycyathus atlanticus*		✓			🟧	Boekschoten & Borel-Best, 1988
n/d	Antipatharia	*Cirripathes sp.*			✓		🟩	Wirtz, 2023
TOTAL				**28**	**38**	**21**		

The final dataset used to build the phylogenetic trees was further reduced according to BLAST results identification (Table 3.1.2). Specifically, certain sequences were not corals or genus's classification and preliminary morphological identification needed reviewing. For instance, the sample labelled SVLPA2, based on the degenerate COI (COX1) primer pair was identified as *Millepora alcicornis* (Hydrozoa) and in the same Genus for the 28S (Table 3.1.2), while for the sequences from the 28S dataset, STCR and SVN2 (*Antipathozoanthus cavernus*), SVLFF (*Timea sp.*: a sponge) and SVLPA2 (*Millepora sp.*: a Hydrozoa or fire coral) were not corals either (Table 3.1.2).

Table 3.1.2: Sample identification results from BLASTn, list ordered by sample Subclass (O=Octocorallia, H=Hexacorallia). Sampling location (Island: St = Santiago, SN = Sao Nicolau, SV = Sao Vicente, B = Boavista) is presented. Initial species identification (Initial ID) is compared to GenBank (NCBI) sequence matches for COX1 (COI), 28S and MutS, where cells with (-) represent samples that were not amplified/sequenced for the specific genetic marker.

Subclass	**Order**	**sample label**	**Sampling location**	**sampling location (Island)**	**Initial ID**	**COX1 match**	**ID (%)**	**28S match**	**ID (%)**	**MutS match**	**ID (%)**
O	Alcyonacea	ST CR	Tarrafal	St	*Carijoa riisei* or *Antipathozoanthus macaronesicus*	-	-	*Antipathozoanthus cavernus***	99.23	-	-
O	Alcyonacea	SN CR	House reef-love auditorium	SN	*Carijoa riisei*	*C. riisei*	99.89	*C. riisei*	99.4	-	-
O	Alcyonacea	SV N2	Cubos dive spot	SV	*Carijoa riisei* or *Antipathozoanthus macaronesicus*	-	-	*Antipathozoanthus cavernus (order: Zoantharia)***	99.53	-	-

O	Alcyonacea	SV N2 EG	Cubos dive spot	SV	*Eunicella granulata*	*Leptogorgia cf. sarmentosa AP-2021*[2, 3]	98.62	*Leptogorgia capverdensis*[3]	96.66	*L. gaini*	99.89
O	Alcyonacea	SVN2 EP	Cubos dive spot	SV	*Eunicella papillifera*	*E. gazella*[2, 3]	98.84	*E. tricoronata***	96.83	*E. tricoronata*[3]	98.14
O	Alcyonacea	SVN2 LG	Cubos dive spot	SV	*Leptogorgia gaini*	*L. gaini*	99.87	*L. capverdensis*[1]	96.78	*L. gaini*	99.13
O	Alcyonacea	SVN2 LC	Cubos dive spot	SV	*Leptogorgia capverdensis*	*L. capverdensis*[3, 4]	100	*L. capverdensis*[3]	99.44	*L. capverdensis*	99.02
O	Alcyonacea	ST EG	Tarrafal	St	*Eunicella granulata*	*E. filiformis*	100	*E.verrucosa*[2]**	98.97	*E. verrucosa*	100
H	Scleractinia	BPG SR	Praia das gatas	B	*Siderastrea radians*	*S. radians*[3]	99.53	*S. radians**	99.85	N/A	-
H	Scleractinia	BPG FF	Praia das gatas	B	*Favia fragum*	*F. fragum*[1]	97.41	-		N/A	-
H	Scleractinia	BPG PP	Praia das gatas	B	*porites porites*	*P. porites*[3]	99.84	*Porites sp. NG17*	98.19	N/A	-
H	Scleractinia	BPG SR3	Praia das gatas	B	*Siderastrea radians*	*S. radians*[3]	99.84	*S. radians**	99.85	N/A	-
H	Scleractinia	BPG PA2	Praia das gatas	B	*Porites astreoides*	*P. astreoides*[3]	99.84	*Porites sp. NG17*	99.86	N/A	-
H	Scleractinia	BPG FF2	Praia das gatas	B	*Favia fragum*	-	-	-	-	N/A	-
H	Scleractinia	BPG PP2	Praia das gatas	B	*Porites porites*	*P. porites*[3]	99.84	*Porites sp. NG17*	98.19	N/A	-
H	Scleractinia	BBSR PP	Bahia de Sal rei (Praia Diante)	B	*Porites porites*	*P. porites*	100	*Porites sp. NG17*[2]	98.19	N/A	-
H	Scleractinia	BBSR PA	Bahia de Sal rei (Praia Diante)	B	*Porites astreoides*	*P. astreoides*[3]	99.84	*Porites sp. NG17*	99.86	N/A	-
H	Scleractinia	BBSR SR	Bahia de Sal rei (Praia Diante)	B	*Siderastrea radians*	*S. radians*[3]	99.69	*S. radians**	99.85	N/A	-
H	Scleractinia	BISR PA	Ilheu Sal Rei	B	*Porites astreoides*	*P. astreoides*[3]	99.68	*Porites sp. NG17*	99.86	N/A	-
H	Scleractinia	BISR P?	Ilheu Sal Rei	B	*Porites*	*P. porites*[3]	99.69	*Porites sp. NG17*[2]	98.18	N/A	-
H	Scleractinia	BISR FF	Ilheu Sal Rei	B	*Favia fragum*	-	-	-	-	N/A	-
H	Scleractinia	BISR PP	Ilheu Sal Rei	B	*Porites porites*	*P. porites*	100	*Porites sp. NG17*[2]	98.18	N/A	-
H	Scleractinia	ST TA	Tarrafal	St	*Tubastraea aurea (Australopsammia aurea)*	*T. micranthus*[2, 3, 4]	98.59	*Leptopsammia pruvoti*[1]*	96.43	N/A	-
H	Scleractinia	PBG PA (BPG PA)	Praia das gatas	B	*Porites astreoides*	*P. astreoides*[3]	99.84	*Porites sp. NG17*	99.86	N/A	-
H	Scleractinia	ST TA 2	Tarrafal	St	*Tubastraea aurea (Australopsammia aurea)*	*T. micranthus*[2]	98	*Leptopsammia pruvoti*[1]*	96.82	N/A	-

H	Scleractinia	BPG SR2	Praia das gatas	B	*Sideratrea radians*	*S. radians* [3]	99.84	*S. radians**	99.85	N/A	-
H	Scleractinia	SVBG SR4	Baia das gatas	SV	*Siderastrea radians*	*S. radians* [3]	99.84	*S. radians**	99.85	N/A	-
H	Scleractinia	SVN2 AC3	Cubos dive spot	SV	*Atlantia caboverdiana*	*Tubastraea micranthus* [2, 3]	98.75	*Leptopsammia pruvoti* [1]*	96.83	N/A	-
H	Scleractinia	SVN FF	Ninho de Guincho	SV	*Favia fragum*	-	-	-	-	N/A	-
H	Scleractinia	SVL SR3	Enseada de Coral da Laginha	SV	*Siderastrea radians*	*S. radians* [3]	99.84	*S. radians**	99.85	N/A	-
H	Scleractinia	SVL PA3	Enseada de Coral da Laginha	SV	*Porites astreoides*	*P. astreoides* [3]	99.84	*Porites sp. NG17*	99.72	N/A	-
H	Scleractinia	SVL MP 2	Enseada de Coral da Laginha	SV	*Madracis pharensis*	-	-	-	-	N/A	-
H	Scleractinia	SVL PS (SVL MP)	Enseada de Coral da Laginha	SV	*Polycyathus senegalensis*	*Oculina patagonica OR Oculina sp. KL-2014* [3]	100	-	-	N/A	-
H	Scleractinia	SVL PP2	Enseada de Coral da Laginha	SV	*Porites porites*	*P. porites* [3]	100	*Porites sp. NG17*	99.72	N/A	-
H	Scleractinia	SVL FF2	Enseada de Coral da Laginha	SV	*Favia fragum*	-	-	-	-	N/A	-
H	Scleractinia	SVL --	Enseada de Coral da Laginha	SV	*porites sp.*	-	-	-	-	N/A	-
H	Scleractinia	SVL AC4	Enseada de Coral da Laginha	SV	*Atlantia caboverdiana*	*T. micranthus* [2, 3]	98.75	*Leptopsammia pruvoti* [1]*	96.55	N/A	-
H	Scleractinia	SVL AC3	Enseada de Coral da Laginha	SV	*Atlantia caboverdiana*	*T. micranthus* [2, 3]	98.59	*Leptopsammia pruvoti* [1]*	96.68	N/A	-
H	Scleractinia	SVL BW	Enseada de Coral da Laginha	SV	*Balanopsammia wirtzi*	**New barcode**		-	-	N/A	-
H	Scleractinia	SVL MR	Enseada de Coral da Laginha	SV	*Madracis sp. (Madracis pharensis)*	-	-	-	-	N/A	-
H	Scleractinia	SVL FF	Enseada de Coral da Laginha	SV	*Favia fragum*	-	-	*Timea sp. G313459*[1]	89.59	N/A	-
H	Scleractinia	SVL PA2	Enseada de Coral da Laginha	SV	*Porites astreoides*	*Millepora alcicornis (order: Anthoathecata)*	99.35	*Millepora sp. AMN-2008*	99.86	N/A	-
H	Scleractinia	SVL PA1	Enseada de Coral da Laginha	SV	*Porites astreoides*	*P. astreoides* [3]	99.69	*Porites sp. NG17*	99.86	N/A	-
H	Scleractinia	SVL SR2	Enseada de Coral da Laginha	SV	*Siderastrea radians*	*S. radians* [3]	99.53	*S. radians**	99.85	N/A	-
H	Scleractinia	SVL SR1	Enseada de Coral da Laginha	SV	*Siderastrea radians*	*S. radians* [3]	99.84	*S. radians**	99.85	N/A	-
H	Scleractinia	SVL PP	Enseada de Coral da Laginha	SV	*Porites porites*	*P.porites* [3]	100	*Porites sp. NG17*	99.72	N/A	-

H	Scleractinia	SVL AC2	Enseada de Coral da Laginha	SV	*Atlantia caboverdiana*	*Tubastraea micranthus* ^{2,3}	98.75	*Leptopsammia pruvoti* ^{1}**	93.15	N/A	-
H	Scleractinia	SVL AC1	Enseada de Coral da Laginha	SV	*Atlantia caboverdiana*	*Tubastraea micranthus* ^{2,3}	98.75	*Leptopsammia pruvoti* ^{1}*	96.53	N/A	-
H	Scleractinia	SVL SS	Enseada de Coral da Laginha	SV	*Siderastrea siderea*	*S. radians* ^{3}	99.84	*S. radians**	99.85	N/A	-
H	Antipatharia	ST TS	Tarrafal	St	*Tanacetipathes spinescens*	-	-	-	-	N/A	-
H	Antipatharia	ST S? 1	Tarrafal	St	*Stichopathes sp.*	-	-	-	-	N/A	-
H	Antipatharia	ST SL 2	Tarrafal	St	*Stichopathes sp.*	-	-	-	-	N/A	-
H	Antipatharia	ST S? 3	Tarrafal	St	*Stichopathes sp.*	-	-	-	-	N/A	-
H	Antipatharia	ST AW	Tarrafal	St	*Antipathella wollastoni*	-	-	-	-	N/A	-
H	Antipatharia	ST TS2	Tarrafal	St	*Tanacetipathes spinescens*	-	-	-	-	N/A	-
H	Antipatharia	SN T ?	House reef-love auditorium	SN	*Tanacetipathes sp.*	-	-	-	-	N/A	-
H	Antipatharia	SV N2 AW3	Cubos dive spot	SV	*Antipathella wollastoni*	-	-	-	-	N/A	-
H	Antipatharia	SVN AW2	Ninho de Guincho	SV	*Antipathella wollastoni*	-	-	-	-	N/A	-
H	Antipatharia	SVN AW1	Ninho de Guincho	SV	*Antipathella wollastoni*	-	-	-	-	N/A	-
H	Antipatharia	SVN TS	Ninho de Guincho	SV	*Tanacetipathes spinescens*	-	-	-	-	N/A	-
H	Antipatharia	SVN SL 2	Ninho de Guincho	SV	*Stichopathes luetkeni*	-	-	-	-	N/A	-
H	Antipatharia	SVN SL 1	Ninho de Guincho	SV	*Stichopathes luetkeni*	-	-	-	-	N/A	-

Blue is 2nd match 100 ID corresponding to Initial ID but query of 90-98

1 ID < 98%	🟩	Green is 2nd match close to the 1st for ID and query %, but 1st match is 100% ID
2 ID % between 98-99%	🟦	
3 Specie with 2 or more potential match (high ID% but low Query 90-100%)		(red) : specie from totally different taxonomic group
4 Specie identified through targeted Blast and sequence similarity with other specific sequence (it can be with entire mitogenome)		*** Query coverage of < 90%*

** Query coverage of 90-95%*

Figure 3.1.1: Specimen morphologically identified as *Balanopsammia wirtzi* during field sampling (Solitary to small colonies, short densely packet calyces, attached to rocky substrate, Pink, reddish and orange, 5-25 mm height and 5x5 to 15x10 mm in diameter (Ocaña & Brito, 2013)).

While the sample SVLBW was previously identified as *Balanopsammia wirtzi*, COI sequence match was 98.44% with both *Tubastraea micranthus* and *Tubastraea tagusensis*. However, these results are in contradiction with morphological features (Figure 3.1.1) and therefore for this specimen, COI marker could not confidently resolve its identity. Thus, it was listed as a new barcode (Table 3.1.2).

3.1.1 28S rDNA nuclear gene

Specifically concerning identification results for the nuclear 28S rDNA gene, as suspected, STCR and SVN2 samples were from the genus *Antipathozoanthus* (order: Zoantharia) but 28S sequences were not sufficient to confidently distinguish between potential identities suggesting either *A. cavernus* (STCR: 99.23%, SVN2: 99.53) or *A. remengesaui* (STCR: 99.23%, SVN2: 100%) (Supplementary material Tables S3). Sequences from the genus *Tubastraea, Atlantia, Eunicella* (except for STEG), and for the sample SVN2LC (initial ID: *Leptogorgia gaini*)'specie level identification resolution yielded low percentage of ID (93-97%) with query coverage generally under 90% (Supplementary material Tables S3). Most 28S BLAST results were totally different from COI results across genus, as per evident lower ID and query coverage percentages (Table 3.1.2). Sequence alignments were extremely complex and for most genus, could not be completed for further phylogenetic analysis due to unresolved nucleotide gaps or variation in the gene fragment region and size when compared to preexisting 28S coral sequences.

3.2 *MITOCHONDRIAL PHYLOGENETIC TREES*

3.2.1 Genus's overview

As previously mentioned, sequences identities obtained from BLAST revealed the need to correct both species and genus' taxonomic assignments for certain samples. Nine Genus were identified to build the phylogenetic trees (three Alcyonacea, six Scleractinia), with a change for the expected *Polycyathus* genus to *Oculina/Cladocora*, although identified as the first, by local researchers. Most other initial identification of species turned out to be classified, at least, in the same genus, except for *Atlantia* and *Tubastraea*, which seemingly corresponded closer to sequences of species included in *Astroides* or *Dendrophyllia* than to *Atlantia caboverdiana* or *Tubastraea aurea* (Figure 3.2.1). Those two genus also represented a challenge during field identification, sharing almost identical morphologies.

<table>
<tr><th colspan="3">Genus</th></tr>
<tr>
<td><i>Atlantia</i>

→ <i>Astroides / Dendrophyllia (sp.)</i>
</td>
<td><i>Tubastraea</i>

→ <i>Tubastraea</i> (middle) / <i>Astroides</i> (down)
[1]
[2]</td>
<td><i>Porites</i>

<u>SVLPP</u>

<u>SVLPA3</u></td>
</tr>
</table>

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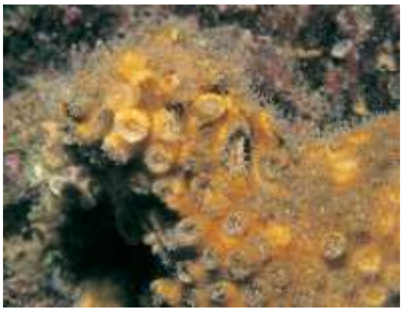
[1] *Note:* From *Tubastraea coccinea, orange cup coral*, by J.M. Gradot, 2018, Reeflex (https://www.reeflex.net/tiere/628_Tubastraea_coccinea.htm#)

[2] *Note:* From *Corail orange (Astroides calycularis)*, by Azzopardi, B, March 2014, Atlantis diving (https://www.atlantisgozo.com/fr/orange-coral-astroides-calycularis/)

Siderastrea 	*Favia* 	*Polycyathus*  → *Cladocora* (middle) / *Oculina* (down)  [3]  [4]
Carijoa  **SNCR**	*Leptogorgia*  **SVN2LC**  **SVN2LG**	*Eunicella*  **SVN2EP**  [5]

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[3] *Note:* From *Cladocora caespitosa*, by M. Fine, 2000, Corals of the World (http://www.coralsoftheworld.org/species_factsheets/species_factsheet_summary/cladocora-caespitosa/)

[4] *Note:* From *Oculina patagonica*, by M. Fine, 2000, Corals of the World (http://www.coralsoftheworld.org/species_factsheets/species_factsheet_summary/oculina-patagonica/)

[5] Note: From *Libro 300 especies cabo verde* (Biotecmar), Cnidarios (pp. 105-111), C. Fernandez-Gil et al., 2013, Espécies Marinhas de Cabo Verde (https://issuu.com/oceanografica/docs/libro_300_especies_cabo_verde_web/111)

Figure 3.2.1: Genus included in Hexacorallia and Octocorallia phylogenies. Images of representative species taken during field sampling (bold and underlined) or from online resources.

3.2.2 Octocorallia trees

Phylogenetic trees of Octocorallia species from the order Alcyonacea were reconstructed for both mitochondrial MutS and COI genes for *Eunicella* and *Leptogorgia*, and only for COI for the *Carijoa*. Genetic distance values (p-distance using Pairwise gap deletion) were obtained for haplotype groups and within and between species and subspecies and are available in the supplementary material (Octocorallia: Table S4-S8, Hexacorallia: Table S9-S14).

- *Eunicella*

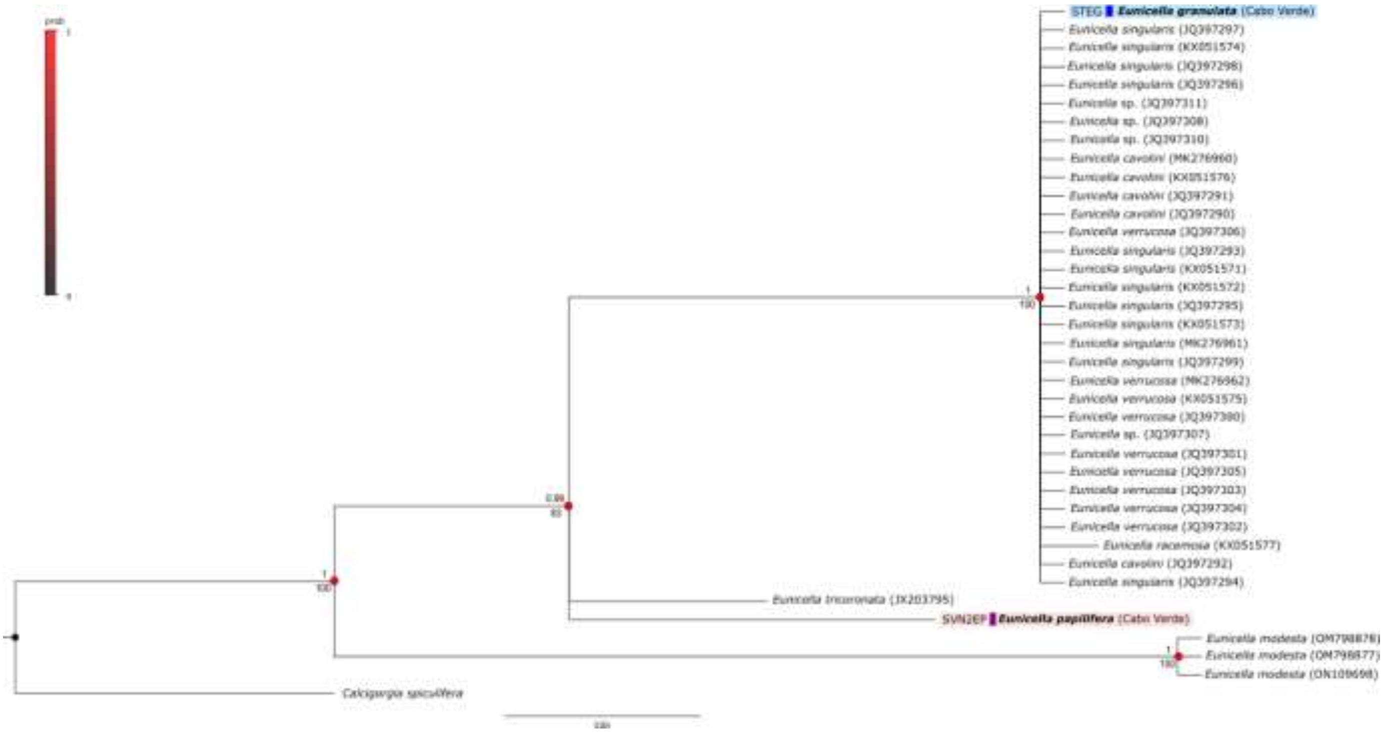

Figure 3.2.2: Phylogenetic tree of the *Eunicella* genus for the Octocorallia mtMutS gene using two model-based methods of phylogenetic inference: Bayesian Inference (BI) and Maximum-Likelihood (ML) analysis, for concatenated sequences of 38 specimens (2 sequences from this study's samples, 36 sequences from GenBank). *Calcigorgia spiculifera* (KF856128.1) is used as outgroup to root the tree. BI analyses were performed running four MCMC chain, and Bayesian posterior probabilities (BPP) are represented by circles and values above nodes (red circles indicate that the clade cluster is strongly supported). Bootstrap percentages of the ML analysis are given below nodes.

Tree reconstruction (Figure 3.2.2, Figure 3.2.3) for *Eunicella* showed high confidence (BI = 1, ML = 100) in the clade grouping for the sample STEG (initially identified as *Eunicella granulata*) with MutS, and slightly lower with COI ((BI = 0.99, ML = 65). MutS and COI tree show close genetic proximity with many sequences of *Eunicella cavolini*, *Eunicella verrucosa*, *Eunicella singularis*. This clustering follows results from Blast identification (MutS) which gave 100% identity and query coverage for the sample STEG to both *E. verrucosa* and *E. cavolini*, notwithstanding, *E. verrucosa*'s distribution makes it the most likely candidate as presented in Table 3.1.2. The MutS marker was therefore not sufficient to confidently distinguish the specie. 28S Blast results also suggested the identity of the sample as *E. verrucosa* (98.97%) but query coverage was low (87%)(Table 3.1.2). Similar percentage values could also be observed for STEG when used with COI and was matched to *E. filiformis* (100%) but with a second potential ID, *E. gazella* (Suppl. Material TableS3). It is interesting to note also that p-distance for mutation rate was null (0.00) between STEG sequence and *E. granulata* (KJ685927) (Suppl. Material Table S5), but this value was also observed with other specimens of *Eunicella* found clustered in the COI tree (Figure 3.2.3). While *E. granulata* is included in our sample's clade for the COI tree, it is not present in the MutS, but this is consistent with the reduced dataset and sequence availability for that species for other markers than the COI. SVN2EP, preliminarily identified as *E. papilifera,* was blasted as *E. tricoronata* (28S: 96.83%, MutS: 98.14%, COI: 98.84%) (Figure 3.2.3), but sequence match was low for 28S and of equal value for another specie for COI (*E. gazella*) (Table S2, S3).

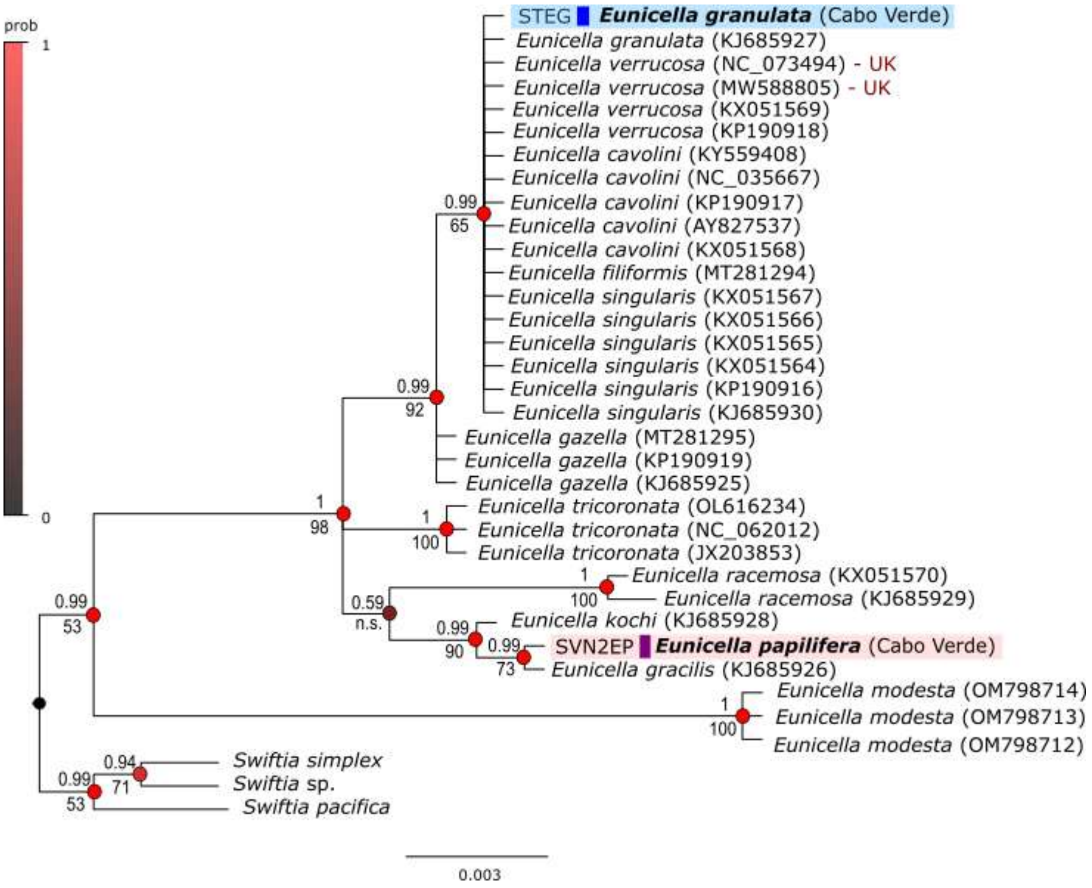

Figure 3.2.3: Phylogenetic tree of the *Eunicella* genus for the mitochondrial gene COI using two model-based methods of phylogenetic inference: Bayesian Inference (BI) and Maximum-Likelihood (ML) analysis, for concatenated sequences of 35 specimens (2 sequences from this study's samples, 33 sequences from GenBank). Three specimens of the genus *Swiftia* (KX904980.1, FJ264906.1, MT281301.1) were used as outgroup to root the tree. BI analyses were performed running four

MCMC chain, and Bayesian posterior probabilities (BPP) are represented by circles and values above nodes (red circles indicate that the clade cluster is strongly supported). Bootstrap percentages of the ML analysis are given below nodes.

➢ *Leptogorgia*

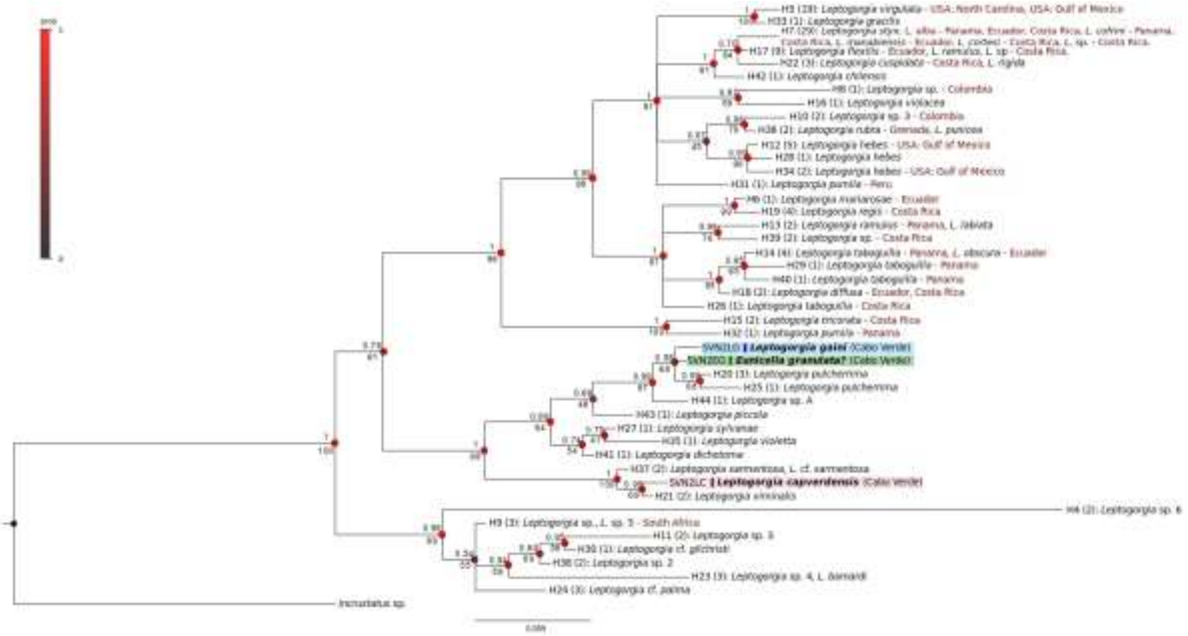

Figure 3.2.4: Phylogenetic tree of the *Leptogorgia* genus for the Octocorallia mtMutS gene using two model-based methods of phylogenetic inference: Bayesian Inference (BI) and Maximum-Likelihood (ML) analysis, for 45 concatenated haplotype groups (3 sequences from this study's samples, 128 sequences from GenBank). *Incrustatus sp.* (MW166876.1) was used as outgroup to root the tree. BI analyses were performed running four MCMC chain, and Bayesian posterior probabilities (BPP) are represented by circles and values above nodes (red circles indicate that the clade cluster is strongly supported). Bootstrap percentages of the ML analysis are given below nodes.

Barcodes and their metadata regarding geographic location for the genus *Leptogorgia* were much more complete compared to the other Octocorallia genus. While the three samples from Cabo Verde each were classified in a separate haplotype group in the MutS tree (Hap_1: SVN2LC_ND4L2475-F_Lcapverdensis, Hap_2: SVN2LG_ND4L2475-F_Lgainii, Hap_3: SVN2EG_ND4L2475-F_Egranulata) most sequences included in this phylogeny (MutS: Figure 3.2.4 and COI: Figure 3.2.5) were samples originating from the USA, central America, and the Caribbean. In both trees, *L. capverdensis* was the single sequence in its own clade but shared similar branch length to *L. cf. sarmentosa* in terms of genetic change, with high support in clade separation (COI: BI:1, ML: 90, MutS: BI: 1, ML: 100). Each one of the three markers matches for SVN2LC gave two best hits for the sequence, of either *L. sarmentosa* or *L. capverdensis* with the highest hit occurring with COI fragment (*L. cf. sarmentosa AP-2021* or *L. capverdensis* both ID and query coverage: 100%) (Tables S2).

SVN2LG and SVN2EG were identified as *L. gaini*, corroborated by their sequence divergence of 0.2% for MutS (Suppl. Material Table S6) and 0.0% for COI (Suppl. Material Table S7).

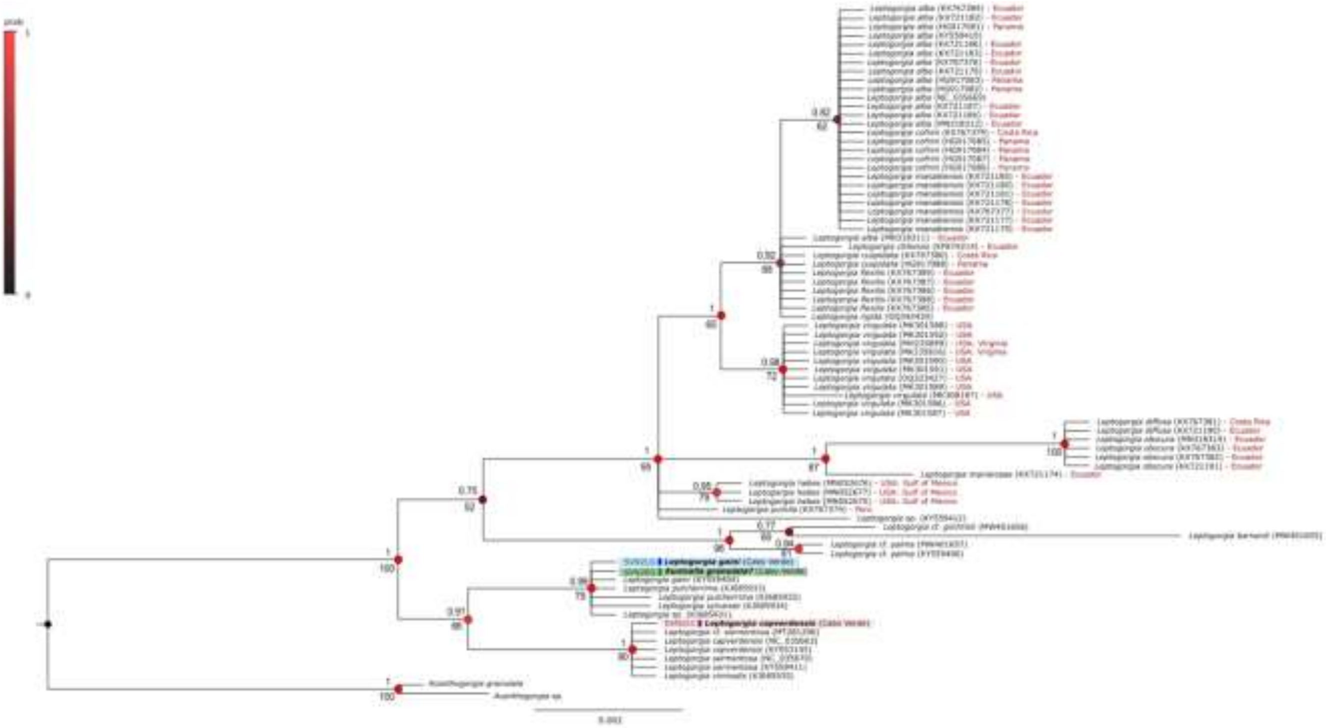

Figure 3.2.5: Phylogenetic tree of the *Leptogorgia* genus for the mitochondrial gene COI using two model-based methods of phylogenetic inference: Bayesian Inference (BI) and Maximum-Likelihood (ML) analysis, for concatenated sequences of 79 specimens (3 sequences from this study's samples, 76 sequences from GenBank). *Acanthogorgia granulata* (FJ264903.1) and *Acanthogorgia sp.* (FJ264902.1) were used as outgroup to root the tree. BI analyses were performed running four MCMC chain, and Bayesian posterior probabilities (BPP) are represented by circles and values above nodes (red circles indicate that the clade cluster is strongly supported). Bootstrap percentages of the ML analysis are given below nodes.

- *Carijoa*

Carijoa riisei was successfully identified across all three nuclear and mitochondrial markers. Our sequence (SNCR) was grouped with sequences from the Caribbean region encompassing Panama and the USA, and morphological identity validated this claim (Figure 3.2.1).

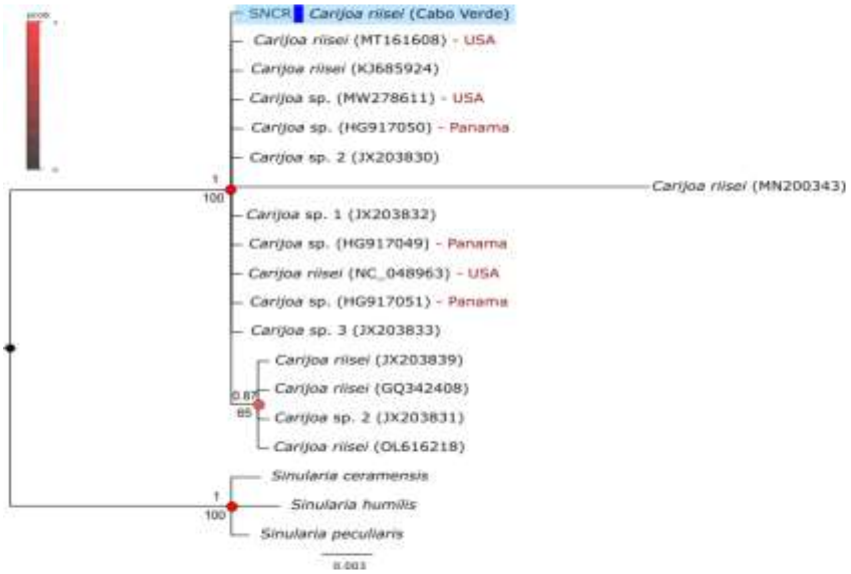

Figure 3.2.6: : Phylogenetic tree of the *Carijoa* genus for the mitochondrial gene COI using two model-based methods of phylogenetic inference: Bayesian Inference (BI) and Maximum-Likelihood (ML) analysis, for concatenated sequences of 19 specimens (1 sequences from this study's samples, 18 sequences from GenBank). Three sequences from the genus *Sinularia*

(NC_044122.1, OK641586.1, NC_018379.1) were used as outgroup to root the tree. BI analyses were performed running four MCMC chain, and Bayesian posterior probabilities (BPP) are represented by circles and values above nodes (red circles indicate that the clade cluster is strongly supported). Bootstrap percentages of the ML analysis are given below nodes.

3.2.3 Hexacorallia trees

- *Atlantia*

Atlantia is well established in Cabo Verde and has been the subject of recent molecular and phylogenetic analyses (Capel et al., 2020). Even so, sequences of the genus presented a challenge and comparative sequences for COI or 28S were lacking in GenBank database. All sequences matched to either other *Tubastraea* specimens (92-98.75) outside their theoretical geographic distribution, or to two additional genus *Astroides* (98.87), *Dendrophyllia* (96-98.75%) (Suppl. Material TableS2). Similarity distance between haplotype 1 (green) and haplotype 2 (our sequences in blue) was quite low (0.4%: Table S9) but clade separation was highly supported nevertheless.

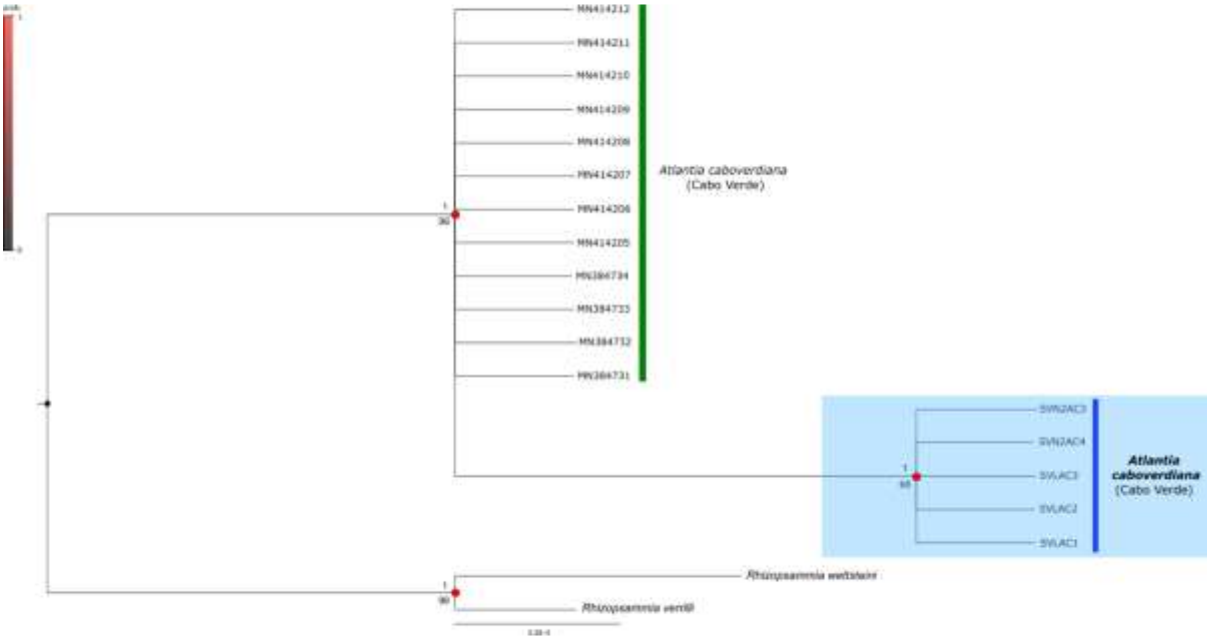

Figure 3.2.7: Phylogenetic tree of the *Atlantia* genus for the mitochondrial gene COI using two model-based methods of phylogenetic inference: Bayesian Inference (BI) and Maximum-Likelihood (ML) analysis, for concatenated sequences of 19 specimens (5 sequences from this study's samples, 14 sequences from GenBank). Three sequences from the genus *Rhizopsammia* (OR394761.1, OR394768.1) were used as outgroup to root the tree. BI analyses were performed running four MCMC chain, and Bayesian posterior probabilities (BPP) are represented by circles and values above nodes (red circles indicate that the clade cluster is strongly supported). Bootstrap percentages of the ML analysis are given below nodes.

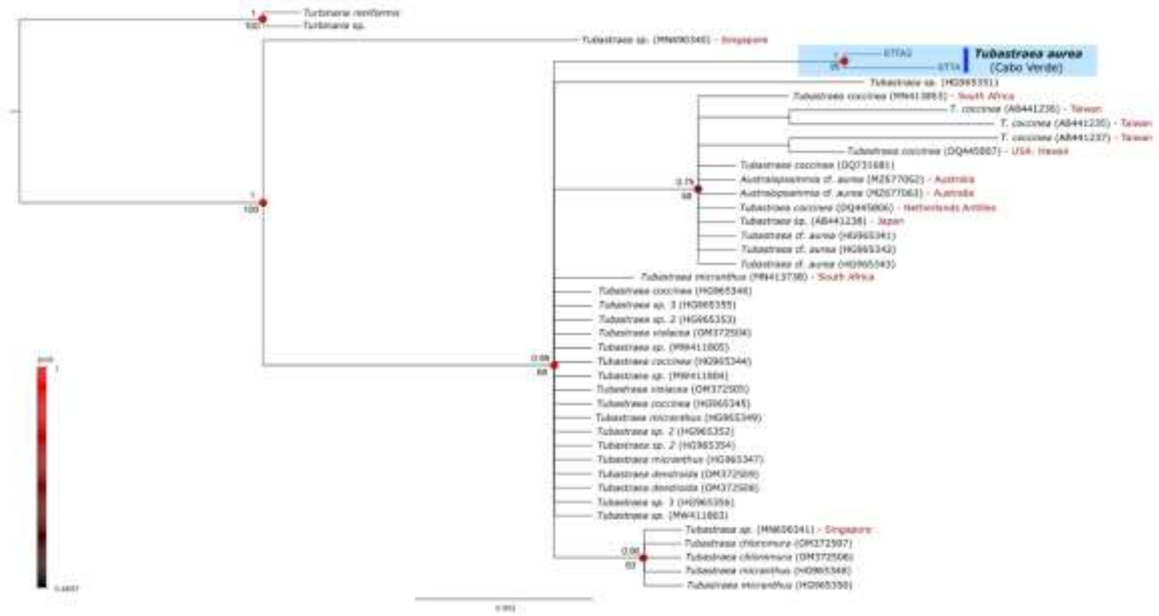

Figure 3.2.8: Phylogenetic tree of the *Tubastraea* genus for the mitochondrial gene COI using two model-based methods of phylogenetic inference: Bayesian Inference (BI) and Maximum-Likelihood (ML) analysis, for concatenated sequences of 42 specimens (2 sequences from this study's samples, 40 sequences from GenBank). *Turbinaria_reniformis* (MZ701621.1) and *Turbinaria mesenterina* (MZ701598.1) were used as outgroup to root the tree. BI analyses were performed running four MCMC chain, and Bayesian posterior probabilities (BPP) are represented by circles and values above nodes (red circles indicate that the clade cluster is strongly supported). Bootstrap percentages of the ML analysis are given below nodes.

Tubastraea tree reconstruction showed very widely distributed regional affinities across different oceans. Previously classified as *Australopsammia* (superseded name), our samples, were initially identified as the specie *Tubastraea aurea,* but seemed to hold important genetic divergence in relation to the *Australopsammia cf. aurea* species from Australia (Figure 3.2.8). Sequences gave also close percentage of identification to three other specimens barcode.

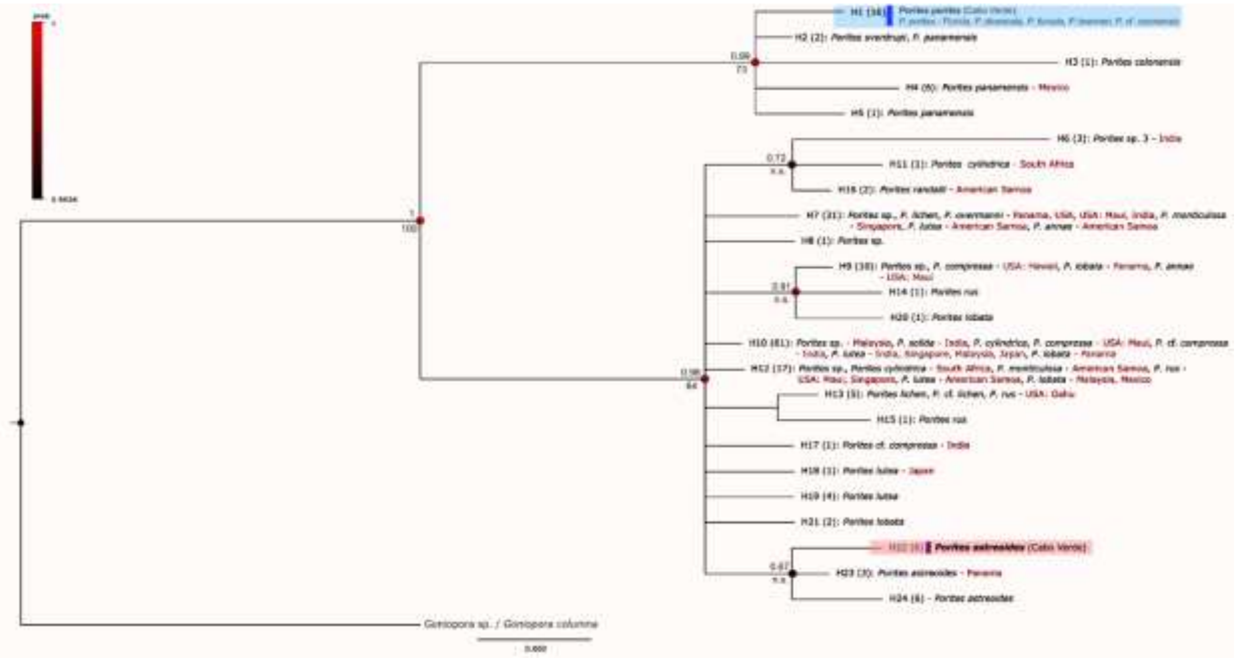

Figure 3.2.9: Phylogenetic tree of the *Porites* genus for the mitochondrial gene COI using two model-based methods of phylogenetic inference: Bayesian Inference (BI) and Maximum-Likelihood (ML) analysis, for 25 concatenated haplotype groups (12 sequences from this study's samples, 171 sequences from GenBank). All sequences were collapsed into identical sequences, followed by haplotype groups. *Goniopora columna* (MN690336.1) and *Goniopora sp.* (LC565115.1) were used as outgroup to root the tree. BI analyses were performed running four MCMC chain, and Bayesian posterior probabilities (BPP) are represented by circles and values above nodes (red circles indicate that the clade cluster is strongly supported). Bootstrap percentages of the ML analysis are given below nodes.

All *Porites porites* samples from this study were included in the Haplotype group 1, which was paired with *P. porites* samples from Florida. Species from this study shared close genetic proximity to species from both Florida and Mexico (H4) (Figure 3.2.9). Blast results for *P. porites* gave 100% match to *P. porites* sequences from GenBank for the mitochondrial gene COI (Table S2) but matched to Porites sp. NG17 (98.19%) (KY786090.1) with the nuclear 28S gene (Table S3). Samples of P. astreoides also matched with this sequence but to a higher percentage (99.86%). Caution in using the 28S nuclear gene as a reliable barcode for specie identification for this genus is appropriate as both species were morphologically distinct in the field. The next best id match for *P. porites* was with *P. panamensis* (99.54-99.84 %), which showed an interspecific divergence between 3.4 and 3.7% (Table S11). *Porites astreoides* Blast results corresponded to initial identification (COI: Tables S2), followed closely by matches with *P. rus* (99.38%) and *P. harrisoni* (99.69%) sequences.

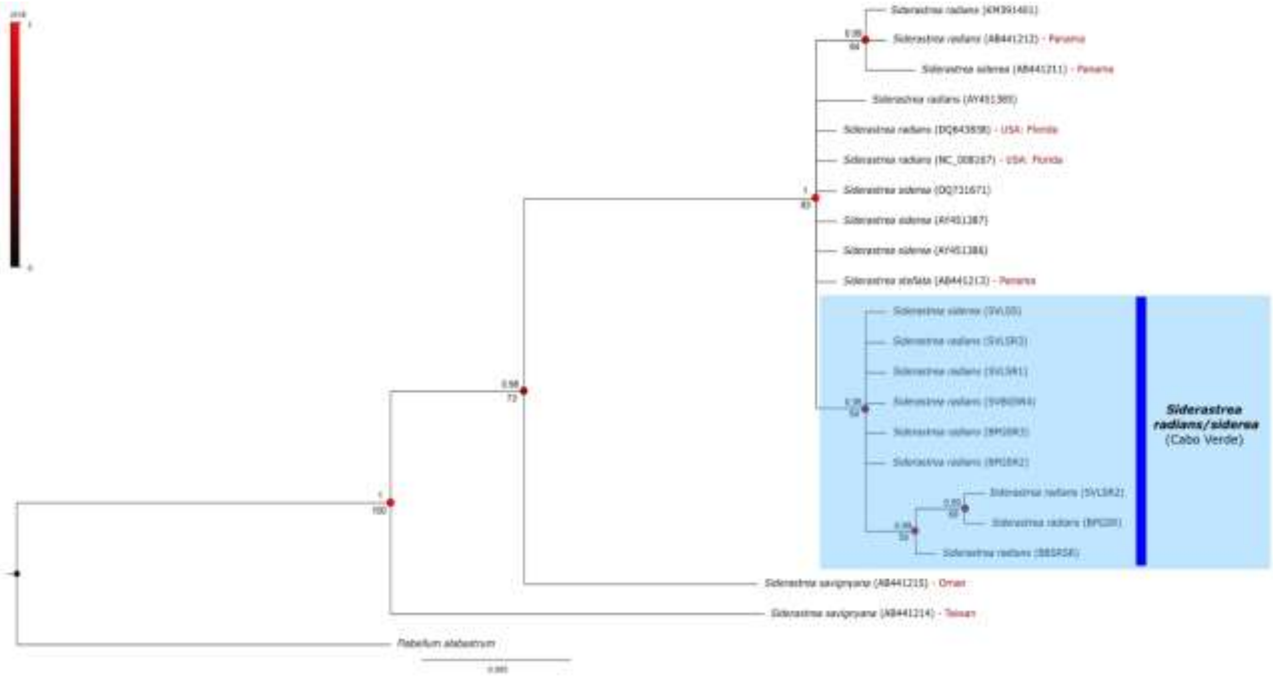

Figure 3.2.10: Phylogenetic tree of the *Siderastrea* genus for the mitochondrial gene COI using two model-based methods of phylogenetic inference: Bayesian Inference (BI) and Maximum-Likelihood (ML) analysis, for concatenated sequences of 22 specimens (9 sequences from this study's samples, 13 sequences from GenBank). *Flabellum alabastrum* (OQ731672.1) was used as outgroup to root the tree. BI analyses were performed running four MCMC chain, and Bayesian posterior probabilities (BPP) are represented by circles and values above nodes (red circles indicate that the clade cluster is strongly supported). Bootstrap percentages of the ML analysis are given below nodes.

All *Siderastrea radians* samples matched the same specie for both genes tested. For COI, ID% and Query coverage were high and matched *S. radians* (99.84%), closely followed by *S.siderea* (99.69%) (Table S2). They matched *S.radians* sequences at 99.85% but with a low query coverage (90-91%) for the 28S gene (Tables S3). While *S. radians* sampled sequences were separated in three haplogroups, their intraspecific divergence appeared low (0.2-0.3%) as well as their interspecific divergence (0.2-0.5%) with *S. siderea* (haplotype 6) (Table S12). Specimens shared close genetic proximity to species from Panama and Florida (Figure 3.2.10).

In the *Favia* phylogenetic tree, sample BPGFF haplotype grouping was not so evident with a divergence from *F.fragum* (Figure 3.2.11). Genetic distance between my sample and *F. fragum* sequences was 2.3% (Table S13) for the COI gene analysis. Clustering of my sample was not strongly supported and blast identification matched to *Favia fragum* but with a 97.41% correspondence (100% Query) (Table S2). Most samples that had been morphologically identified as *F.fragum* were difficult to manage during molecular analyses, at that, percentage of high quality reading from sequencing for BGPFF was lower than for other samples (28.5%).

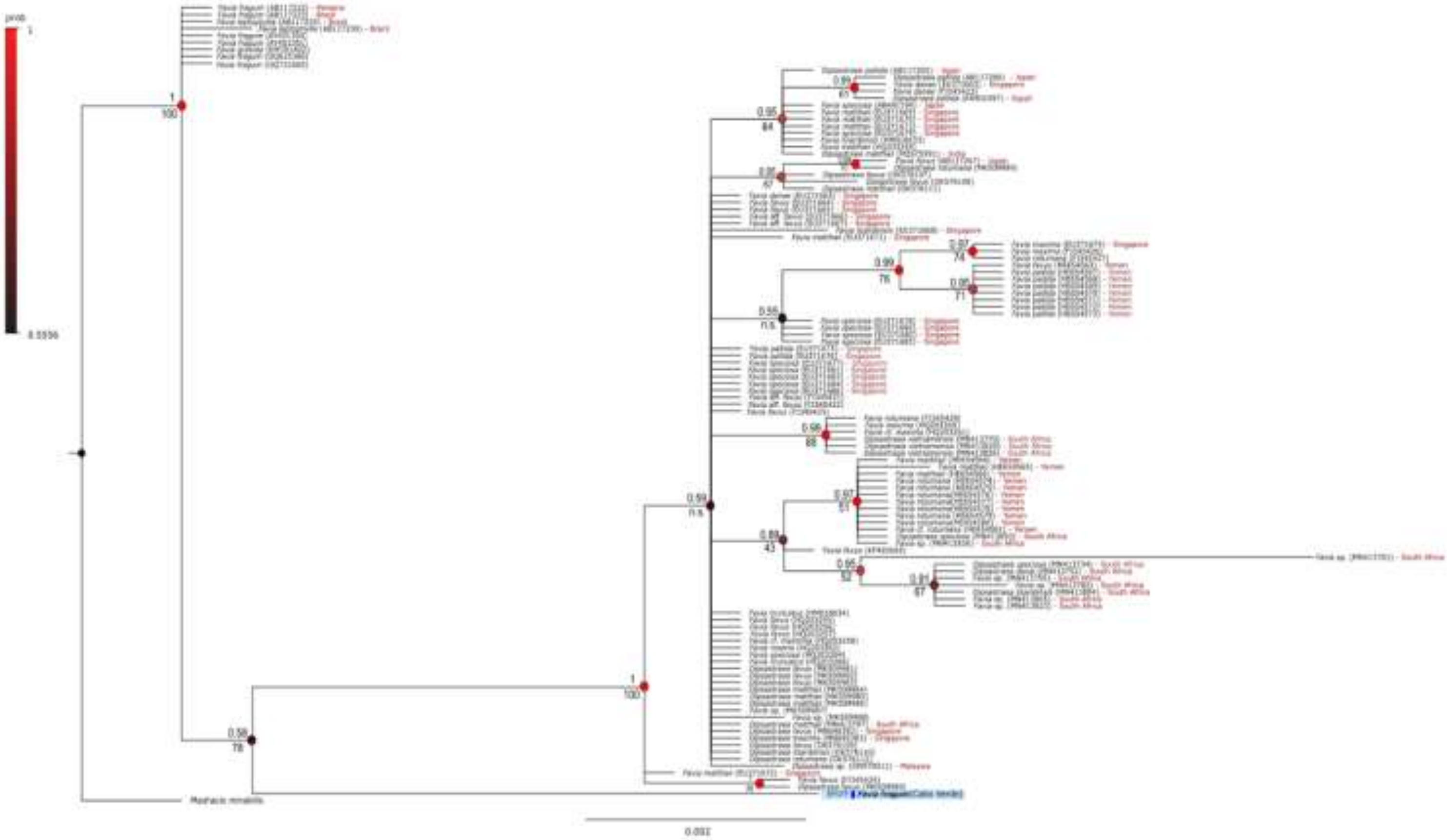

Figure 3.2.11: Phylogenetic tree of the *Favia* genus for the mitochondrial gene COI using two model-based methods of phylogenetic inference: Bayesian Inference (BI) and Maximum-Likelihood (ML) analysis, for concatenated sequences of 115 specimens (1 sequences from this study's samples, 114 sequences from GenBank, 26 haplotype groups). *Madracis mirabilis* (AY451344.1) was used as outgroup to root the tree. BI analyses were performed running four MCMC chain, and Bayesian posterior probabilities (BPP) are represented by circles and values above nodes (red circles indicate that the clade cluster is strongly supported). Bootstrap percentages of the ML analysis are given below nodes.

SVLMP sample was initially identified as *Polycyathus senegalensis*. After molecular analysis, a mitochondrial DNA match was found for the *Oculina* genus (*Oculina patagonica, Oculina sp. KL-2014*) with 100% identification and query coverage (Table S2). Clade clustering in the tree based on COI was strongly supported and our sequence shared close similarity in the amount of genetic change to both *Oculina* and *Cladocora* genus. *Oculina Patagonica* (LN614380) which was one of the highest identity match (100%) is a sequence from Spain while most Cladocora are from Cyprus or Greece. SVLMP presented a similarity distance of 0.00% with different species from both previously mentioned genus (*Cladocora caespitosa*, *Oculina cf. varicose*, *O. diffusa*, *O. patagonica*, *O. robusta*) (Table S14).

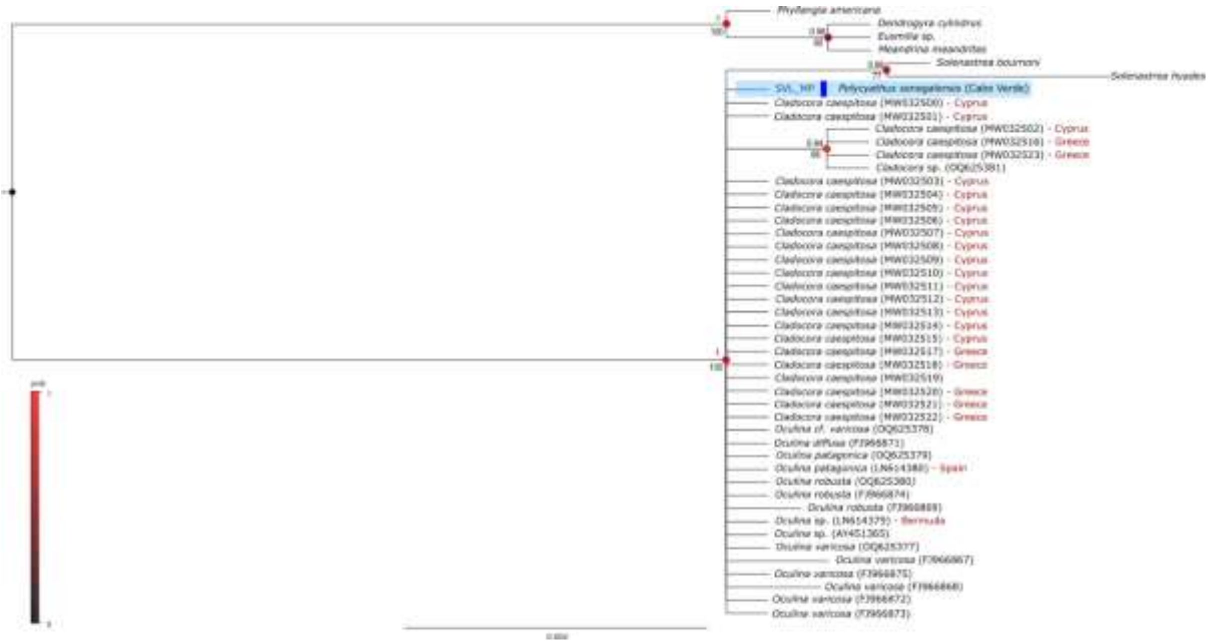

Figure 3.2.12: Phylogenetic tree of the *Cladocora/Oculina* genus for the mitochondrial gene COI using two model-based methods of phylogenetic inference: Bayesian Inference (BI) and Maximum-Likelihood (ML) analysis, for concatenated sequences of 47 specimens (1 sequences from this study's samples, 46 sequences from GenBank). *Phyllangia americana* (MK309944), *Dendrogyra cylindrus* (OQ625384), *Eusmilia sp.* (AY451345), *Meandrina meandrites* (OQ625382), *Solenastrea bournoni* (AY451359), *and Solenastrea hyades* (FJ966870) were used as outgroups to root the tree. BI analyses were performed running four MCMC chain, and Bayesian posterior probabilities (BPP) are represented by circles and values above nodes (red circles indicate that the clade cluster is strongly supported). Bootstrap percentages of the ML analysis are given below nodes.

3.3 LIST OF SPECIES FROM MACARONESIA

In order to comprehend the shared species between Cabo Verde and the islands of Macaronesia, a list of species was created to better illustrate commonality. No common species of Alcyonacea are shared between the Azores and Cabo Verde. Only the genus *Keratoisis* could be found in both islands. *Eunicella verrucosa* was the only common Alcyonacea species between the Canary islands, Madeira and Cabo Verde. Five species of Scleractinia were shared with Cabo Verde from the Canary islands and Madeira mostly from the genus *Madracis*, *Polycyathus* and *Phyllangia* (Table 3.3.1). *Pourtalosmilia anthophyllites* is found in Madeira, Azores and Cabo Verde. The specie *Anthipatella wollastoni* is widely distributed across all Macaronesia islands and Cabo Verde. At the genus level, species from *Stichopathes* and *Tanacetipathes* could be found in all Macaronesia islands, genus's commonly found in Cabo Verde, but did not boast the same species included in those genus except for *S. setacea* (Canry Islands) and *T. wirtzi* (Madeira) (Table 3.3.1). It is worth nothing that and exhaustive list exists regarding coral species found in Azores (Braga et al., 2013), however, only a partial list was presented here, mostly focusing to include species from the same genus or family. No records could be found for the Selvagens islands precisely.

Table 3.3.1: List of species of Alcyonacea (orange), Scleractinia (green), Antipatharia (blue) from the litterature of three islands of Macaronesia: the Canary Islands, Azores and Madeira. Common species to Cabo Verde are in **bold.** Common genus are underlined (reference list associated can be found in Suppl. material Table S15).

Canary Islands	Source	Madeira	Source	Azores	Source
Alcyonium coralloides	16	*Bebryce mollis*	17	*Acanella arbuscula*	12
Alcyonium glomeratum	15	*Dentomuricea meteor*	17	*Alcyonium glomeratum*	10
Acanthogorgia hirsuta	16	***Eunicella verrucosa***	2, 9	*Alcyonium acaule*	18
Acanthogorgia armata	16	*Eunicella sp.*	9	*Anthothela grandiflora*	18
Berbryce mollis	16	*Paramuricea cf. grayi*	17	*Azoriella bayeri*	10
Callogorgia verticillata	16	*Paracalyptrophora josephinae*	17	*Bebryce mollis*	12
Corallium niobe	16	*Sarcophyton sp.*	17	*Chelidonisis aurantiaca*	12
Corallium tricolor	16	*Viminella flagellum*	17	*Callogorgia verticillata*	12
Ellisella paraplexauroides	16			*Candidella imbricata*	12
Eunicella verrucosa	16	*Balanophyllia regia*	8	*Chrysogorgia agassizii*	12
Leptogorgia ruberrima	16	*Caryophyllia inornata*	8	*Chrysogorgia elegans*	12
Leptogorgia vimnalis	15	*Caryophyllia smithii*	5	*Chrysogorgia fewkesii*	12
Metallogorgia melanothrichos	16	*Cladocora debilis*	5, 8	*Chrysogorgia quadruplex*	12
Narella bellissima	16	*Dendrophyllia ramea*	8	*Chrysogorgia squamata*	12
Paramuricea grayi	16	*Hoplangia durotrix*	8	*Dacrygorgia modesta (Eunicella modesta)*	12
Paramuricea biscaya	16	***Madracis asperula***	5, 8	*Dentomuricea meteor*	12
Placogorgia sp.	16	***Madracis pharensis***	8	*Heteropolypus sol*	18
Pteroeides griseum	16	*Paracyathus pulchellus*	8	*Isidella longiflora*	12
Swiftia pallida	16	***Polycyathus senegalensis***	4	*Iridogorgia pourtalesii*	12
Villogorgia bebrycoides	16	*Polycyathus muelleri*	8	*Keratoisis grayi*	12
Viminella flagellum	16	***Phyllangia americana mouchezii***	8	*Lepidisis cyanae*	12
		Pourtalosmilia anthophyllites	8	*Metallogorgia melanotrichos*	12
Anomocora fecunda (Coenosmilia fecunda)	16			*Muriceides lepida*	12
Anomocora elongata	16	***Antipathella wollastoni***	1, 8	*Muriceides paucituberculata*	12
Balanophyllia regia	15, 16	*Antipathes sp.*	17	*Narella bellissima*	12
Caryophyllia calveri	16	*Antipathes furcata*	8	*Narella versluysi*	12
Caryophyllia cyathus	4	*Distichopathes sp.*	17	*Nicella granifera*	12
Caryophyllia inornata	15, 16	*Parantipathes sp.*	17	*Paracalyptrophora josephinae*	12
Caryophyllia seguenzae	5	***Stichopathes sp.***	17	*Paramuricea candida*	12
Caryophyllia smithii	5	*Stichopathes dissimilis*	6	*Placogorgia becena*	12
Coenocyathus cylindricus	16	*Stichopathes gracilis*	8	*Placogorgia coronata*	12
Cladocora debilis	15	***Tanacetipathes sp.***	17	*Placogorgia intermedia*	12
Coesnosmilia fecunda	16	*Tanacetipathes cavernicola*	8	*Placogorgia terceira*	12
Deltocyathus moseleyi	16	***Tanacetipathes wirtzi***	8	*Pseudoanthomastus agaricus*	18
Deltocyathus eccentricus	16			*Pseudoanthomastus mariejosae*	18
Dendrophyllia alternata	16			*Radicipes fragilis*	12
Dendrophyllia laboreli	16			*Swiftia dubia*	12
Dendrophyllia ramea	15			*Thesea rigida*	12
Desmophyllum dianthus	4			*Thouarella (Thouarella) variabilis*	12
Eguchipsammia gaditana	16			*Thouarella (Euthouarella) grasshoffi*	12
Enallopsammia rostrata	16			*Villogorgia bebrycoides*	12
Hoplangia durotrix	16			*Viminella flagellum*	12
Leptopsammia pruvoti	16				
Madracis asperula	5			*Anomocora fecunda*	12
Madracis pharensis	15			*Aulocyathus atlanticus*	12

Madrepora oculata	16			*Balanophyllia (Balanophyllia) cellulosa*	12
Paracyathus pulchellus	15			*Cladocora cf. debilis*	11
Phyllangia americana mouchezii	15, 16			*Caryophyllia inornata*	11, 12
Polycyathus sp.	16			*Caryophyllia smithii*	5, 11, 12
Polycyathus muellerae	16			*Caryophyllia (Caryophyllia) abyssorum*	12
Polycyathus senegalensis	**4**			*Caryophyllia (Caryophyllia) alberti*	12
Oculina Patagonica	14			*Caryophyllia (Caryophyllia) ambrosia*	12
Tubastraea sp.	14			*Caryophyllia (Caryophyllia) atlantica*	12
Tubastraea coccinea	3			*Caryophyllia (Caryophyllia) calveri*	12
Tubastraea tagusensis	3			*Caryophyllia (Caryophyllia) cyathus*	12
				Caryophyllia (Caryophyllia) foresti	12
Antipathella wollastoni	1			*Caryophyllia (Caryophyllia) inornata*	12
Antipathes furcata	16			*Caryophyllia (Caryophyllia) sarsiae*	12
Antipathes flabellum	16			*Caryophyllia (Caryophyllia) smithii*	12
Paranthipathes cf. larix	16			*Coenocyathus cylindricus*	12
Stichopathes sp.	12, 16			*Concentrotheca laevigata*	12
Stichopathes gracilis	16			*Dasmosmilia lymani*	12
Stichopathes setacea	16			*Dasmosmilia variegata*	12
Tanacetipathes cavernicola	16			*Deltocyathus eccentricus*	12
				Deltocyathoides stimpsonii	12
				Deltocyathus italicus	12
				Deltocyathus moseleyi	12
				Desmophyllum dianthus	12
				Dendrophyllia ramea	12
				Dendrophyllia cornigera	12
				Fungiacyathus (Bathyactis) crispus	12
				Fungiacyathus (Bathyactis) marenzelleri	12
				Fungiacyathus (Bathyactis) symmetricus	12
				Fungiacyathus (Fungiacyathus) fragilis	12
				Guynia annulata	11
				Leptopsammia formosa	12
				Desmophyllum pertusum	12
				Madrepora oculata	12
				Madracis pharensis	11, 12
				Madracis profunda	12
				Paracyathus pulchellus	11, 12
				Pourtalosmilia anthophyllites	12
				Premocyathus cornuformis	12
				Solenosmilia variabilis	12
				Stephanocyathus (Odontocyathus) nobilis	12
				Stephanocyathus (Stephanocyathus) crassus	12
				Stephanocyathus (Stephanocyathus) diadema	12
				Stephanocyathus (Stephanocyathus) moseleyanus	12
				Tethocyathus variabilis	12
				Trochocyathus (Trochocyathus) spinosocostatus	12
				Vaughanella concinna	12
				Antipathella wollastoni	1
				Antipathella subpinnata	12
				Antipathes erinaceus	12
				Antipathes grayi	12
				Antipathes virgata	12
				Bathypathes patula	12

				Distichopathes sp.	12,13
				Elatopathes aff. abietina	12
				Leiopathes glaberrima	12
				Leiopathe sgrimaldii	12
				Leiopathes sp.	12, 13
				Parantipathes hirondelle	12
				Schizophytum echinatum	12, 13
				Stichopathes flagellum	7
				Stichopathes dissimilis	6
				Stauropathes punctata	12
				Stichopathes gravieri	12
				Stichopathes richardi	12
				Tanacetipathes squamosa	12

4 DISCUSSION

4.1 DNA BARCODING AND GENETIC SPECIES DELIMITATION

To the best of our knowledge, this study constitutes the first comprehensive DNA barcoding and phylogenetic analysis of coral species of Cabo Verde across different taxa. Our focus was on shallow water species and a total of 21 species were expected at first, further reduced at 14 species following sequencing step (*Atlantia caboverdiana, Porites porites, Siderastrea radians, Siderastrea siderea, Porites astreoides, Balanopsammia wirtzi, Favia fragum, Leptogorgia capverdensis, Leptogorgia gaini, Eunicella papillifera, Eunicella granulata, Carijoa riisei, Tubastraea aurea, Polycyathus senegalensis*). When only looking at the final phylogenetic analysis, including BLAST output, these resulted in the identification of two samples at the species level and 30 other samples at the genus level, across seven genus, and seven other samples, with insufficient genetic resolution even at the genus level. Now when we look at both the phylogenetic data, morphological identification and species list from the litterature, we can put forward that 27 samples were identified at the species level (eight species), included within six genus (*Siderastrea, Porites, Oculina, Leptogorgia, Carijoa, Balanopsammia*), and three, at the genus level (*Eunicella*). Some samples showed conflicting morphologic/molecular identifications and underwent taxonomic assignation corrections.

The identified species strictly based on phylogenetic analysis, were the following: a new barcode for presumed *Balanopsammia wirtzi*, and *Carijoa riisei*. Concerning *C. riisei*, all three tested primers showed consistency in identification. This specie was previously successfully confirmed in Cape Verde using the cox1 Folmer region as barcode (Lopes et al., 2021). As for *B. wirtzi,* this specimen therefore constituted a new barcode whose definite identification will require further investigation into nucleotide mutation and specie-specific primer are needed. As a matter of fact, all species from the Dendrophylliidae family for Cabo Verde are needing revision and precise molecular research.

In the same vein, seven samples, which were initially classified in the genus *Atlantia* and *Tubastraea* did not have sufficient genetic resolution to be classified at the genus level. *Atlantia* was only recently defined as a new genus and little to no molecular studies exists for it (Capel et al., 2020). As for the genus *Tubastraea*, misidentification of its underlying species has already been noted, with previously recorded confusion of deposited sequences in GenBank with the genus *Dendrophyllia* (Capel et al., 2016). The corrected taxa for our sample SVLMP, as *Oculina patagonica,* initially identified as *Polycyathus senegalensis,* could be accurate. Even though the species was never recorded in Cabo Verde before, it was deemed invasive and recently established in the Canary islands (López et al., 2019b). While *Polycyathus* is theoretically present in the archipelago, its field identification has already proven problematic, as one of the less-understood scleractinian genera (Lin et al., 2012). *Leptogorgia Capverdensis* samples BLAST identification and haplotype groups in the phylogeny were similar for both COI and MutS and while morphological identification helped us to distinguish this specie, basing ourselves solely on the BLAST identification and phylogenetic trees would not help resolve specific classification. Genetic distance between *L. capverdensis* and *L. sarmentosa* sequences from GenBank were less than 0.01%, congruent with the values of 0.05% for the mitogenomes of *L. capverdensis* and *L. sarmentosa* (Poliseno et al., 2017).

While eight species were identified, most of the blasted sequences had more than one species-level match and different ID and query percentage. It is also worth noting that many Cabo Verdean species initially identified were taxonomically recorded in recent times, lacking any preliminary official molecular identification, explaning the substantial amount of unidentified samples. Prior to this research, there were no existing barcode library for Cabo Verde or any West African species, so sequences necessarily blasted, in most instances, against specimens (conspecific or not) collected in other biogeographical regions (Caribean, Pacific, etc...). Interspecific divergence values were also very low (Table S4-14) across genus and intergeneric genetic divergence, when comparing the targeted genus sequences to the outgroup genus, were lower for COI (around 3%) than for MutS (around 7.9%) (Shearer & Coffroth, 2008).

Overall, mitochondrial genetic resolution at the specie level was similar for COI and MutS gene fragments and often did not allow to distinguish a specimen at the specie level solely based on the molecular data. The low variability within the mitochondrial genome has been a difficult problem to solve in the search for a barcoding marker for both Octocorallia (Korphage et al., 2022) and Scleractinia (Shearer & Coffroth, 2008). Approaches using multiple nuclear and mitochondrial markers are considered the most promising, but as this study shows, some inherent variability problems persist. In any case, the use of a suite of mitochondrial and nuclear genes, rather than a single gene, remains the best approach, , and COI has proven more useful when employed complementarely with other genes (Shearer & Coffroth, 2008; Forsman et al., 2009; McFadden et al., 2014).

4.1.1 Unresolved molecular analysis: 28S

Most nuclear 28S BLAST results were totally different from COI results across genus, and yielded lower ID and query coverage percentages. While most markers were only useful to identify up to the genus level, all barcodes based on the nuclear (28S) marker showed low identification resolution with variable barcode lengths. This could be partly explained by the limited database for dna barcoding based on the 28S, especially for eastern Atlantic species. Phylogenetic interpretation took into account BLAST identifications from 28S but was mostly based on COI and MutS sequences, for octocorals, as phylogenies should be prioritized over uncertain BLAST results where approximation of phylogenetic relationships is needed (Smith & Pease, 2017). As previously mentioned, 28S and mitochondrial BLAST results were often conflicting , sequence alignments for 28S amplicons were extremely complex and for most genus, could not be completed, ultimately compromising phylogenetic analysis. This limitation is attributable to the nuclear rDNA gene containing indels, which generally makes DNA alignments in corals difficult, and which is why COI sequences provide an advantage in coral phylogenetics (Kitahara et al., 2010).

4.2 CAPE VERDE CORAL REGIONAL AFFINITIES

As previously mentioned, specie delimitation was successful for 27 samples at species, and all most other samples, resolved at the genus level, in part because of marker resolution, in part because reference databases are still very incomplete and are plagued with conflicting results. Phylogenies nevertheless revealed important and interesting relationship to species from the USA, Caribbean and South/central America for three of the dominating hermatypic corals of Cabo Verde: *P. porites, P. astreoides* and *S. radians* (*S. siderea*) (Moses et al., 2003; Monteiro et al., 2008; Lopes et al., 2014). While this could be attributable to many sequences from

GenBank lacking geographical data, it seems most two of the Octocorallia genus (*Leptogorgia* and *Carijoa*) were sharing affinities to the aforementioned three regions. Hexacorallia on the other hand revealed more divergence in region relatedness, with 1) the genus *Porites* and *Siderastrea* (four species) closer to Carribean clades, 2) *Favia,* more cosmopolite with affinities to Oceania, Africa, America, and 3) *Oculina/Caldocora* genus, more related to Mediterranean species (Cyprus, Greece).

These findings deepen understanding of coral community composition and affinities as previously explored by Morri & Bianchi (1995), Morri et al. (2000) and Lopes et al. (2014). Most shallow hermatypic species found in Cabo Verde were closely related to Caribbean species, however, colony size for *S. radians* grew significatly larger than reported caribbean colonies, a unique feature deserving further investigation (Moses et al., 2003; Lewis, 1989). Regarding Alcyonacea, the Gorgonian species initially identified as *Leptogorgia capverdensis* could be attributed to either *L. capverdensis* or *L. sarmentosa.* While Watling & Auster (2005) associated both species to the Lusitanian-Mediteranean region, a revised comparative mitogenomic analysis of the genus *Leptogorgia* clearly seperated *L. capverdensis*'s distribution in a West African group and *L. sarmentosa* in a strictly Mediteranean group (Poliseno et al., 2017). *L. gaini* was also found not only in Cabo Verde but also throughout West African countries (Grasshoff, 1988; 1992) and while phylogenies of the *Leptogorgia* genus obtained here only show geographical data of related species from Central and South America, the Caribbean and USA, these findings are congruent with geographical relationships established for the widely encompassing genus by Poliseno et al. (2017). According to our *Carijoa* phylogenetic tree, our *Carijoa riisei* sample, consistently identified through both mitochondrial and nuclear gene, was closely affiliated with species from Panama and the USA which was consistent with findings by Lopes et al. (2021) and Concepcion et al. (2010). This specie, deemed invasive, is native to the Indo-West Pacific and has a wide geographic distribution, found in the Caribbean, the Western Atlantic (West Africa), the Gulf of Mexico and Hawaii. While confirmation of identification for samples previously assigned as *Eunicella papilifera* and *E. granulata* were not 100% reliable, the sample STEG was identified as *E. verrucosa* with the MutS primer (100%) (Table S2). While phylogenetic metadata for *Eunicella* was absent, the species was previously recorded in Cabo Verde by Grasshoff (1992) and can be found in Northern Atlantic, the Mediterranean, and in Madeira (Grasshoff, 1992) and the Canary Islands (Provencio & Munoz, 2013).

Regarding affinities with Macaronesia, identification at species level revealed substantial differences with Cabo Verde. From DNA barcoding match and GenBank sequence database, most sequences matching our sample sequences were not from Macaronesia. Looking at the phylogenies for *S. radians, P. porites* and *P. astreoides,* these shallow dominant hermatypic species of Cabo Verde (Monteiro et al., 2008), cannot be found in the three other Macaronesia archipelagos (Brito et al., 2007). As advanced by Molodtsova (2006), it seems deep Anthipatharia species (black corals) such as *Antipathella wollastoni,* some *Tanacetipathes* and *Stichopathes* species are found in Azores, Canary, Madeira and Cabo Verde but not necessarily the same species. *Antipathella wollastoni* could be found throughout all the four archipelagos and unidentified specimens from the same genus could be common between Macaronesia and Cabo Verde. This phenomenon could be attributable to the bridging effects of deep sea seamounts in dispersal patterns for Antipatharia (Braga-Henriques et al., 2013). This claim regarding the preceeding order would need further investigation as no molecular data was obtained for any Antipatharia corals sampled in Cape Verde due to PCR amplification failure. A potential cause for this failure was hypothesized to be related to the preservation agent (70% ethanol) which might have degraded the DNA. Saturated sodium chloride (DESS) might have been a better option as it has been shown to be superior to ethanol for coral tissue DNA preservation (Gaither et al., 2011). Cox1 intron also exists within the order Antipatharia which could have caused a DNA fragment mismatch regarding the complementary primer region (Barrett et al., 2020). Cryptic species of the Antipatharia order were previously singled out by Wirtz (2022b, 2023) and represent important knowledge gaps which render coral biodiversity and richness of Cabo verde incomplete.

To summarize, this study does not provide a complete DNA barcode of all the species of Cabo Verde, but it is still the first to provide sequences and phylogenetic data on many of the species present and, successfully identify seven species of the Archipelago based on genetic data, morphological identification, and through litterature-based lists. While cryptic species had been anticipated to be discovered, they were mostly comprised in the order Antipatharia, which ended up being set aside from the molecular analysis. Notwithstanding, morphological taxonomic classification were corrected for certain species such as *Oculina patagonica*, a new barcode for the specie *Balanopsammia wirtzi* was provided, but specifically designed primers, and more importantly better reference databases, for which this study represents a great contribution, would be needed to provide better genetic resolution. As for the species affinities of Cabo Verde, a general trend could be seen across some Scleractinia taxa towards Western

Atlantic and Carribean corals, especially in the dominating four hermatypic species. While from the exhaustive Macaronesia taxa lists (Table 3.3.1), some Antipatharia species could be commonly found in three of the four Macaronesia islands and Cabo Verde, sporadically distributed but commonality was more related to genus level as very few species were widely distributed. A distinction following observation from Monteiro et al. (2008) could be made in the species affinities, while certain taxa from Scleractinia, Alcyonacea, and Antipatharia could be found throughout the Macaronesia islands and Cabo Verde, species compositions of the four islands compared (Azores, Madeira, Canary Islands, Cabo Verde) was often different, and Cabo Verde shallow dominating hermatypic coral species seem to constitute distinct communities from Macaronesia and from West Africa.

5 CONCLUSION

As threats to coral habitats increase globally, the ongoing monitoring and evaluation of these ecosystems is critical, especially as it supports the establishment of protected areas. Within the geographic context of Western Africa, with heavy reliance on fishery cultures as part of their economic development, it is likewise important to ensure that the natural environment is not severely degraded at the cost of economic progress. This remains, fundamentally, the presumption of sustainable development: whereby sustainable resource use, must couple with economic and social progress, as opposed to at the expense of it. In this region that has been systematically oppressed under the legacy of colonial resource extraction, it is extremely important, that in meaningful partnership, scientists continue to work with residents to ensure that their natural environment is protected, rather than destroyed. In this study, we aimed to provide preliminary scientific information of the geographic distinctness and biodiversity importance of the Cape Verde coral reefs, through the identification of endemic and cryptic species to this region, and through articulating the unique biodiversity of this region. Specifically, Hexacorallia and Octocorallia tissue samples were used to create a preliminary barcode library for coral species. In meaningful partnership with this region, future work needs to continue to identify species within this unique geography, while utilizing a non-invasive method, such as eDNA, as it is pivotal in this region that research does not further exacerbate negative environmental impacts on the species in which it seeks to conserve and protect. Furthermore, particular attention to citizen-led projects should be bolstered, including Enseada the Coral and close to Mindelo, as indigenous-led conservation efforts consistently have proven to be effective and respectful the natural environment.

This study represents the first attempt to characterize coral communities of Cape Verde based on molecular methods, and a first attempt at a DNA barcode library based on multiple nuclear and plastid markers. This effort revealed that barcode databases remain very incomplete and sometimes conflicting when it comes to western African species and communities, highlighting how much basic research is still necessary to satisfactorily inventory coral diversity and endemism and biogeographic/evolutionary affinities of this important Cape Verde assemblage. As it is held globally, to ensure the protection of biodiversity, all countries need come together to protect 30% of the ocean by 2030. Regrettably, in Cape Verde, less than 1% of its coastal waters are protected. Through articulating the biodiversity of this region, and its distinctness, we hope these results can support further designations of Cape Verde coral reefs within marine protected areas. In large, protecting global biodiversity is pivotal, as it is their innate interconnectedness across social and economic realms that allows modern society to thrive. This is pivotal, now, more than ever, in the fight to mitigate and adapt to the Western-initiated anthropogenic modification of the natural environment.

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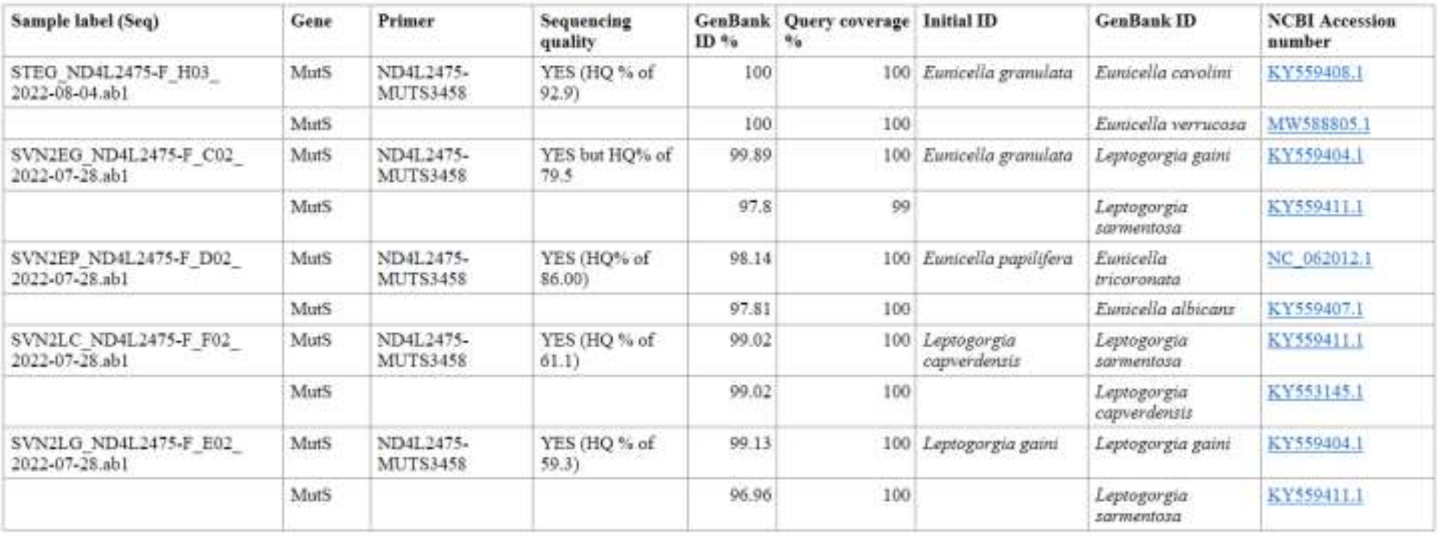
8 SUPPLEMENTARY MATERIAL

Table S1: Best NCBI blast results for sample sequences based on the 2 best hits (MUTS)



Sample label (Seq)	**Gene**	**Primer**	**Sequencing quality**	**GenBank ID %**	**Query coverage %**	**Initial ID**	**GenBank ID**	**NCBI Accession number**
STEG_ND4L2475-F_H03_ 2022-08-04.ab1	MutS	ND4L2475-MUTS3458	YES (HQ % of 92.9)	100	100	*Eunicella granulata*	*Eunicella cavolini*	KY559408.1
	MutS			100	100		*Eunicella verrucosa*	MW588805.1
SVN2EG_ND4L2475-F_C02_ 2022-07-28.ab1	MutS	ND4L2475-MUTS3458	YES but HQ% of 79.5	99.89	100	*Eunicella granulata*	*Leptogorgia gaini*	KY559404.1
	MutS			97.8	99		*Leptogorgia sarmentosa*	KY559411.1
SVN2EP_ND4L2475-F_D02_ 2022-07-28.ab1	MutS	ND4L2475-MUTS3458	YES (HQ% of 86.00)	98.14	100	*Eunicella papilifera*	*Eunicella tricoronata*	NC_062012.1
	MutS			97.81	100		*Eunicella albicans*	KY559407.1
SVN2LC_ND4L2475-F_F02_ 2022-07-28.ab1	MutS	ND4L2475-MUTS3458	YES (HQ % of 61.1)	99.02	100	*Leptogorgia capverdensis*	*Leptogorgia sarmentosa*	KY559411.1
	MutS			99.02	100		*Leptogorgia capverdensis*	KY553145.1
SVN2LG_ND4L2475-F_E02_ 2022-07-28.ab1	MutS	ND4L2475-MUTS3458	YES (HQ % of 59.3)	99.13	100	*Leptogorgia gaini*	*Leptogorgia gaini*	KY559404.1
	MutS			96.96	100		*Leptogorgia sarmentosa*	KY559411.1

Table S2: Best NCBI blast results for sample sequences based on the 2-4 best hits (COX1)

Sample label (Seq.)	**Gene**	**Primer**	**HQ % of the sequencing**	**GenBank ID %**	**Query coverage %**	**Initial ID**	**GenBank ID**	**NCBI Accession number**
SNCR_COII8068F-COIOCTR cons	COX1	COII8068F-COIOCTR	97.4	99.89	100	*Carijoa riisei*	*Carijoa riisei*	OL616218.1
				100	98		*Carijoa sp. HMG115*	HG917049.1
STEG_A04_COII8068-F-COIOCT-R cons VC	COX1	COII8068F-COIOCTR	66.5	100	100	*Eunicella granulata*	*Eunicella filiformis*	MT281294.1
				99.89	100		*Eunicella gazella*	MT281295.1
SVN2EG_B04_COII8068-F-COIOCT-R cons	COX1	COII8068F-COIOCTR	64.4	98.62	100	*Eunicella granulata*	*Leptogorgia cf. sarmentosa AP-2021*	MT281296.1
				98.4	100		*Swiftia pacifica*	FJ264906.1
SVN2EP_C04_COII8068-F-COIOCt-R cons	COX1	COII8068F-COIOCTR	80.5	98.84	100	*Eunicella papilifera*	*Eunicella gazzella*	MT281295.1
				98.84	100		*Eunicella tricoro nata*	NC_062012.1
SVN2LC_E04_COII8068-F-COIOCT-R cons	COX1	COII8068F-COIOCTR	72.9	100	100	*Leptogorgia capverdensis*	*Leptogorgia cf. sarmentosa AP-2021*	MT281296.1

				100	100		*Leptogorgia capverdensis*	NC_035663.1
SVN2LG_COII8068F-COIOCT-R VC cons	COX1	COII8068F-COIOCTR	43.4	99.87	100	*Leptogorgia gaini*	*Leptogorgia gaini*	KY559404.1
SVLMP_LCO1490_C01_2022-09-29 cons	COX1	LCO1490-HCO2198	98.4%	100	100	*Polycyathus senegalensis*	*Oculina patagonica*	LN614380.1
				100	100		*Oculina sp. KL-2014*	LN614379.1
BBSRPA_JGLCO1490-F_G04_2022-08-04.ab1	COX1	JGLCO1490-JGHCO2198	93.7	99.84	96	*Porites astreoides*	*Porites astreoides*	FJ423961.1
BBSRPP_JGLCO1490-F_F04_2022-08-04.ab1	COX1	JGLCO1490-JGHCO2198	94.0	100	98	*Porites porites*	*Porites porites*	DQ643837.1
				99.84	98		*Porites panamensis*	KU761953.1
BBSRSR_JGLCO1490-F_B03_2022-07-28.ab1	COX1	JGLCO1490-JGHCO2198	62.6	99.69	98	*Siderastrea radians*	*Siderastrea radians*	DQ643838.1
				99.68	97		*Siderastrea siderea*	AY451386.1
BISRP._JGLCO1490-F_H04_2022-08-04.ab1	COX1	JGLCO1490-JGHCO2198	91.4	99.69	100	*Porites sp.*	*Porites porites*	DQ643837.1
				99.54	100		*Porites panamensis*	KU761953.1
BISRPA_JGLCO1490-F_C03_2022-07-28.ab1	COX1	JGLCO1490-JGHCO2198	88.7	99.68	99	*Porite astreoides*	*Porites astreoides*	OQ731679.1
				99.38	99		*Porites rus*	MN690339.1
BISRPP_JGLCO1490-F_D03_2022-07-28.ab1	COX1	JGLCO1490-JGHCO2198	93.7	100	98	*Porites porites*	*Porites porites*	DQ643837.1
				99.84	98		*Porites panamensis*	KU761953.1
BPGPA2_JGLCO1490-F_D04_2022-08-04.ab1	COX1	JGLCO1490-JGHCO2198	92.1	99.84	96	*Porite astreoides*	*Porites astreoides*	FJ423961.1
				99.69	99		*Porites harrisoni*	NC_037435.1
BPGPP2_JGLCO1490-F_E04_2022-08-04.ab1	COX1	JGLCO1490-JGHCO2198	93.4	99.84	98	*Porites porites*	*Porites porites*	DQ643837.1
				99.69	98		*Porites panamensis*	KU761953.1
BPGPP_JGLCO1490-F_H02_2022-07-28.ab1	COX1	JGLCO1490-JGHCO2198	91.5	99.84	98	*Porites porites*	*Porites porites*	DQ643837.1

				99.69	98		*Porites panamensis*	KU761953.1
BPGSR2_JGLCO1490-F_G03_2022-07-28.ab1	COX1	JGLCO1490 - JGHCO2198	63.8	99.84	98	*Siderastrea radians*	*Siderastrea radians*	DQ643838.1
				99.84	97		*Siderastrea siderea*	AY451386.1
BPGSR3_JGLCO1490-F_A03_2022-07-28.ab1	COX1	JGLCO1490 - JGHCO2198	62.7	99.84	98	*Siderastrea radians*	*Siderastrea radians*	DQ643838.1
				99.84	97		*Siderastrea siderea*	AY451386.1
BPGSR_JGLCO1490-F_B04_2022-08-04.ab1	COX1	JGLCO1490 - JGHCO2198	72.9	99.53	98	*Siderastrea radians*	*Siderastrea radians*	DQ643838.1
				99.53	97		*Siderastrea siderea*	AY451386.1
PBGPA_JGLCO1490-F_A05_2022-08-04.ab1	COX1	JGLCO1490 - JGHCO2198	92.6	99.84	96	*Porite astreoides*	*Porites astreoides*	FJ423961.1
				99.69	99		*Porites harrisoni*	NC_037435.1
STTA2_JGLCO1490-F_F03_2022-07-28.ab1	COX1	JGLCO1490 - JGHCO2198	65.6	92	99.17	*Tubastraea aurea*	*Tubastraea coccinea*	HG965344.1
				96	98.72		*Dendrophyllia sp. YC-2017*	KY887482.1
				98	98.59		*Tubastraea micranthus*	NC_056883.1
				98.15	99		*Tubastraea sp. IP0356 cytochrome oxidase subunit I (COI) gene, partial cds; mitochondrial*	MN690341.1
STTA_JGLCO1490-F_E03_2022-07-28.ab1	COX1	JGLCO1490 - JGHCO2198	66.2	98.71	95	*Tubastraea aurea*	*Astroides calycularis*	JQ343126.1
				98.59	98		*Tubastraea micranthus*	NC_056883.1
				98.44	98		*Australopsammia cf. aurea WAMZ97774*	MZ677062
SVBGSR4_JGLCO1490-F_B05_2022-08-04.ab1	COX1	JGLCO1490 - JGHCO2198	65.4	99.84	98	*Siderastrea radians*	*Siderastrea radians*	DQ643838.1
				99.84	97		*Siderastrea siderea*	AY451386.1

SVLAC1_JGLCO1490-F_D04_2022-07-28.ab1	COX1	JGLCO1490-JGHCO2198	61.3%	98.87	95	*Atlantia caboverdiana*	*Astroides calycularis*	JQ343126.1
				98.75	98		*Tubastraea micranthus*	NC_056883.1
				98.75	98		*Tubastraea tagusensis*	NC_030352.1
SVLAC2_JGLCO1490-F_C06_2022-08-04.ab1	COX1	JGLCO1490-JGHCO2198	59.6%	98.87	95	*Atlantia caboverdiana*	*Astroides calycularis*	JQ343126.1
				98.75	98		*Tubastraea micranthus*	NC_056883.1
				98.75	98		*Tubastraea micranthus*	NC_056883.1
				98.75	98		*Tubastraea tagusensis*	NC_030352.1
SVLAC3_JGLCO1490-F_C04_2022-07-28.ab1	COX1	JGLCO1490-JGHCO2198	63.3%	98.72	96	*Atlantia caboverdiana*	*Dendrophyllia sp. YC-2017*	KY887482.1
				98.71	95		*Astroides calycularis*	JQ343126.1
				98.59	98		*Tubastraea micranthus*	NC_056883.1
				98.59	98		*Tubastraea tagusensis*	NC_030352.1
SVLAC4_JGLCO1490-F_D05_2022-08-04.ab1	COX1	JGLCO1490-JGHCO2198	62.7%	98.87	95	*Atlantia caboverdiana*	*Astroides calycularis*	JQ343126.1
				98.75	98		*Tubastraea micranthus*	NC_056883.1
SVLBW_JGLCO1490-F_E05_2022-08-04.ab1	COX1	JGLCO1490-JGHCO2198	63.1%	98.44	98	*Balanopsammia wirtzi*	*Tubastraea micranthus*	NC_056883.1
				98.44	98		*Tubastraea tagusensis*	KX024567.1
SVLPA1_JGLCO1490-F_G05_2022-08-04.ab1	COX1	JGLCO1490-JGHCO2198	77.0%	99.69	99	*Porites astreoides*	*Porites astreoides*	OQ731679.1
				99.38	99		*Porites rus*	MN690339.1
SVLPA2_JGLCO1490-F_F05_2022-08-04.ab1	COX1	JGLCO1490-JGHCO2198	54.1%	99.35	73	*Porites astreoides*	*Millepora alcicornis*	MK034169.1
SVLPA3_JGLCO1490-F_A04_2022-07-28.ab1	COX1	JGLCO1490-JGHCO2198	94.1%	99.84	96	*Porites astreoides*	*Porites astreoides*	FJ423961.1
				99.69	99		*Porites harrisoni*	NC_037435.1

SVLPP2_JGLCO1490-F_B04_2022-07-28.ab1	COX1	JGLCO1490-JGHCO2198	93.5%	100	98	*Porites porites*	*Porites porites*	DQ643837.1
				99.84	98		*Porites panamensis*	KU761953.1
SVLPP_JGLCO1490-F_B06_2022-08-04.ab1	COX1	JGLCO1490-JGHCO2198	93.2%	100	98	*Porites porites*	*Porites porites*	DQ643837.1
				99.84	98		*Porites panamensis*	KU761953.1
SVLSR1_JGLCO1490-F_A06_2022-08-04.ab1	COX1	JGLCO1490-JGHCO2198	53.0%	99.84	98	*Siderastrea radians*	*Siderastrea radians*	NC_008167.1
				99.69	98		*Siderastrea siderea*	OQ731671.1
SVLSR2_JGLCO1490-F_G09_2022-09-17.ab1	COX1	JGLCO1490-JGHCO2198	50.8%	99.53	98	*Siderastrea radians*	*Siderastrea radians*	NC_008167.1
				99.37	98		*Siderastrea siderea*	OQ731671.1
SVLSR3_JGLCO1490-F_C05_2022-08-04.ab1	COX1	JGLCO1490-JGHCO2198	59.2%	99.84	98	*Siderastrea radians*	*Siderastrea radians*	DQ643838.1
				99.84	97		*Siderastrea siderea*	AY451386.1
SVLSS_JGLCO1490-F_D06_2022-08-04.ab1	COX1	JGLCO1490-JGHCO2198	61.2%	99.84	98	*Siderastrea siderea*	*Siderastrea radians*	NC_008167.1
				99.69	98		*Siderastrea siderea*	OQ731671.1
SVN2AC3_JGLCO1490-F_H03_2022-07-28.ab1	COX1	JGLCO1490-JGHCO2198	60.2%	98.87	95	*Atlantia caboverdiana*	*Astroides calycularis*	JQ343126.1
				98.75	98		*Tubastraea micranthus*	NC_056883.1
				98.75	98		*Tubastraea tagusensis*	KX024567.1
				98.75	98		*dendrophyllia minuscula*	NC_060606.1
				98.30	99		*Tubastraea sp. IP0356*	MN690341.1
BPGFF_JGLCO1490-F_C04_2022-08-04.ab1	COX1	JGLCO1490-F	28.5%	97.41	100	*Favia fragum*	*Favia fragum*	OQ731665.1
				97.41	100		*Favia fragum*	OQ625386.1

Table S3: Best NCBI blast results for sample sequences based on the 2 best hits (28S)

Sample label (Seq.)	**Gene**	**Primer**	**GenBank ID %**	**Query coverage %**	**Initial ID**	**GenBank ID**	**NCBI Accession number**
STEG_28sFAR-RAR cons	28S	FAR-RAR	98.97	87	*Eunicella granulata*	*Eunicella verrucosa*	MT276789.1
			98.59	87		*Eunicella singularis*	MT276788.1
SVN2EP_28sFAR-RAR cons	28S	FAR-RAR	96.83	89	*Eunicella papillifera*	*Eunicella tricoronata*	JX203707.1
			96.79	87		*Eunicella verrucosa*	MT276789.1
SNCR_28sFAR-RAB_align consensus sequence_w/split	28S	FAR-RAB	99.4	91	*Carijoa riisei*	*Carijoa riisei*	JX203673.1
			98.95	91		*Carijoa sp. 3 CSM-2012*	JX203676.1
STCR_28sFAR.RAB_align consensus sequence_w/split	28S	FAR-RAB	99.23	86	*Antipathozoanthus macaronesicus*	*Antipathozoanthus cavernus*	MW652766.1
			99.68	82		*Antipathozoanthus remengesaui*	MW652767.1
SVN2_28sFAR-RAB_align consensus sequence_w/split	28S	FAR-RAB	99.53	91	*Antipathozoanthus macaronesicus*	*Antipathozoanthus cavernus*	MW652766.1
			100	87		*Antipathozoanthus remengesaui*	MW652767.1
SVN2EG_28sFAR-RAB_align consensus sequence_w/split	28S	FAR-RAB	96.66	99	*Eunicella granulata*	*Leptogorgia capverdensis*	FJ642931.1
			96.21	91		*Leptogorgia cf. lusitanica AP-2020*	MT276790.1
SVN2LC_28sFAR-RAB_align consensus sequence_w/split	28S	FAR-RAB	99.44	99	*Leptogorgia capverdensis*	*Leptogorgia capverdensis*	FJ642931.1
			99.39	91		*Leptogorgia cf. lusitanica AP-2020*	MT276790.1
SVN2LG_28sFAR-RAB_align consensus sequence_w/split	28S	FAR-RAB	96.78	100	*Leptogorgia gaini*	*Leptogorgia capverdensis*	FJ642931.1
			95.05	98		*Pacifigorgia rubinoffi*	KX767456.1
BBSRPA_28sFAR-RAB cons	28S	FAR-RAB	99.86	99	*Porites astreoides*	*Porites sp. NG17*	KY786090.1
			100	90		*Porites astreoides*	EU262821.1
BBSRPP_28sFAR-RAB cons	28S	FAR-RAB	98.19	99	*Porites porites*	*Porites sp. NG17*	KY786090.1
			100	90		*Porites porites*	EU262831.1
BBSRSR_28sFAR_RAB cons	28S	FAR-RAB	99.85	91	*Siderastrea radians*	*Siderastrea radians*	EU262848.1
			91.94	100		*Orbicella franksi*	AY026375.1
BISRP_28sFAR-RAB cons	28S	FAR-RAB	98.18	99	*Porites sp.*	*Porites sp. NG17*	KY786090.1
			97.9	99		*Porites sp. NG08*	KY786088.1
BISRPA_28sFAR-RAB cons	28S	FAR-RAB	99.86	99	*Porites astreoides*	*Porites sp. NG17*	KY786090.1
			100	90		*Porites astreoides*	EU262821.1
BISRPP_28sFAR-RAB cons	28S	FAR-RAB	98.18	99	*Porites porites*	*Porites sp. NG17*	KY786090.1
			100	90		*Porites porites*	EU262831.1

BPGPA2_28sFAR-RAB cons	28S	FAR-RAB	99.86	99	*Porites astreoides*	*Porites sp. NG17*	KY786090.1
			100	90		*Porites astreoides*	EU262821.1
BPGPP2_28sFAR-RAB cons	28S	FAR-RAB	98.19	99	*Porites porites*	*Porites sp. NG17*	KY786090.1
			100	90		*Porites porites*	EU262831.1
BPGPP_28sFAR-RAB cons	28S	FAR-RAB	98.19	99	*Porites porites*	*Porites sp. NG17*	KY786090.1
			100	90		*Porites porites*	EU262831.1
BPGSR2_28sFAR-RAB cons	28S	FAR-RAB	99.85	90	*Siderastrea radians*	*Siderastrea radians*	EU262848.1
			91.84	98		*Orbicella franksi*	AY026375.1
BPGSR3_28sFAR-RAB cons	28S	FAR-RAB	99.85	91	*Siderastrea radians*	*Siderastrea radians*	EU262848.1
			91.82	100		*Orbicella franksi*	AY026375.1
BPGSR_28sFAR-RAB cons	28S	FAR-RAB	99.85	91	*Siderastrea radians*	*Siderastrea radians*	EU262848.1
			91.79	100		*Orbicella franksi*	AY026375.1
PBGPA(BPGPA)_28sFAR-RAB cons	28S	FAR-RAB	99.86	99	*Porites astreoides*	*Porites sp. NG17*	KY786090.1
			100	90		*Porites astreoides*	EU262821.1
STTA2_28sFAR-RAB cons	28S	FAR-RAB	96.82	90	*Tubastraea aurea*	*Leptopsammia pruvoti*	EU262851.1
			96.23	90		*Balanophyllia regia*	EU262813.1
STTA_28sFAR-RAB cons	28S	FAR-RAB	96.43	90	*Tubastraea aurea*	*Leptopsammia pruvoti*	EU262851.1
			95.48	90		*Balanophyllia regia*	EU262813.1
SVBGSR4_28sFAR-RAB cons	28S	FAR-RAB	99.85	91	*Siderastrea radians*	*Siderastrea radians*	EU262848.1
			91.84	99		*Orbicella franksi*	AY026375.1
SVLAC1_28sFAR-RAB cons	28S	FAR-RAB	96.53	90	*Atlantia caboverdiana*	*Leptopsammia pruvoti*	EU262851.1
			95.5	90		*Balanophyllia regia*	EU262813.1
SVLAC2_28sFAR-RAB cons	28S	FAR-RAB	93.15	86	*Atlantia caboverdiana*	*Leptopsammia pruvoti*	EU262851.1
			88.95	96		*Turbinaria sp. G20*	KY798869.1
SVLAC3_28sFAR-RAB cons	28S	FAR-RAB	96.68	90	*Atlantia caboverdiana*	*Leptopsammia pruvoti*	EU262851.1
			95.8	90		*Balanophyllia regia*	EU262813.1
SVLAC4_28sFAR-RAB cons	28S	FAR-RAB	96.55	90	*Atlantia caboverdiana*	*Leptopsammia pruvoti*	EU262851.1
			95.52	90		*Balanophyllia regia*	EU262813.1
SVLFF_28sFAR-RAB cons	28S	FAR-RAB	89.59	100	*Favia Fragum*	*Timea sp. G313459*	AY626303.2
			88.71	100		*Xenospongia patelliformis*	
SVLPA1_28sFAR-RAB cons	28S	FAR-RAB	99.86	99	*99*	*Porites sp. NG17*	KY786090.1

			100	90		*Porites astreoides*	EU262821.1
SVLPA2_28sFAR-RAB cons	28S	FAR-RAB	99.86	99	*Porites astreoides*	*Millepora sp. AMN-2008*	KY786090.1
			100	90		*Millepora alcicornis*	EU262821.1
SVLPA3_28sFAR-RAB cons	28S	FAR-RAB	99.72	99	*Porites astreoides*	*Porites sp. NG17*	KY786090.1
			99.44	99		*Porites sp. NG08*	KY786088.1
SVLPP2_28sFAR-RAB cons	28S	FAR-RAB	99.72	99	*Porites astreoides*	*Porites sp. NG17*	KY786090.1
			99.44	99		*Porites sp. NG08*	KY786088.1
SVLPP_28sFAR-RAB cosn	28S	FAR-RAB	99.72	99	*Porites astreoides*	*Porites sp. NG17*	KY786090.1
			100	90		*Porites porites*	EU262831.1
SVLSR1_28sFAR-RAB cons	28S	FAR-RAB	99.85	90	*Siderastrea radians*	*Siderastrea radians*	EU262848.1
			91.75	100		*Orbicella franksi*	AY026375.1
SVLSR2_28sFAR-RAB cons	28S	FAR-RAB	99.85	90	*Siderastrea radians*	*Siderastrea radians*	EU262848.1
			91.75	100		*Orbicella franksi*	AY026375.1
SVLSR3_28sFAR-RAB cons	28S	FAR-RAB	99.85	90	*Siderastrea radians*	*Siderastrea radians*	EU262848.1
			91.84	99		*Orbicella franksi*	AY026375.1
SVLSS_28sFAR-RAB cons	28S	FAR-RAB	99.85	90	*Siderastrea siderea*	*Siderastrea radians*	EU262848.1
			91.84	99		*Orbicella franksi*	AY026375.1
SVN2AC3_28sFAR-RAB cons	28S	FAR-RAB	96.83	90	*Atlantia caboverdiana*	*Leptopsammia pruvoti*	EU262851.1
			95.95	90		*Balanophyllia regia*	EU262813.1

Table S4: Genetic distances (p-distance) values for *Eunicella* (MutS) within and between haplotype groups and species/subspecies (p-distance: number of nucleotide substitutions per site between DNA sequences. MEGA X)

Haplotype groups *Eunicella* MutS						
	Hapl1	Hapl2	Hapl3	Hapl4	Hapl5	Hapl6
Hapl1						
Hapl2	0,030					
Hapl3	0,052	0,054				
Hapl4	0,025	0,021	0,045			
Hapl5	0,001	0,032	0,054	0,023		
Hapl6	0,044	0,045	0,054	0,037	0,044	

	STEG_ND4L2475-F_Egranulata_{Hapl1}	SVN2EP_ND4L2475-F_Epapilifera_{Hapl2}	JQ397297-Eunicella_singularis_{Hapl1}	KX051574-Eunicella_singularis_{Hapl1}	JQ397298-Eunicella_singularis_{Hapl1}	JQ397296-Eunicella_singularis_{Hapl1}	JQ397311-Eunicella_sp._Gori50_{Hapl1}	JQ397308-Eunicella_sp._Gori11_{Hapl1}	OM798878-Eunicella_modesta_{Hapl3}	OM798877-Eunicella_modesta_{Hapl3}	ON109698-Eunicella_modesta_{Hapl3}	JQ397310-Eunicella_sp._Gori49_{Hapl1}	MK276960-Eunicella_cavolini_{Hapl1}	KX051576-Eunicella_cavolini_{Hapl1}	JQ397291-Eunicella_cavolini_{Hapl1}	JQ397290-Eunicella_cavolini_{Hapl1}	JQ397306-Eunicella_verrucosa_{Hapl1}	JQ397293-Eunicella_singularis_{Hapl1}	KX051571-Eunicella_singularis_{Hapl1}	KX051572-Eunicella_singularis_{Hapl1}	JQ397295-Eunicella_singularis_{Hapl1}	KX051573-Eunicella_singularis_{Hapl1}	MK276961-Eunicella_singularis_{Hapl1}	JQ397299-Eunicella_singularis_{Hapl1}	MK276962-Eunicella_verrucosa_{Hapl1}	KX051575-Eunicella_verrucosa_{Hapl1}	JQ397300-Eunicella_verrucosa_{Hapl1}	JX203795-Eunicella_tricoronata_{Hapl4}	JQ397307-Eunicella_sp._Gori6_{Hapl1}	JQ397301-Eunicella_verrucosa_{Hapl1}	JQ397305-Eunicella_verrucosa_{Hapl1}	JQ397303-Eunicella_verrucosa_{Hapl1}	JQ397304-Eunicella_verrucosa_{Hapl1}	JQ397302-Eunicella_verrucosa_{Hapl1}	KX051577-Eunicella_racemosa_{Hapl5}	JQ397292-Eunicella_cavolini_{Hapl1}	JQ397294-Eunicella_singularis_{Hapl1}
STEG_ND4L2475-F_Egranulata_{Hapl1}																																					
SVN2EP_ND4L2475-F_Epapilifera_{Hapl2}	0,030																																				
JQ397297-Eunicella_singularis_{Hapl1}	0,000	0,030																																			
KX051574-Eunicella_singularis_{Hapl1}	0,000	0,030	0,000																																		
JQ397298-Eunicella_singularis_{Hapl1}	0,000	0,030	0,000	0,000																																	
JQ397296-Eunicella_singularis_{Hapl1}	0,000	0,030	0,000	0,000	0,000																																
JQ397311-Eunicella_sp._Gori50_{Hapl1}	0,000	0,030	0,000	0,000	0,000	0,000																															
JQ397308-Eunicella_sp._Gori11_{Hapl1}	0,000	0,030	0,000	0,000	0,000	0,000	0,000																														
OM798878-Eunicella_modesta_{Hapl3}	0,052	0,054	0,052	0,052	0,052	0,052	0,052	0,052																													
OM798877-Eunicella_modesta_{Hapl3}	0,052	0,054	0,052	0,052	0,052	0,052	0,052	0,052	0,000																												
ON109698-Eunicella_modesta_{Hapl3}	0,052	0,054	0,052	0,052	0,052	0,052	0,052	0,052	0,000	0,000																											
JQ397310-Eunicella_sp._Gori49_{Hapl1}	0,000	0,030	0,000	0,000	0,000	0,000	0,000	0,000	0,052	0,052	0,052																										
MK276960-Eunicella_cavolini_{Hapl1}	0,000	0,030	0,000	0,000	0,000	0,000	0,000	0,000	0,052	0,052	0,052	0,000																									
KX051576-Eunicella_cavolini_{Hapl1}	0,000	0,030	0,000	0,000	0,000	0,000	0,000	0,000	0,052	0,052	0,052	0,000	0,000																								
JQ397291-Eunicella_cavolini_{Hapl1}	0,000	0,030	0,000	0,000	0,000	0,000	0,000	0,000	0,052	0,052	0,052	0,000	0,000	0,000																							
JQ397290-Eunicella_cavolini_{Hapl1}	0,000	0,030	0,000	0,000	0,000	0,000	0,000	0,000	0,052	0,052	0,052	0,000	0,000	0,000	0,000																						
JQ397306-Eunicella_verrucosa_{Hapl1}	0,000	0,030	0,000	0,000	0,000	0,000	0,000	0,000	0,052	0,052	0,052	0,000	0,000	0,000	0,000	0,000																					
JQ397293-Eunicella_singularis_{Hapl1}	0,000	0,030	0,000	0,000	0,000	0,000	0,000	0,000	0,052	0,052	0,052	0,000	0,000	0,000	0,000	0,000	0,000																				
KX051571-Eunicella_singularis_{Hapl1}	0,000	0,030	0,000	0,000	0,000	0,000	0,000	0,000	0,052	0,052	0,052	0,000	0,000	0,000	0,000	0,000	0,000	0,000																			
KX051572-Eunicella_singularis_{Hapl1}	0,000	0,030	0,000	0,000	0,000	0,000	0,000	0,000	0,052	0,052	0,052	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000																		
JQ397295-Eunicella_singularis_{Hapl1}	0,000	0,030	0,000	0,000	0,000	0,000	0,000	0,000	0,052	0,052	0,052	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000																	
KX051573-Eunicella_singularis_{Hapl1}	0,000	0,030	0,000	0,000	0,000	0,000	0,000	0,000	0,052	0,052	0,052	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000																
MK276961-Eunicella_singularis_{Hapl1}	0,000	0,030	0,000	0,000	0,000	0,000	0,000	0,000	0,052	0,052	0,052	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000															
JQ397299-Eunicella_singularis_{Hapl1}	0,000	0,030	0,000	0,000	0,000	0,000	0,000	0,000	0,052	0,052	0,052	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000														
MK276962-Eunicella_verrucosa_{Hapl1}	0,000	0,030	0,000	0,000	0,000	0,000	0,000	0,000	0,052	0,052	0,052	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000													
KX051575-Eunicella_verrucosa_{Hapl1}	0,000	0,030	0,000	0,000	0,000	0,000	0,000	0,000	0,052	0,052	0,052	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000												
JQ397300-Eunicella_verrucosa_{Hapl1}	0,000	0,030	0,000	0,000	0,000	0,000	0,000	0,000	0,052	0,052	0,052	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000											
JX203795-Eunicella_tricoronata_{Hapl4}	0,025	0,021	0,025	0,025	0,025	0,025	0,025	0,025	0,045	0,045	0,045	0,025	0,025	0,025	0,025	0,025	0,025	0,025	0,025	0,025	0,025	0,025	0,025	0,025	0,025	0,025	0,025										
JQ397307-Eunicella_sp._Gori6_{Hapl1}	0,000	0,030	0,000	0,000	0,000	0,000	0,000	0,000	0,052	0,052	0,052	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,025									
JQ397301-Eunicella_verrucosa_{Hapl1}	0,000	0,030	0,000	0,000	0,000	0,000	0,000	0,000	0,052	0,052	0,052	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,025	0,000								
JQ397305-Eunicella_verrucosa_{Hapl1}	0,000	0,030	0,000	0,000	0,000	0,000	0,000	0,000	0,052	0,052	0,052	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,025	0,000	0,000							
JQ397303-Eunicella_verrucosa_{Hapl1}	0,000	0,030	0,000	0,000	0,000	0,000	0,000	0,000	0,052	0,052	0,052	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,025	0,000	0,000	0,000						
JQ397304-Eunicella_verrucosa_{Hapl1}	0,000	0,030	0,000	0,000	0,000	0,000	0,000	0,000	0,052	0,052	0,052	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,025	0,000	0,000	0,000	0,000					
JQ397302-Eunicella_verrucosa_{Hapl1}	0,000	0,030	0,000	0,000	0,000	0,000	0,000	0,000	0,052	0,052	0,052	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,025	0,000	0,000	0,000	0,000	0,000				
KX051577-Eunicella_racemosa_{Hapl5}	0,001	0,032	0,001	0,001	0,001	0,001	0,001	0,001	0,054	0,054	0,054	0,001	0,001	0,001	0,001	0,001	0,001	0,001	0,001	0,001	0,001	0,001	0,001	0,001	0,001	0,001	0,001	0,023	0,001	0,001	0,001	0,001	0,001	0,001			
JQ397292-Eunicella_cavolini_{Hapl1}	0,000	0,030	0,000	0,000	0,000	0,000	0,000	0,000	0,052	0,052	0,052	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,025	0,000	0,000	0,000	0,000	0,000	0,000	0,001		
JQ397294-Eunicella_singularis_{Hapl1}	0,000	0,030	0,000	0,000	0,000	0,000	0,000	0,000	0,052	0,052	0,052	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,025	0,000	0,000	0,000	0,000	0,000	0,000	0,001	0,000	
KF856128.1-Calcigorgia_spiculifera_{Hapl6}	0,044	0,045	0,044	0,044	0,044	0,044	0,044	0,044	0,054	0,054	0,054	0,044	0,044	0,044	0,044	0,044	0,044	0,044	0,044	0,044	0,044	0,044	0,044	0,044	0,044	0,044	0,044	0,037	0,044	0,044	0,044	0,044	0,044	0,044	0,044	0,044	0,044

Table S5: Genetic distances (p-distance) values for *Eunicella* (COI) within and between haplotype groups and species/subspecies (p-distance: number of nucleotide substitutions per site between DNA sequences. MEGA X)

Haplotype groups Eunicella COI														
	Hapl1	Hapl2	Hapl3	Hapl4	Hapl5	Hapl6	Hapl7	Hapl8	Hapl9	Hapl10	Hapl11	Hapl12	Hapl13	Hapl14
Hapl1														
Hapl2	0,0099													
Hapl3	0,0100	0,0000												
Hapl4	0,0408	0,0408	0,0399											
Hapl5	0,0087	0,0087	0,0087	0,0371										
Hapl6	0,0087	0,0012	0,0012	0,0396	0,0074									
Hapl7	0,0124	0,0124	0,0125	0,0458	0,0136	0,0111								
Hapl8	0,0137	0,0137	0,0137	0,0461	0,0149	0,0125	0,0012							
Hapl9	0,0012	0,0087	0,0087	0,0386	0,0075	0,0075	0,0112	0,0125						
Hapl10	0,0000	0,0100	0,0100	0,0399	0,0087	0,0087	0,0125	0,0137	0,0012					
Hapl11	0,0087	0,0012	0,0012	0,0386	0,0075	0,0000	0,0112	0,0125	0,0075	0,0087				
Hapl12	0,0235	0,0235	0,0237	0,0359	0,0223	0,0223	0,0285	0,0299	0,0224	0,0237	0,0224			
Hapl13	0,0223	0,0223	0,0224	0,0347	0,0210	0,0210	0,0272	0,0286	0,0212	0,0224	0,0212	0,0087		
Hapl14	0,0223	0,0223	0,0224	0,0347	0,0186	0,0210	0,0272	0,0286	0,0212	0,0224	0,0212	0,0087	0,0050	

	SVN2EP_C04_COII8068-F-COIOCt-Epapilifera_{Hapl1}	STEG_A04_COII8068-F-COIOCT-R_Egranulata_{Hapl2}	KJ685927-Eunicella_granulata_{Hapl3}	OM798714-Eunicella_modesta_{Hapl4}	OM798713-Eunicella_modesta_{Hapl4}	OM798712-Eunicella_modesta_{Hapl4}	OL616234-Eunicella_tricoronata_{Hapl5}	NC_062012-Eunicella_tricoronata_{Hapl5}	NC_073494-Eunicella_verrucosa_{Hapl2}	MW588805-Eunicella_verrucosa_{Hapl2}	KX051569-Eunicella_verrucosa_{Hapl2}	KP190918-Eunicella_verrucosa_{Hapl2}	KY559408-Eunicella_cavolini_{Hapl2}	NC_035667-Eunicella_cavolinii_{Hapl2}	KP190917-Eunicella_cavolini_{Hapl2}	AY827537-Eunicella_cavolini_{Hapl2}	KX051568-Eunicella_cavolini_{Hapl2}	MT281295-Eunicella_gazella_{Hapl6}	KP190919-Eunicella_gazella_{Hapl6}	MT281294-Eunicella_filiformis_{Hapl2}	KX051570-Eunicella_racemosa_{Hapl7}	KJ685929-Eunicella_racemosa_{Hapl8}	KX051567-Eunicella_singularis_{Hapl2}	KX051566-Eunicella_singularis_{Hapl2}	KX051565-Eunicella_singularis_{Hapl2}	KX051564-Eunicella_singularis_{Hapl2}	KP190916-Eunicella_singularis_{Hapl2}	KJ685930-Eunicella_singularis_{Hapl3}	KJ685928-Eunicella_kochi_{Hapl9}	KJ685926-Eunicella_gracilis_{Hapl10}	KJ685925-Eunicella_gazella_{Hapl11}	JX203853-Eunicella_tricoronata_{Hapl5}	FJ264906.1-Swiftia_pacifica_{Hapl12}	KX904980.1-Swiftia_simplex_{Hapl13}	MT281301.1-Swiftia_sp._{Hapl14}
SVN2EP_C04_COII8068-F-COIOCt-																																			
STEG_A04_COII8068-F-COIOCT-R_Egranulata_{H	0,0099																																		
KJ685927-Eunicella_granulata_{Hapl3}	0,0100	0,0000																																	
OM798714-Eunicella_modesta_{Hapl4}	0,0408	0,0408	0,0399																																
OM798713-Eunicella_modesta_{Hapl4}	0,0408	0,0408	0,0399	0,0000																															
OM798712-Eunicella_modesta_{Hapl4}	0,0408	0,0408	0,0399	0,0000	0,0000																														
OL616234-Eunicella_tricoronata_{Hapl5}	0,0087	0,0087	0,0087	0,0371	0,0371	0,0371																													
NC_062012-Eunicella_tricoronata_{Hapl5}	0,0087	0,0087	0,0087	0,0371	0,0371	0,0371	0,0000																												
NC_073494-Eunicella_verrucosa_{Hapl2}	0,0099	0,0000	0,0000	0,0408	0,0408	0,0408	0,0087	0,0087																											
MW588805-Eunicella_verrucosa_{Hapl2}	0,0099	0,0000	0,0000	0,0408	0,0408	0,0408	0,0087	0,0087	0,0000																										
KX051569-Eunicella_verrucosa_{Hapl2}	0,0099	0,0000	0,0000	0,0408	0,0408	0,0408	0,0087	0,0087	0,0000	0,0000																									
KP190918-Eunicella_verrucosa_{Hapl2}	0,0099	0,0000	0,0000	0,0408	0,0408	0,0408	0,0087	0,0087	0,0000	0,0000	0,0000																								
KY559408-Eunicella_cavolini_{Hapl2}	0,0099	0,0000	0,0000	0,0408	0,0408	0,0408	0,0087	0,0087	0,0000	0,0000	0,0000	0,0000																							
NC_035667-Eunicella_cavolinii_{Hapl2}	0,0099	0,0000	0,0000	0,0408	0,0408	0,0408	0,0087	0,0087	0,0000	0,0000	0,0000	0,0000	0,0000																						
KP190917-Eunicella_cavolini_{Hapl2}	0,0099	0,0000	0,0000	0,0408	0,0408	0,0408	0,0087	0,0087	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000																					
AY827537-Eunicella_cavolini_{Hapl2}	0,0099	0,0000	0,0000	0,0408	0,0408	0,0408	0,0087	0,0087	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000																				
KX051568-Eunicella_cavolini_{Hapl2}	0,0099	0,0000	0,0000	0,0408	0,0408	0,0408	0,0087	0,0087	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000																			
MT281295-Eunicella_gazella_{Hapl6}	0,0087	0,0012	0,0012	0,0396	0,0396	0,0396	0,0074	0,0074	0,0012	0,0012	0,0012	0,0012	0,0012	0,0012	0,0012	0,0012	0,0012																		
KP190919-Eunicella_gazella_{Hapl6}	0,0087	0,0012	0,0012	0,0396	0,0396	0,0396	0,0074	0,0074	0,0012	0,0012	0,0012	0,0012	0,0012	0,0012	0,0012	0,0012	0,0012	0,0000																	
MT281294-Eunicella_filiformis_{Hapl2}	0,0099	0,0000	0,0000	0,0408	0,0408	0,0408	0,0087	0,0087	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0012	0,0012																
KX051570-Eunicella_racemosa_{Hapl7}	0,0124	0,0124	0,0125	0,0458	0,0458	0,0458	0,0136	0,0136	0,0124	0,0124	0,0124	0,0124	0,0124	0,0124	0,0124	0,0124	0,0124	0,0111	0,0111	0,0124															
KJ685929-Eunicella_racemosa_{Hapl8}	0,0137	0,0137	0,0137	0,0461	0,0461	0,0461	0,0149	0,0149	0,0137	0,0137	0,0137	0,0137	0,0137	0,0137	0,0137	0,0137	0,0137	0,0125	0,0125	0,0137	0,0012														
KX051567-Eunicella_singularis_{Hapl2}	0,0099	0,0000	0,0000	0,0408	0,0408	0,0408	0,0087	0,0087	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0012	0,0012	0,0000	0,0124	0,0137													
KX051566-Eunicella_singularis_{Hapl2}	0,0099	0,0000	0,0000	0,0408	0,0408	0,0408	0,0087	0,0087	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0012	0,0012	0,0000	0,0124	0,0137	0,0000												
KX051565-Eunicella_singularis_{Hapl2}	0,0099	0,0000	0,0000	0,0408	0,0408	0,0408	0,0087	0,0087	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0012	0,0012	0,0000	0,0124	0,0137	0,0000	0,0000											
KX051564-Eunicella_singularis_{Hapl2}	0,0099	0,0000	0,0000	0,0408	0,0408	0,0408	0,0087	0,0087	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0012	0,0012	0,0000	0,0124	0,0137	0,0000	0,0000	0,0000										
KP190916-Eunicella_singularis_{Hapl2}	0,0099	0,0000	0,0000	0,0408	0,0408	0,0408	0,0087	0,0087	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0012	0,0012	0,0000	0,0124	0,0137	0,0000	0,0000	0,0000	0,0000									
KJ685930-Eunicella_singularis_{Hapl3}	0,0100	0,0000	0,0000	0,0399	0,0399	0,0399	0,0087	0,0087	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0000	0,0012	0,0012	0,0000	0,0125	0,0137	0,0000	0,0000	0,0000	0,0000	0,0000								
KJ685928-Eunicella_kochi_{Hapl9}	0,0012	0,0087	0,0087	0,0386	0,0386	0,0386	0,0075	0,0075	0,0087	0,0087	0,0087	0,0087	0,0087	0,0087	0,0087	0,0087	0,0087	0,0075	0,0075	0,0087	0,0112	0,0125	0,0087	0,0087	0,0087	0,0087	0,0087	0,0087							
KJ685926-Eunicella_gracilis_{Hapl10}	0,0000	0,0100	0,0100	0,0399	0,0399	0,0399	0,0087	0,0087	0,0100	0,0100	0,0100	0,0100	0,0100	0,0100	0,0100	0,0100	0,0100	0,0087	0,0087	0,0100	0,0125	0,0137	0,0100	0,0100	0,0100	0,0100	0,0100	0,0100	0,0012						
KJ685925-Eunicella_gazella_{Hapl11}	0,0087	0,0012	0,0012	0,0386	0,0386	0,0386	0,0075	0,0075	0,0012	0,0012	0,0012	0,0012	0,0012	0,0012	0,0012	0,0012	0,0012	0,0000	0,0000	0,0012	0,0112	0,0125	0,0012	0,0012	0,0012	0,0012	0,0012	0,0012	0,0075	0,0087					
JX203853-Eunicella_tricoronata_{Hapl5}	0,0087	0,0087	0,0087	0,0371	0,0371	0,0371	0,0000	0,0000	0,0087	0,0087	0,0087	0,0087	0,0087	0,0087	0,0087	0,0087	0,0087	0,0074	0,0074	0,0087	0,0136	0,0149	0,0087	0,0087	0,0087	0,0087	0,0087	0,0087	0,0075	0,0087	0,0075				
FJ264906.1-Swiftia_pacifica_{Hapl12}	0,0235	0,0235	0,0237	0,0359	0,0359	0,0359	0,0223	0,0223	0,0235	0,0235	0,0235	0,0235	0,0235	0,0235	0,0235	0,0235	0,0235	0,0223	0,0223	0,0235	0,0285	0,0299	0,0235	0,0235	0,0235	0,0235	0,0235	0,0237	0,0224	0,0237	0,0224	0,0223			
KX904980.1-Swiftia_simplex_{Hapl13}	0,0223	0,0223	0,0224	0,0347	0,0347	0,0347	0,0210	0,0210	0,0223	0,0223	0,0223	0,0223	0,0223	0,0223	0,0223	0,0223	0,0223	0,0210	0,0210	0,0223	0,0272	0,0286	0,0223	0,0223	0,0223	0,0223	0,0223	0,0224	0,0212	0,0224	0,0212	0,0210	0,0087		
MT281301.1-Swiftia_sp._{Hapl14}	0,0223	0,0223	0,0224	0,0347	0,0347	0,0347	0,0186	0,0186	0,0223	0,0223	0,0223	0,0223	0,0223	0,0223	0,0223	0,0223	0,0223	0,0210	0,0210	0,0223	0,0272	0,0286	0,0223	0,0223	0,0223	0,0223	0,0223	0,0224	0,0212	0,0224	0,0212	0,0186	0,0087	0,0050	

Table S6: Genetic distances (p-distance) values for *Leptogorgia* (MutS) within and between haplotype groups (p-distance: number of nucleotide substitutions per site between DNA sequences. MEGA X)

	Hapl1	Hapl2	Hapl3	Hapl4	Hapl5	Hapl6	Hapl7	Hapl8	Hapl9	Hapl10	Hapl11	Hapl12	Hapl13	Hapl14	Hapl15	Hapl16	Hapl17	Hapl18	Hapl19	Hapl20	Hapl21	Hapl22	Hapl23	Hapl24	Hapl25	Hapl26	Hapl27	Hapl28	Hapl29	Hapl30	Hapl31	Hapl32	Hapl33	Hapl34	Hapl35	Hapl36	Hapl37	Hapl38	Hapl39	Hapl40	Hapl41	Hapl42	Hapl43	Hapl44	Hapl45
Hapl1																																													
Hapl2	0,030																																												
Hapl3	0,029	0,002																																											
Hapl4	0,089	0,089	0,091																																										
Hapl5	0,052	0,056	0,055	0,091																																									
Hapl6	0,053	0,052	0,050	0,083	0,029																																								
Hapl7	0,050	0,055	0,053	0,091	0,017	0,027																																							
Hapl8	0,055	0,053	0,052	0,091	0,024	0,027	0,023																																						
Hapl9	0,038	0,038	0,036	0,061	0,045	0,041	0,044	0,042																																					
Hapl10	0,053	0,055	0,053	0,094	0,021	0,027	0,020	0,024	0,044																																				
Hapl11	0,048	0,048	0,047	0,071	0,056	0,052	0,055	0,053	0,011	0,048																																			
Hapl12	0,050	0,052	0,050	0,088	0,018	0,024	0,017	0,021	0,041	0,009	0,052																																		
Hapl13	0,053	0,052	0,050	0,080	0,029	0,014	0,029	0,029	0,041	0,029	0,052	0,026																																	
Hapl14	0,053	0,048	0,047	0,080	0,029	0,012	0,027	0,027	0,041	0,024	0,052	0,021	0,014																																
Hapl15	0,052	0,050	0,048	0,092	0,041	0,039	0,042	0,041	0,042	0,042	0,053	0,039	0,038	0,039																															
Hapl16	0,058	0,056	0,055	0,094	0,026	0,027	0,024	0,014	0,045	0,014	0,056	0,014	0,029	0,024	0,044																														
Hapl17	0,047	0,052	0,050	0,088	0,014	0,024	0,003	0,020	0,041	0,017	0,052	0,014	0,026	0,024	0,039	0,021																													
Hapl18	0,052	0,047	0,045	0,082	0,027	0,011	0,026	0,026	0,039	0,023	0,050	0,020	0,012	0,002	0,038	0,023	0,023																												
Hapl19	0,055	0,053	0,052	0,085	0,030	0,002	0,029	0,029	0,042	0,029	0,053	0,026	0,015	0,014	0,041	0,029	0,026	0,012																											
Hapl20	0,030	0,003	0,002	0,092	0,056	0,052	0,055	0,053	0,038	0,055	0,048	0,052	0,052	0,048	0,050	0,056	0,052	0,047	0,053																										
Hapl21	0,002	0,029	0,027	0,088	0,050	0,052	0,048	0,053	0,036	0,052	0,047	0,048	0,052	0,052	0,050	0,056	0,045	0,050	0,053	0,029																									
Hapl22	0,048	0,053	0,052	0,091	0,017	0,027	0,006	0,023	0,044	0,020	0,055	0,017	0,029	0,027	0,042	0,024	0,003	0,026	0,029	0,053	0,047																								
Hapl23	0,050	0,050	0,048	0,073	0,064	0,058	0,062	0,061	0,018	0,062	0,026	0,059	0,058	0,058	0,058	0,064	0,059	0,056	0,059	0,050	0,048	0,062																							
Hapl24	0,044	0,044	0,042	0,067	0,052	0,047	0,050	0,048	0,006	0,050	0,017	0,047	0,044	0,047	0,048	0,052	0,047	0,045	0,048	0,044	0,042	0,050	0,024																						
Hapl25	0,033	0,006	0,005	0,092	0,059	0,055	0,058	0,056	0,041	0,058	0,052	0,055	0,055	0,052	0,053	0,059	0,055	0,050	0,056	0,003	0,032	0,056	0,053	0,047																					
Hapl26	0,050	0,048	0,047	0,080	0,026	0,009	0,024	0,024	0,038	0,024	0,048	0,021	0,011	0,009	0,036	0,024	0,021	0,008	0,011	0,048	0,048	0,024	0,055	0,044	0,052																				
Hapl27	0,024	0,009	0,008	0,086	0,053	0,048	0,052	0,050	0,032	0,052	0,042	0,048	0,048	0,045	0,047	0,053	0,048	0,044	0,050	0,009	0,023	0,050	0,044	0,038	0,012	0,045																			
Hapl28	0,052	0,053	0,052	0,086	0,020	0,026	0,018	0,023	0,042	0,011	0,053	0,002	0,027	0,023	0,041	0,015	0,015	0,021	0,027	0,053	0,050	0,018	0,061	0,048	0,056	0,023	0,050																		
Hapl29	0,056	0,050	0,050	0,082	0,032	0,015	0,030	0,030	0,044	0,027	0,055	0,024	0,017	0,003	0,042	0,027	0,027	0,005	0,017	0,052	0,055	0,030	0,061	0,050	0,055	0,012	0,048	0,026																	
Hapl30	0,044	0,044	0,042	0,064	0,052	0,047	0,050	0,048	0,006	0,044	0,008	0,047	0,047	0,047	0,048	0,052	0,047	0,045	0,048	0,044	0,042	0,050	0,020	0,012	0,047	0,044	0,038	0,048	0,050																
Hapl31	0,050	0,052	0,050	0,091	0,017	0,024	0,015	0,020	0,041	0,017	0,052	0,014	0,026	0,021	0,039	0,021	0,012	0,020	0,026	0,052	0,048	0,015	0,059	0,047	0,055	0,021	0,048	0,015	0,024	0,047															
Hapl32	0,052	0,050	0,048	0,092	0,041	0,039	0,042	0,041	0,042	0,042	0,053	0,039	0,035	0,036	0,009	0,044	0,039	0,035	0,041	0,050	0,050	0,042	0,058	0,045	0,053	0,036	0,047	0,041	0,039	0,048	0,036														
Hapl33	0,050	0,055	0,053	0,091	0,002	0,027	0,015	0,023	0,044	0,020	0,055	0,017	0,029	0,027	0,039	0,024	0,012	0,026	0,029	0,055	0,048	0,015	0,062	0,050	0,058	0,024	0,052	0,018	0,030	0,050	0,015	0,039													
Hapl34	0,052	0,053	0,052	0,089	0,020	0,026	0,018	0,023	0,042	0,011	0,053	0,002	0,027	0,023	0,041	0,015	0,015	0,021	0,027	0,053	0,050	0,018	0,061	0,048	0,056	0,023	0,050	0,003	0,026	0,048	0,015	0,041	0,018												
Hapl35	0,026	0,014	0,012	0,089	0,052	0,050	0,050	0,052	0,036	0,050	0,047	0,047	0,052	0,047	0,050	0,055	0,047	0,045	0,052	0,014	0,024	0,048	0,048	0,042	0,017	0,047	0,005	0,048	0,050	0,042	0,047	0,050	0,050	0,048											
Hapl36	0,050	0,052	0,050	0,091	0,018	0,024	0,017	0,021	0,041	0,003	0,052	0,006	0,026	0,021	0,039	0,011	0,014	0,020	0,026	0,052	0,048	0,017	0,059	0,047	0,055	0,021	0,048	0,008	0,024	0,047	0,014	0,039	0,017	0,008	0,047										
Hapl37	0,003	0,027	0,026	0,086	0,048	0,050	0,047	0,052	0,035	0,050	0,045	0,047	0,050	0,050	0,048	0,055	0,044	0,048	0,052	0,027	0,002	0,045	0,047	0,041	0,030	0,047	0,021	0,048	0,053	0,041	0,047	0,048	0,047	0,048	0,023	0,047									
Hapl38	0,042	0,042	0,041	0,062	0,050	0,045	0,048	0,047	0,005	0,045	0,009	0,045	0,045	0,045	0,047	0,050	0,045	0,044	0,047	0,042	0,041	0,048	0,018	0,011	0,045	0,042	0,036	0,047	0,048	0,002	0,045	0,047	0,048	0,047	0,041	0,045	0,039								
Hapl39	0,052	0,050	0,048	0,079	0,023	0,014	0,023	0,023	0,039	0,024	0,050	0,021	0,006	0,014	0,038	0,024	0,020	0,012	0,015	0,050	0,050	0,023	0,056	0,042	0,053	0,011	0,047	0,023	0,017	0,045	0,020	0,035	0,023	0,023	0,048	0,021	0,048	0,044							
Hapl40	0,055	0,050	0,048	0,082	0,030	0,014	0,029	0,029	0,042	0,026	0,053	0,023	0,015	0,002	0,041	0,026	0,026	0,003	0,015	0,050	0,053	0,029	0,059	0,048	0,053	0,011	0,047	0,024	0,005	0,048	0,023	0,038	0,029	0,024	0,048	0,023	0,052	0,047	0,015						
Hapl41	0,023	0,011	0,009	0,085	0,052	0,047	0,050	0,048	0,030	0,050	0,041	0,047	0,047	0,044	0,045	0,052	0,047	0,042	0,048	0,011	0,021	0,048	0,042	0,036	0,014	0,044	0,002	0,048	0,047	0,036	0,047	0,045	0,050	0,048	0,006	0,047	0,020	0,035	0,045	0,045					
Hapl42	0,050	0,052	0,050	0,091	0,017	0,024	0,006	0,020	0,041	0,017	0,052	0,014	0,026	0,024	0,039	0,021	0,003	0,023	0,026	0,052	0,048	0,006	0,059	0,047	0,055	0,021	0,048	0,015	0,027	0,047	0,012	0,039	0,015	0,015	0,047	0,014	0,047	0,045	0,020	0,026	0,047				
Hapl43	0,024	0,009	0,008	0,086	0,053	0,048	0,052	0,050	0,032	0,052	0,042	0,048	0,048	0,048	0,047	0,053	0,048	0,047	0,050	0,009	0,023	0,050	0,044	0,038	0,012	0,045	0,009	0,050	0,052	0,038	0,048	0,047	0,052	0,050	0,014	0,048	0,021	0,036	0,047	0,050	0,008	0,048			
Hapl44	0,030	0,005	0,003	0,092	0,056	0,052	0,055	0,053	0,038	0,053	0,048	0,050	0,052	0,048	0,050	0,055	0,052	0,047	0,053	0,005	0,029	0,053	0,050	0,044	0,008	0,048	0,009	0,052	0,052	0,044	0,052	0,050	0,055	0,052	0,014	0,050	0,027	0,042	0,050	0,050	0,011	0,052	0,009		
Hapl45	0,079	0,074	0,076	0,111	0,083	0,085	0,082	0,086	0,068	0,088	0,079	0,082	0,085	0,082	0,089	0,089	0,079	0,080	0,086	0,077	0,077	0,082	0,083	0,074	0,080	0,079	0,076	0,083	0,083	0,074	0,082	0,086	0,082	0,083	0,080	0,085	0,076	0,073	0,083	0,080	0,074	0,082	0,076	0,076	

Table S7: Genetic distances (p-distance) values for *Leptogorgia* (COI) within and between haplotype groups and species/subspecies (p-distance: number of nucleotide substitutions per site between DNA sequences. MEGA X)

Haplotype groups *Leptogorgia* COI																				
	Hapl1	Hapl2	Hapl3	Hapl4	Hapl5	Hapl6	Hapl7	Hapl8	Hapl9	Hapl10	Hapl11	Hapl12	Hapl13	Hapl14	Hapl15	Hapl16	Hapl17	Hapl18	Hapl19	Hapl20
Hapl1																				
Hapl2	0,009																			
Hapl3	0,018	0,017																		
Hapl4	0,018	0,014	0,005																	
Hapl5	0,018	0,017	0,020	0,018																
Hapl6	0,017	0,015	0,019	0,017	0,001															
Hapl7	0,031	0,029	0,015	0,015	0,031	0,029														
Hapl8	0,018	0,017	0,020	0,018	0,003	0,001	0,031													
Hapl9	0,027	0,025	0,029	0,027	0,017	0,015	0,039	0,017												
Hapl10	0,015	0,014	0,018	0,015	0,005	0,004	0,028	0,005	0,014											
Hapl11	0,022	0,020	0,024	0,022	0,011	0,010	0,034	0,011	0,010	0,009										
Hapl12	0,008	0,001	0,015	0,013	0,015	0,014	0,028	0,015	0,024	0,013	0,019									
Hapl13	0,009	0,003	0,017	0,014	0,017	0,015	0,029	0,017	0,025	0,014	0,020	0,001								
Hapl14	0,009	0,003	0,014	0,011	0,017	0,015	0,027	0,017	0,025	0,014	0,020	0,001	0,003							
Hapl15	0,015	0,014	0,018	0,015	0,005	0,004	0,028	0,005	0,014	0,003	0,009	0,013	0,014	0,014						
Hapl16	0,017	0,015	0,019	0,017	0,004	0,003	0,028	0,004	0,015	0,004	0,010	0,014	0,015	0,015	0,004					
Hapl17	0,018	0,017	0,020	0,018	0,005	0,004	0,029	0,005	0,017	0,005	0,011	0,015	0,017	0,017	0,005	0,001				
Hapl18	0,019	0,018	0,022	0,018	0,010	0,009	0,032	0,010	0,017	0,008	0,011	0,017	0,018	0,018	0,008	0,009	0,010			
Hapl19	0,031	0,029	0,036	0,036	0,031	0,029	0,045	0,031	0,042	0,031	0,037	0,028	0,029	0,029	0,031	0,032	0,033	0,036		
Hapl20	0,031	0,032	0,038	0,038	0,033	0,032	0,047	0,033	0,045	0,033	0,039	0,031	0,032	0,032	0,033	0,034	0,036	0,038	0,003	

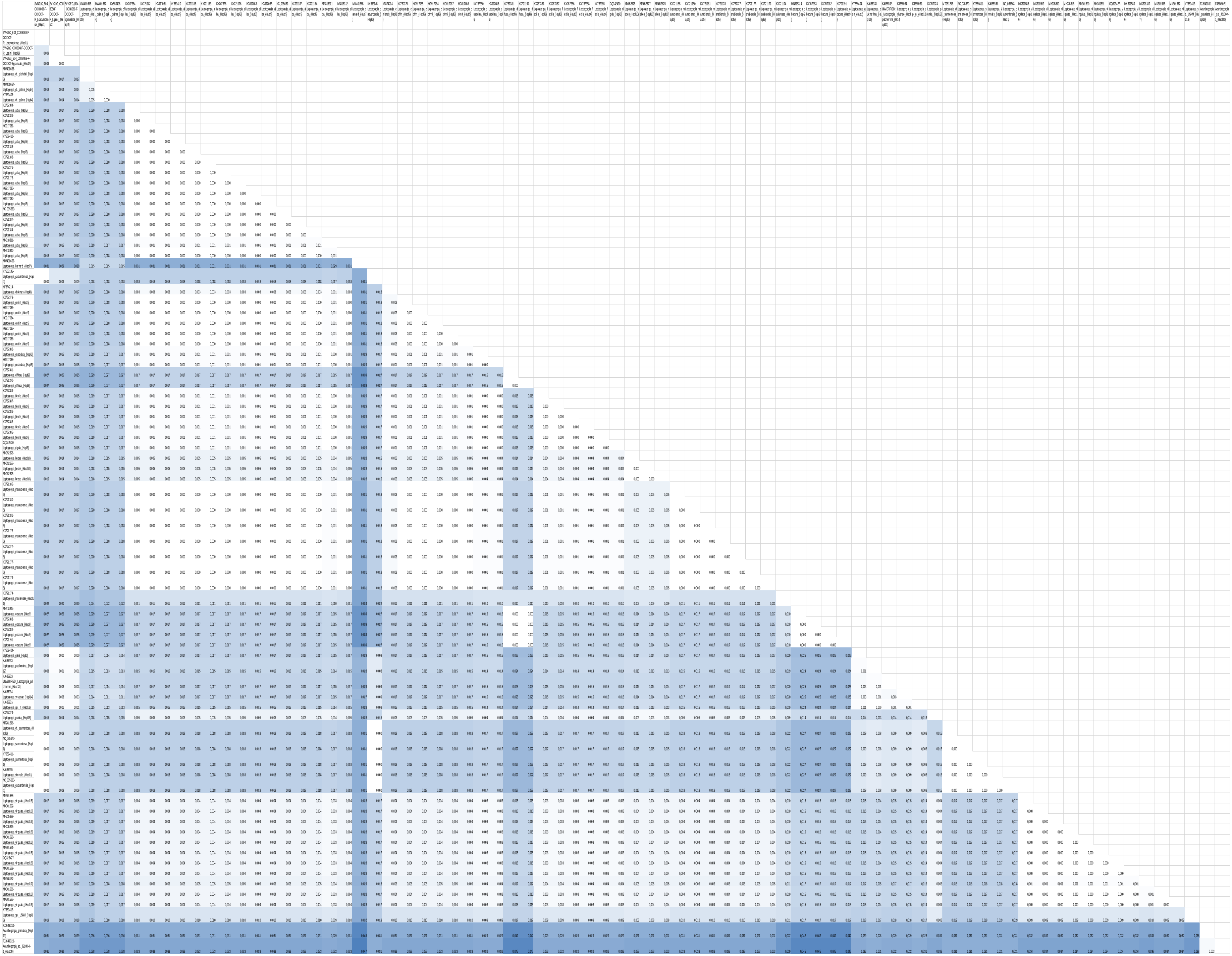


Table S8: Genetic distances (p-distance) values for *Carijoa* (COI) within and between haplotype groups and species/subspecies (p-distance: number of nucleotide substitutions per site between DNA sequences. MEGA X)

Haplotype groups *Carijoa* COI						
	Hapl1	Hapl2	Hapl3	Hapl4	Hapl5	Hapl6
Hapl1						
Hapl2	0,001					
Hapl3	0,039	0,040				
Hapl4	0,037	0,039	0,072			
Hapl5	0,040	0,042	0,072	0,006		
Hapl6	0,039	0,040	0,070	0,003	0,004	

	SNCR_COII8068F-COIOCTR_Criisei_{Hapl1}	MT161608-Carijoa_riisei_{Hapl1}	KJ685924-Carijoa_riisei_{Hapl1}	MW278611-Carijoa_sp._HAW01_{Hapl1}	HG917050-Carijoa_sp._HMG90_{Hapl1}	JX203829-Carijoa_riisei_{Hapl2}	JX203830-Carijoa_sp._2_{Hapl1}	GQ342408-Carijoa_riisei_{Hapl2}	JX203831-Carijoa_sp._2_{Hapl2}	MN200343-Carijoa_riisei_{Hapl3}	OL616218-Carijoa_riisei_{Hapl2}	JX203832-Carijoa_sp._1_{Hapl1}	HG917049-Carijoa_sp._HMG115_{Hapl1}	NC_048963-Carijoa_riisei_{Hapl1}	HG917051-Carijoa_sp._HMG68_{Hapl1}	JX203833-Carijoa_sp._3_{Hapl1}	NC_044122.1-Sinularia_ceramensis_{Hapl4}	OK641586.1-Sinularia_humilis_{Hapl5}	NC_018379.1-Sinularia_peculiaris_{Hapl6}
SNCR_COII8068F-COIOCTR_Criisei_{Hapl1}																			
MT161608-Carijoa_riisei_{Hapl1}	0,000																		
KJ685924-Carijoa_riisei_{Hapl1}	0,000	0,000																	
MW278611-Carijoa_sp._HAW01_{Hapl1}	0,000	0,000	0,000																
HG917050-Carijoa_sp._HMG90_{Hapl1}	0,000	0,000	0,000	0,000															
JX203829-Carijoa_riisei_{Hapl2}	0,001	0,001	0,001	0,001	0,001														
JX203830-Carijoa_sp._2_{Hapl1}	0,000	0,000	0,000	0,000	0,000	0,001													
GQ342408-Carijoa_riisei_{Hapl2}	0,001	0,001	0,001	0,001	0,001	0,000	0,001												
JX203831-Carijoa_sp._2_{Hapl2}	0,001	0,001	0,001	0,001	0,001	0,000	0,001	0,000											
MN200343-Carijoa_riisei_{Hapl3}	0,039	0,039	0,039	0,039	0,039	0,040	0,039	0,040	0,040										
OL616218-Carijoa_riisei_{Hapl2}	0,001	0,001	0,001	0,001	0,001	0,000	0,001	0,000	0,000	0,040									
JX203832-Carijoa_sp._1_{Hapl1}	0,000	0,000	0,000	0,000	0,000	0,001	0,000	0,001	0,001	0,039	0,001								
HG917049-Carijoa_sp._HMG115_{Hapl1}	0,000	0,000	0,000	0,000	0,000	0,001	0,000	0,001	0,001	0,039	0,001	0,000							
NC_048963-Carijoa_riisei_{Hapl1}	0,000	0,000	0,000	0,000	0,000	0,001	0,000	0,001	0,001	0,039	0,001	0,000	0,000						
HG917051-Carijoa_sp._HMG68_{Hapl1}	0,000	0,000	0,000	0,000	0,000	0,001	0,000	0,001	0,001	0,039	0,001	0,000	0,000	0,000					
JX203833-Carijoa_sp._3_{Hapl1}	0,000	0,000	0,000	0,000	0,000	0,001	0,000	0,001	0,001	0,039	0,001	0,000	0,000	0,000	0,000				
NC_044122.1-Sinularia_ceramensis_{Hapl4}	0,037	0,037	0,037	0,037	0,037	0,039	0,037	0,039	0,039	0,072	0,039	0,037	0,037	0,037	0,037	0,037			
OK641586.1-Sinularia_humilis_{Hapl5}	0,040	0,040	0,040	0,040	0,040	0,042	0,040	0,042	0,042	0,072	0,042	0,040	0,040	0,040	0,040	0,040	0,006		
NC_018379.1-Sinularia_peculiaris_{Hapl6}	0,039	0,039	0,039	0,039	0,039	0,040	0,039	0,040	0,040	0,070	0,040	0,039	0,039	0,039	0,039	0,039	0,003	0,004	

Table S9: Genetic distances (p-distance) values for *Atlantia* (COI) within and between haplotype groups and species/subspecies (p-distance: number of nucleotide substitutions per site between DNA sequences. MEGA X)

Haplotype groups *Atlantia* COI				
	Hapl1	Hapl2	Hapl3	Hapl4
Hapl1				
Hapl2	0,004			
Hapl3	0,012	0,009		
Hapl4	0,011	0,007	0,002	

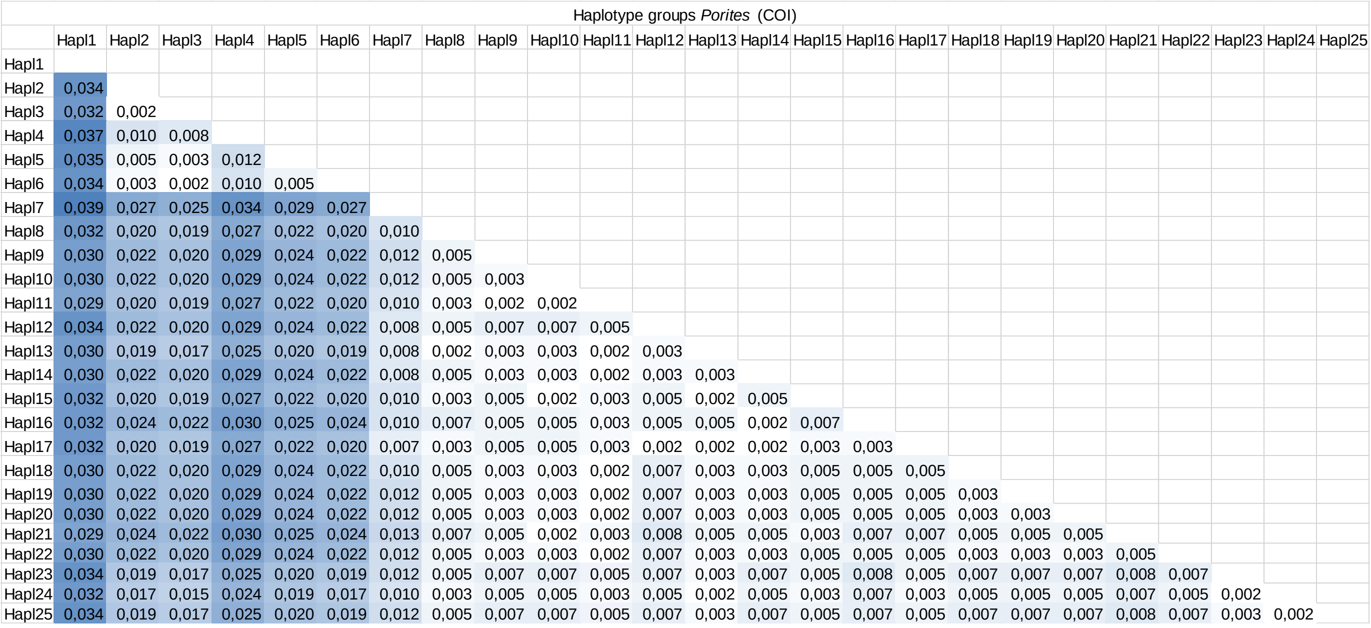
	SVN2AC3_JGLCO1490-Acaboverdiana_{Hapl1}	SVLAC4_JGLCO1490-Acaboverdiana_{Hapl1}	SVLAC3_JGLCO1490-Acaboverdiana_{Hapl1}	SVLAC2_JGLCO1490-Acaboverdiana_{Hapl1}	SVLAC1_JGLCO1490-Acaboverdiana_{Hapl1}	MN414212-Dendrophylliidae_{Hapl2}	MN414211-Dendrophylliidae_{Hapl2}	MN414210-Dendrophylliidae_{Hapl2}	MN414209-Dendrophylliidae_{Hapl2}	MN414208-Dendrophylliidae_{Hapl2}	MN414207-Dendrophylliidae_{Hapl2}	MN414206-Dendrophylliidae_{Hapl2}	MN414205-Dendrophylliidae_{Hapl2}	MN384734-Dendrophylliidae_{Hapl2}	MN384733-Dendrophylliidae_{Hapl2}	MN384732-Dendrophylliidae_{Hapl2}	MN384731-Dendrophylliidae_{Hapl2}	OR394768.1-Rhizopsammia_wettste	OR394761.1-Rhizopsammia_verrilli_{
SVN2AC3_JGLCO1490-Acaboverdiana_{Hapl1}																			
SVLAC4_JGLCO1490-Acaboverdiana_{Hapl1}	0,000																		
SVLAC3_JGLCO1490-Acaboverdiana_{Hapl1}	0,000	0,000																	
SVLAC2_JGLCO1490-Acaboverdiana_{Hapl1}	0,000	0,000	0,000																
SVLAC1_JGLCO1490-Acaboverdiana_{Hapl1}	0,000	0,000	0,000	0,000															
MN414212-Dendrophylliidae_{Hapl2}	0,004	0,004	0,004	0,004	0,004														
MN414211-Dendrophylliidae_{Hapl2}	0,004	0,004	0,004	0,004	0,004	0,000													
MN414210-Dendrophylliidae_{Hapl2}	0,004	0,004	0,004	0,004	0,004	0,000	0,000												
MN414209-Dendrophylliidae_{Hapl2}	0,004	0,004	0,004	0,004	0,004	0,000	0,000	0,000											
MN414208-Dendrophylliidae_{Hapl2}	0,004	0,004	0,004	0,004	0,004	0,000	0,000	0,000	0,000										
MN414207-Dendrophylliidae_{Hapl2}	0,004	0,004	0,004	0,004	0,004	0,000	0,000	0,000	0,000	0,000									
MN414206-Dendrophylliidae_{Hapl2}	0,004	0,004	0,004	0,004	0,004	0,000	0,000	0,000	0,000	0,000	0,000								
MN414205-Dendrophylliidae_{Hapl2}	0,004	0,004	0,004	0,004	0,004	0,000	0,000	0,000	0,000	0,000	0,000	0,000							
MN384734-Dendrophylliidae_{Hapl2}	0,004	0,004	0,004	0,004	0,004	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000						
MN384733-Dendrophylliidae_{Hapl2}	0,004	0,004	0,004	0,004	0,004	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000					
MN384732-Dendrophylliidae_{Hapl2}	0,004	0,004	0,004	0,004	0,004	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000				
MN384731-Dendrophylliidae_{Hapl2}	0,004	0,004	0,004	0,004	0,004	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000			
OR394768.1-Rhizopsammia_wettsteini_{Hapl3}	0,012	0,012	0,012	0,012	0,012	0,009	0,009	0,009	0,009	0,009	0,009	0,009	0,009	0,009	0,009	0,009	0,009		
OR394761.1-Rhizopsammia_verrilli_{Hapl4}	0,011	0,011	0,011	0,011	0,011	0,007	0,007	0,007	0,007	0,007	0,007	0,007	0,007	0,007	0,007	0,007	0,007	0,002	

Table S10: Genetic distances (p-distance) values for *Tubastraea* (COI) within and between haplotype groups and species/subspecies (p-distance: number of nucleotide substitutions per site between DNA sequences. MEGA X)

Haplotype groups *Tubastraea* COI														
	Hapl1	Hapl2	Hapl3	Hapl4	Hapl5	Hapl6	Hapl7	Hapl8	Hapl9	Hapl10	Hapl11	Hapl12	Hapl13	Hapl14
Hapl1														
Hapl2	0,022													
Hapl3	0,025	0,020												
Hapl4	0,027	0,022	0,002											
Hapl5	0,030	0,025	0,017	0,018										
Hapl6	0,023	0,022	0,013	0,015	0,013									
Hapl7	0,020	0,018	0,010	0,012	0,010	0,003								
Hapl8	0,022	0,017	0,008	0,010	0,008	0,005	0,002							
Hapl9	0,023	0,018	0,010	0,012	0,010	0,007	0,003	0,002						
Hapl10	0,030	0,025	0,017	0,018	0,015	0,007	0,010	0,008	0,010					
Hapl11	0,032	0,027	0,018	0,020	0,015	0,008	0,012	0,010	0,012	0,008				
Hapl12	0,027	0,022	0,013	0,015	0,010	0,003	0,007	0,005	0,007	0,007	0,005			
Hapl13	0,032	0,027	0,018	0,020	0,017	0,008	0,012	0,010	0,012	0,008	0,010	0,008		
Hapl14	0,025	0,020	0,012	0,013	0,012	0,002	0,005	0,003	0,005	0,005	0,007	0,002	0,007	

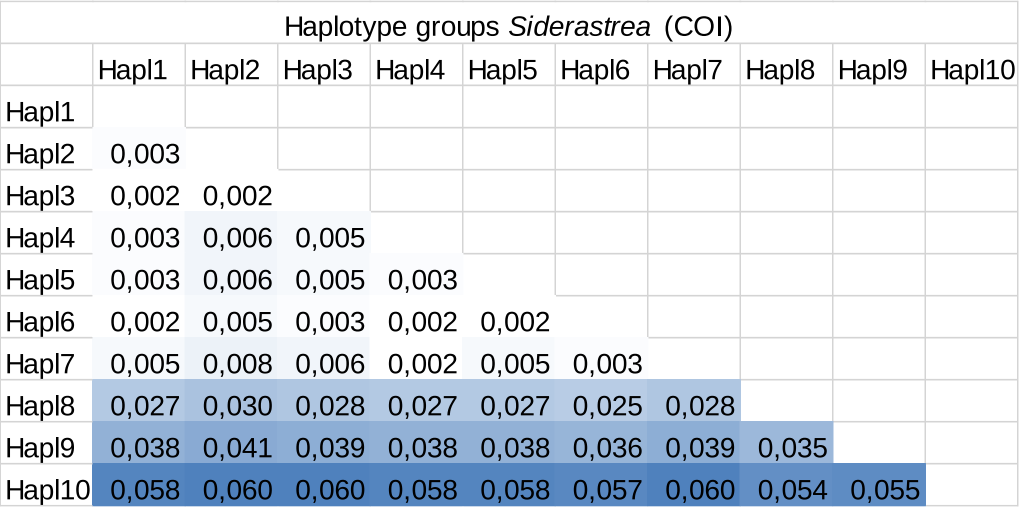
	MZ701621.1-Turbinaria_reniformis_{Hapl1}	MZ701598.1_Turbinaria_{Hapl1}	MN690340-Tubastraea_sp._IP0355_{Hapl2}	STTA2_JGLCO1490-Taurea_{Hapl3}	STTA_JGLCO1490-Taurea_{Hapl4}	HG965351-Tubastraea_sp._1_{Hapl5}	MN413853-Tubastraea_coccinea_{Hapl6}	MN413738-Tubastraea_micranthus_{Hapl7}	HG965346-Tubastraea_coccinea_{Hapl8}	HG965355-Tubastraea_sp._3_{Hapl8}	HG965353-Tubastraea_sp._2_{Hapl8}	OM372504-Tubastraea_violacea_{Hapl8}	MW411805-Tubastraea_sp._n._{Hapl8}	HG965344-Tubastraea_coccinea_{Hapl8}	MW411804-Tubastraea_sp._n._{Hapl8}	OM372505-Tubastraea_violacea_{Hapl8}	HG965345-Tubastraea_coccinea_{Hapl8}	HG965349-Tubastraea_micranthus_{Hapl8}	HG965352-Tubastraea_sp._2_{Hapl8}	HG965354-Tubastraea_sp._2_{Hapl8}	HG965347-Tubastraea_micranthus_{Hapl8}	OM372509-Tubastraea_dendroida_{Hapl8}	OM372508-Tubastraea_dendroida_{Hapl8}	HG965356-Tubastraea_sp._3_{Hapl8}	MW411803-Tubastraea_sp._n._{Hapl8}	MN690341-Tubastraea_sp._IP0356_{Hapl9}	OM372507-Tubastraea_chloromura_{Hapl9}	OM372506-Tubastraea_chloromura_{Hapl9}	HG965348-Tubastraea_micranthus_{Hapl9}	HG965350-Tubastraea_micranthus_{Hapl9}	AB441236-Tubastraea_coccinea_{Hapl10}	AB441237-Tubastraea_coccinea_{Hapl11}	DQ445807-Tubastraea_coccinea_{Hapl12}	AB441235-Tubastraea_coccinea_{Hapl13}	OQ731681-Tubastraea_coccinea_{Hapl14}	MZ677062-Australopsammia_cf._aurea_{Hapl14}	MZ677063-Australopsammia_cf._aurea_{Hapl14}	DQ445806-Tubastraea_coccinea_{Hapl14}	AB441238-Tubastraea_sp._OKTub_{Hapl14}	HG965341-Tubastraea_cf._aurea_{Hapl14}	HG965342-Tubastraea_cf._aurea_{Hapl14}	HG965343-Tubastraea_cf._aurea_{Hapl14}
MZ701621.1-Turbinaria_reniformis_{Hapl1}																																										
MZ701598.1_Turbinaria_{Hapl1}	0,000																																									
MN690340-Tubastraea_sp._IP0355_{Hapl2}	0,022	0,022																																							
STTA2_JGLCO1490-Taurea_{Hapl3}	0,025	0,025	0,020																																						
STTA_JGLCO1490-Taurea_{Hapl4}	0,027	0,027	0,022	0,002																																					
HG965351-Tubastraea_sp._1_{Hapl5}	0,030	0,030	0,025	0,017	0,018																																				
MN413853-Tubastraea_coccinea_{Hapl6}	0,023	0,023	0,022	0,013	0,015	0,013																																			
MN413738-Tubastraea_micranthus_{Hapl7}	0,020	0,020	0,018	0,010	0,012	0,010	0,003																																		
HG965346-Tubastraea_coccinea_{Hapl8}	0,022	0,022	0,017	0,008	0,010	0,008	0,005	0,002																																	
HG965355-Tubastraea_sp._3_{Hapl8}	0,022	0,022	0,017	0,008	0,010	0,008	0,005	0,002	0,000																																
HG965353-Tubastraea_sp._2_{Hapl8}	0,022	0,022	0,017	0,008	0,010	0,008	0,005	0,002	0,000	0,000																															
OM372504-Tubastraea_violacea_{Hapl8}	0,022	0,022	0,017	0,008	0,010	0,008	0,005	0,002	0,000	0,000	0,000																														
MW411805-Tubastraea_sp._n._{Hapl8}	0,022	0,022	0,017	0,008	0,010	0,008	0,005	0,002	0,000	0,000	0,000	0,000																													
HG965344-Tubastraea_coccinea_{Hapl8}	0,022	0,022	0,017	0,008	0,010	0,008	0,005	0,002	0,000	0,000	0,000	0,000	0,000																												
MW411804-Tubastraea_sp._n._{Hapl8}	0,022	0,022	0,017	0,008	0,010	0,008	0,005	0,002	0,000	0,000	0,000	0,000	0,000	0,000																											
OM372505-Tubastraea_violacea_{Hapl8}	0,022	0,022	0,017	0,008	0,010	0,008	0,005	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000																										
HG965345-Tubastraea_coccinea_{Hapl8}	0,022	0,022	0,017	0,008	0,010	0,008	0,005	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000																									
HG965349-Tubastraea_micranthus_{Hapl8}	0,022	0,022	0,017	0,008	0,010	0,008	0,005	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000																								
HG965352-Tubastraea_sp._2_{Hapl8}	0,022	0,022	0,017	0,008	0,010	0,008	0,005	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000																							
HG965354-Tubastraea_sp._2_{Hapl8}	0,022	0,022	0,017	0,008	0,010	0,008	0,005	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000																						
HG965347-Tubastraea_micranthus_{Hapl8}	0,022	0,022	0,017	0,008	0,010	0,008	0,005	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000																					
OM372509-Tubastraea_dendroida_{Hapl8}	0,022	0,022	0,017	0,008	0,010	0,008	0,005	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000																				
OM372508-Tubastraea_dendroida_{Hapl8}	0,022	0,022	0,017	0,008	0,010	0,008	0,005	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000																			
HG965356-Tubastraea_sp._3_{Hapl8}	0,022	0,022	0,017	0,008	0,010	0,008	0,005	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000																		
MW411803-Tubastraea_sp._n._{Hapl8}	0,022	0,022	0,017	0,008	0,010	0,008	0,005	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000																	
MN690341-Tubastraea_sp._IP0356_{Hapl9}	0,023	0,023	0,018	0,010	0,012	0,010	0,007	0,003	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002																
OM372507-Tubastraea_chloromura_{Hapl9}	0,023	0,023	0,018	0,010	0,012	0,010	0,007	0,003	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,000															
OM372506-Tubastraea_chloromura_{Hapl9}	0,023	0,023	0,018	0,010	0,012	0,010	0,007	0,003	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,000	0,000														
HG965348-Tubastraea_micranthus_{Hapl9}	0,023	0,023	0,018	0,010	0,012	0,010	0,007	0,003	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,000	0,000	0,000													
HG965350-Tubastraea_micranthus_{Hapl9}	0,023	0,023	0,018	0,010	0,012	0,010	0,007	0,003	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,000	0,000	0,000	0,000												
AB441236-Tubastraea_coccinea_{Hapl10}	0,030	0,030	0,025	0,017	0,018	0,015	0,007	0,010	0,008	0,008	0,008	0,008	0,008	0,008	0,008	0,008	0,008	0,008	0,008	0,008	0,008	0,008	0,008	0,008	0,008	0,010	0,010	0,010	0,010	0,010											
AB441237-Tubastraea_coccinea_{Hapl11}	0,032	0,032	0,027	0,018	0,020	0,015	0,008	0,012	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,012	0,012	0,012	0,012	0,012	0,008										
DQ445807-Tubastraea_coccinea_{Hapl12}	0,027	0,027	0,022	0,013	0,015	0,010	0,003	0,007	0,005	0,005	0,005	0,005	0,005	0,005	0,005	0,005	0,005	0,005	0,005	0,005	0,005	0,005	0,005	0,005	0,005	0,007	0,007	0,007	0,007	0,007	0,007	0,005									
AB441235-Tubastraea_coccinea_{Hapl13}	0,032	0,032	0,027	0,018	0,020	0,017	0,008	0,012	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,012	0,012	0,012	0,012	0,012	0,008	0,010	0,008								
OQ731681-Tubastraea_coccinea_{Hapl14}	0,025	0,025	0,020	0,012	0,013	0,012	0,002	0,005	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,005	0,005	0,005	0,005	0,005	0,005	0,007	0,002	0,007							
MZ677062-Australopsammia_cf._aurea_{Hapl14}	0,025	0,025	0,020	0,012	0,013	0,012	0,002	0,005	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,005	0,005	0,005	0,005	0,005	0,005	0,007	0,002	0,007	0,000						
MZ677063-Australopsammia_cf._aurea_{Hapl14}	0,025	0,025	0,020	0,012	0,013	0,012	0,002	0,005	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,005	0,005	0,005	0,005	0,005	0,005	0,007	0,002	0,007	0,000	0,000					
DQ445806-Tubastraea_coccinea_{Hapl14}	0,025	0,025	0,020	0,012	0,013	0,012	0,002	0,005	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,005	0,005	0,005	0,005	0,005	0,005	0,007	0,002	0,007	0,000	0,000	0,000				
AB441238-Tubastraea_sp._OKTub_{Hapl14}	0,025	0,025	0,020	0,012	0,013	0,012	0,002	0,005	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,005	0,005	0,005	0,005	0,005	0,005	0,007	0,002	0,007	0,000	0,000	0,000	0,000			
HG965341-Tubastraea_cf._aurea_{Hapl14}	0,025	0,025	0,020	0,012	0,013	0,012	0,002	0,005	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,005	0,005	0,005	0,005	0,005	0,005	0,007	0,002	0,007	0,000	0,000	0,000	0,000	0,000		
HG965342-Tubastraea_cf._aurea_{Hapl14}	0,025	0,025	0,020	0,012	0,013	0,012	0,002	0,005	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,005	0,005	0,005	0,005	0,005	0,005	0,007	0,002	0,007	0,000	0,000	0,000	0,000	0,000	0,000	
HG965343-Tubastraea_cf._aurea_{Hapl14}	0,025	0,025	0,020	0,012	0,013	0,012	0,002	0,005	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,003	0,005	0,005	0,005	0,005	0,005	0,005	0,007	0,002	0,007	0,000	0,000	0,000	0,000	0,000	0,000	0,000	

Table S11: Genetic distances (p-distance) values for *Porites* (COI) within and between haplotype groups (p-distance: number of nucleotide substitutions per site between DNA sequences. MEGA X)



	Haplotype groups *Porites* (COI)																								
	Hapl1	Hapl2	Hapl3	Hapl4	Hapl5	Hapl6	Hapl7	Hapl8	Hapl9	Hapl10	Hapl11	Hapl12	Hapl13	Hapl14	Hapl15	Hapl16	Hapl17	Hapl18	Hapl19	Hapl20	Hapl21	Hapl22	Hapl23	Hapl24	Hapl25
Hapl1																									
Hapl2	0,034																								
Hapl3	0,032	0,002																							
Hapl4	0,037	0,010	0,008																						
Hapl5	0,035	0,005	0,003	0,012																					
Hapl6	0,034	0,003	0,002	0,010	0,005																				
Hapl7	0,039	0,027	0,025	0,034	0,029	0,027																			
Hapl8	0,032	0,020	0,019	0,027	0,022	0,020	0,010																		
Hapl9	0,030	0,022	0,020	0,029	0,024	0,022	0,012	0,005																	
Hapl10	0,030	0,022	0,020	0,029	0,024	0,022	0,012	0,005	0,003																
Hapl11	0,029	0,020	0,019	0,027	0,022	0,020	0,010	0,003	0,002	0,002															
Hapl12	0,034	0,022	0,020	0,029	0,024	0,022	0,008	0,005	0,007	0,007	0,005														
Hapl13	0,030	0,019	0,017	0,025	0,020	0,019	0,008	0,002	0,003	0,003	0,002	0,003													
Hapl14	0,030	0,022	0,020	0,029	0,024	0,022	0,008	0,005	0,003	0,003	0,002	0,003	0,003												
Hapl15	0,032	0,020	0,019	0,027	0,022	0,020	0,010	0,003	0,005	0,002	0,003	0,005	0,002	0,005											
Hapl16	0,032	0,024	0,022	0,030	0,025	0,024	0,010	0,007	0,005	0,005	0,003	0,005	0,005	0,002	0,007										
Hapl17	0,032	0,020	0,019	0,027	0,022	0,020	0,007	0,003	0,005	0,005	0,003	0,002	0,002	0,002	0,003	0,003									
Hapl18	0,030	0,022	0,020	0,029	0,024	0,022	0,010	0,005	0,003	0,003	0,002	0,007	0,003	0,003	0,005	0,005	0,005								
Hapl19	0,030	0,022	0,020	0,029	0,024	0,022	0,012	0,005	0,003	0,003	0,002	0,007	0,003	0,003	0,005	0,005	0,005	0,003							
Hapl20	0,030	0,022	0,020	0,029	0,024	0,022	0,012	0,005	0,003	0,003	0,002	0,007	0,003	0,003	0,005	0,005	0,005	0,003	0,003						
Hapl21	0,029	0,024	0,022	0,030	0,025	0,024	0,013	0,007	0,005	0,002	0,003	0,008	0,005	0,005	0,003	0,007	0,007	0,005	0,005	0,005					
Hapl22	0,030	0,022	0,020	0,029	0,024	0,022	0,012	0,005	0,003	0,003	0,002	0,007	0,003	0,003	0,005	0,005	0,005	0,003	0,003	0,003	0,005				
Hapl23	0,034	0,019	0,017	0,025	0,020	0,019	0,012	0,005	0,007	0,007	0,005	0,007	0,003	0,007	0,005	0,008	0,005	0,007	0,007	0,007	0,008	0,007			
Hapl24	0,032	0,017	0,015	0,024	0,019	0,017	0,010	0,003	0,005	0,005	0,003	0,005	0,002	0,005	0,003	0,007	0,003	0,005	0,005	0,005	0,007	0,005	0,002		
Hapl25	0,034	0,019	0,017	0,025	0,020	0,019	0,012	0,005	0,007	0,007	0,005	0,007	0,003	0,007	0,005	0,007	0,005	0,007	0,007	0,007	0,008	0,007	0,003	0,002	

Table S12: Genetic distances (p-distance) values for *Siderastrea* (COI) within and between haplotype groups and species/subspecies (p-distance: number of nucleotide substitutions per site between DNA sequences. MEGA X)



	Haplotype groups *Siderastrea* (COI)									
	Hapl1	Hapl2	Hapl3	Hapl4	Hapl5	Hapl6	Hapl7	Hapl8	Hapl9	Hapl10
Hapl1										
Hapl2	0,003									
Hapl3	0,002	0,002								
Hapl4	0,003	0,006	0,005							
Hapl5	0,003	0,006	0,005	0,003						
Hapl6	0,002	0,005	0,003	0,002	0,002					
Hapl7	0,005	0,008	0,006	0,002	0,005	0,003				
Hapl8	0,027	0,030	0,028	0,027	0,027	0,025	0,028			
Hapl9	0,038	0,041	0,039	0,038	0,038	0,036	0,039	0,035		
Hapl10	0,058	0,060	0,060	0,058	0,058	0,057	0,060	0,054	0,055	

	SVLSS_JGLCO1490-Ssiderea_{Hapl1}	SVLSR3_JGLCO1490-Sradians_{Hapl1}	SVLSR2_JGLCO1490-Sradians_{Hapl2}	SVLSR1_JGLCO1490-Sradians_{Hapl1}	SVBGSR4_JGLCO1490-F_Sradians_{Hapl1}	BPGSR_JGLCO1490-Sradians_{Hapl2}	BPGSR3_JGLCO1490-Sradians_{Hapl1}	BPGSR2_JGLCO1490-Sradians_{Hapl1}	BBSRSR_JGLCO1490-Sradians_{Hapl3}	KM391401-Siderastrea_radians_{Hapl4}	AB441212-Siderastrea_radians_{Hapl4}	AY451385-Siderastrea_radians_{Hapl5}	DQ643838-Siderastrea_radians_{Hapl6}	NC_008167-Siderastrea_radians_{Hapl6}	OQ731671-Siderastrea_siderea_{Hapl6}	AY451387-Siderastrea_siderea_{Hapl6}	AY451386-Siderastrea_siderea_{Hapl6}	AB441211-Siderastrea_siderea_{Hapl7}	AB441213-Siderastrea_stellata_{Hapl6}	AB441215-Siderastrea_savignyana_{Hapl8}	AB441214-Siderastrea_savignyana_{Hapl9}	OQ731672.1-Flabellum_alabastrum_{Hapl10}
SVLSS_JGLCO1490-Ssiderea_{Hapl1}																						
SVLSR3_JGLCO1490-Sradians_{Hapl1}	0,0000																					
SVLSR2_JGLCO1490-Sradians_{Hapl2}	0,0031	0,0031																				
SVLSR1_JGLCO1490-Sradians_{Hapl1}	0,0000	0,0000	0,0031																			
SVBGSR4_JGLCO1490-F_Sradians_{Hapl1}	0,0000	0,0000	0,0031	0,0000																		
BPGSR_JGLCO1490-Sradians_{Hapl2}	0,0031	0,0031	0,0000	0,0031	0,0031																	
BPGSR3_JGLCO1490-Sradians_{Hapl1}	0,0000	0,0000	0,0031	0,0000	0,0000	0,0031																
BPGSR2_JGLCO1490-Sradians_{Hapl1}	0,0000	0,0000	0,0031	0,0000	0,0000	0,0031	0,0000															
BBSRSR_JGLCO1490-Sradians_{Hapl3}	0,0016	0,0016	0,0016	0,0016	0,0016	0,0016	0,0016	0,0016														
KM391401-Siderastrea_radians_{Ha	0,0031	0,0031	0,0063	0,0031	0,0031	0,0063	0,0031	0,0031	0,0047													
AB441212-Siderastrea_radians_{Ha	0,0031	0,0031	0,0063	0,0031	0,0031	0,0063	0,0031	0,0031	0,0047	0,0000												
AY451385-Siderastrea_radians_{Ha	0,0031	0,0031	0,0063	0,0031	0,0031	0,0063	0,0031	0,0031	0,0047	0,0031	0,0031											
DQ643838-Siderastrea_radians_{Ha	0,0016	0,0016	0,0047	0,0016	0,0016	0,0047	0,0016	0,0016	0,0031	0,0016	0,0016	0,0016										
NC_008167-Siderastrea_radians_{Ha	0,0016	0,0016	0,0047	0,0016	0,0016	0,0047	0,0016	0,0016	0,0031	0,0016	0,0016	0,0016	0,0000									
OQ731671-Siderastrea_siderea_{Ha	0,0016	0,0016	0,0047	0,0016	0,0016	0,0047	0,0016	0,0016	0,0031	0,0016	0,0016	0,0016	0,0000	0,0000								
AY451387-Siderastrea_siderea_{Ha	0,0016	0,0016	0,0047	0,0016	0,0016	0,0047	0,0016	0,0016	0,0031	0,0016	0,0016	0,0016	0,0000	0,0000	0,0000							
AY451386-Siderastrea_siderea_{Ha	0,0016	0,0016	0,0047	0,0016	0,0016	0,0047	0,0016	0,0016	0,0031	0,0016	0,0016	0,0016	0,0000	0,0000	0,0000	0,0000						
AB441211-Siderastrea_siderea_{Ha	0,0047	0,0047	0,0079	0,0047	0,0047	0,0079	0,0047	0,0047	0,0063	0,0016	0,0016	0,0047	0,0031	0,0031	0,0031	0,0031	0,0031					
AB441213-Siderastrea_stellata_{Ha	0,0016	0,0016	0,0047	0,0016	0,0016	0,0047	0,0016	0,0016	0,0031	0,0016	0,0016	0,0016	0,0000	0,0000	0,0000	0,0000	0,0000	0,0031				
AB441215-Siderastrea_savignyana_{Hapl8}	0,0268	0,0268	0,0299	0,0268	0,0268	0,0299	0,0268	0,0268	0,0283	0,0268	0,0268	0,0268	0,0252	0,0252	0,0252	0,0252	0,0252	0,0283	0,0252			
AB441214-Siderastrea_savignyana_{Hapl9}	0,0378	0,0378	0,0409	0,0378	0,0378	0,0409	0,0378	0,0378	0,0394	0,0378	0,0378	0,0378	0,0362	0,0362	0,0362	0,0362	0,0362	0,0394	0,0362	0,0346		
OQ731672.1-Flabellum_alabastrum_{Hapl10}	0,0583	0,0583	0,0598	0,0583	0,0583	0,0598	0,0583	0,0583	0,0598	0,0583	0,0583	0,0583	0,0567	0,0567	0,0567	0,0567	0,0567	0,0598	0,0567	0,0535	0,0551	

Table S13: Genetic distances (p-distance) values for *Favia* (COI) within and between haplotype groups and species/subspecies (p-distance: number of nucleotide substitutions per site between DNA sequences. MEGA X)

	Haplotype groups *Favia* (COI)																									
	Hapl1	Hapl2	Hapl3	Hapl4	Hapl5	Hapl6	Hapl7	Hapl8	Hapl9	Hapl10	Hapl11	Hapl12	Hapl13	Hapl14	Hapl15	Hapl16	Hapl17	Hapl18	Hapl19	Hapl20	Hapl21	Hapl22	Hapl23	Hapl24	Hapl25	Hapl26
Hapl1																										
Hapl2	0,002																									
Hapl3	0,019	0,021																								
Hapl4	0,021	0,023	0,002																							
Hapl5	0,021	0,023	0,005	0,007																						
Hapl6	0,007	0,009	0,026	0,028	0,028																					
Hapl7	0,023	0,024	0,038	0,040	0,040	0,029																				
Hapl8	0,017	0,019	0,002	0,003	0,003	0,024	0,036																			
Hapl9	0,021	0,023	0,005	0,007	0,007	0,028	0,040	0,003																		
Hapl10	0,019	0,021	0,003	0,005	0,005	0,026	0,038	0,002	0,005																	
Hapl11	0,016	0,017	0,003	0,005	0,005	0,023	0,035	0,002	0,005	0,003																
Hapl12	0,019	0,021	0,009	0,010	0,010	0,026	0,038	0,007	0,010	0,009	0,005															
Hapl13	0,019	0,021	0,003	0,005	0,005	0,026	0,038	0,002	0,005	0,003	0,003	0,005														
Hapl14	0,019	0,021	0,007	0,009	0,009	0,026	0,038	0,005	0,009	0,007	0,003	0,009	0,007													
Hapl15	0,021	0,023	0,005	0,007	0,007	0,028	0,040	0,003	0,007	0,005	0,005	0,010	0,005	0,009												
Hapl16	0,021	0,023	0,009	0,010	0,010	0,028	0,040	0,007	0,010	0,009	0,005	0,003	0,005	0,009	0,010											
Hapl17	0,021	0,023	0,005	0,007	0,007	0,028	0,038	0,003	0,007	0,005	0,005	0,010	0,005	0,009	0,007	0,010										
Hapl18	0,023	0,024	0,007	0,009	0,009	0,029	0,040	0,005	0,009	0,007	0,007	0,009	0,003	0,010	0,009	0,009	0,002									
Hapl19	0,019	0,021	0,003	0,005	0,005	0,026	0,036	0,002	0,005	0,003	0,003	0,009	0,003	0,007	0,005	0,009	0,002	0,003								
Hapl20	0,019	0,021	0,003	0,005	0,005	0,026	0,038	0,002	0,005	0,003	0,003	0,009	0,003	0,007	0,005	0,009	0,005	0,007	0,003							
Hapl21	0,038	0,040	0,023	0,024	0,024	0,045	0,050	0,021	0,024	0,023	0,023	0,028	0,023	0,026	0,024	0,028	0,021	0,023	0,019	0,023						
Hapl22	0,019	0,021	0,007	0,009	0,009	0,026	0,036	0,005	0,009	0,007	0,007	0,010	0,007	0,010	0,009	0,012	0,005	0,007	0,003	0,007	0,019					
Hapl23	0,021	0,023	0,009	0,010	0,010	0,028	0,038	0,007	0,010	0,009	0,009	0,012	0,009	0,012	0,010	0,014	0,007	0,009	0,005	0,009	0,021	0,002				
Hapl24	0,019	0,021	0,003	0,005	0,002	0,026	0,038	0,002	0,005	0,003	0,003	0,009	0,003	0,007	0,005	0,009	0,005	0,007	0,003	0,003	0,023	0,007	0,009			
Hapl25	0,021	0,023	0,005	0,007	0,003	0,028	0,040	0,003	0,007	0,005	0,005	0,010	0,005	0,009	0,007	0,010	0,007	0,009	0,005	0,005	0,024	0,009	0,010	0,002		
Hapl26	0,019	0,021	0,003	0,005	0,005	0,026	0,035	0,002	0,005	0,003	0,003	0,009	0,003	0,007	0,005	0,009	0,005	0,007	0,003	0,003	0,019	0,007	0,009	0,003	0,005	

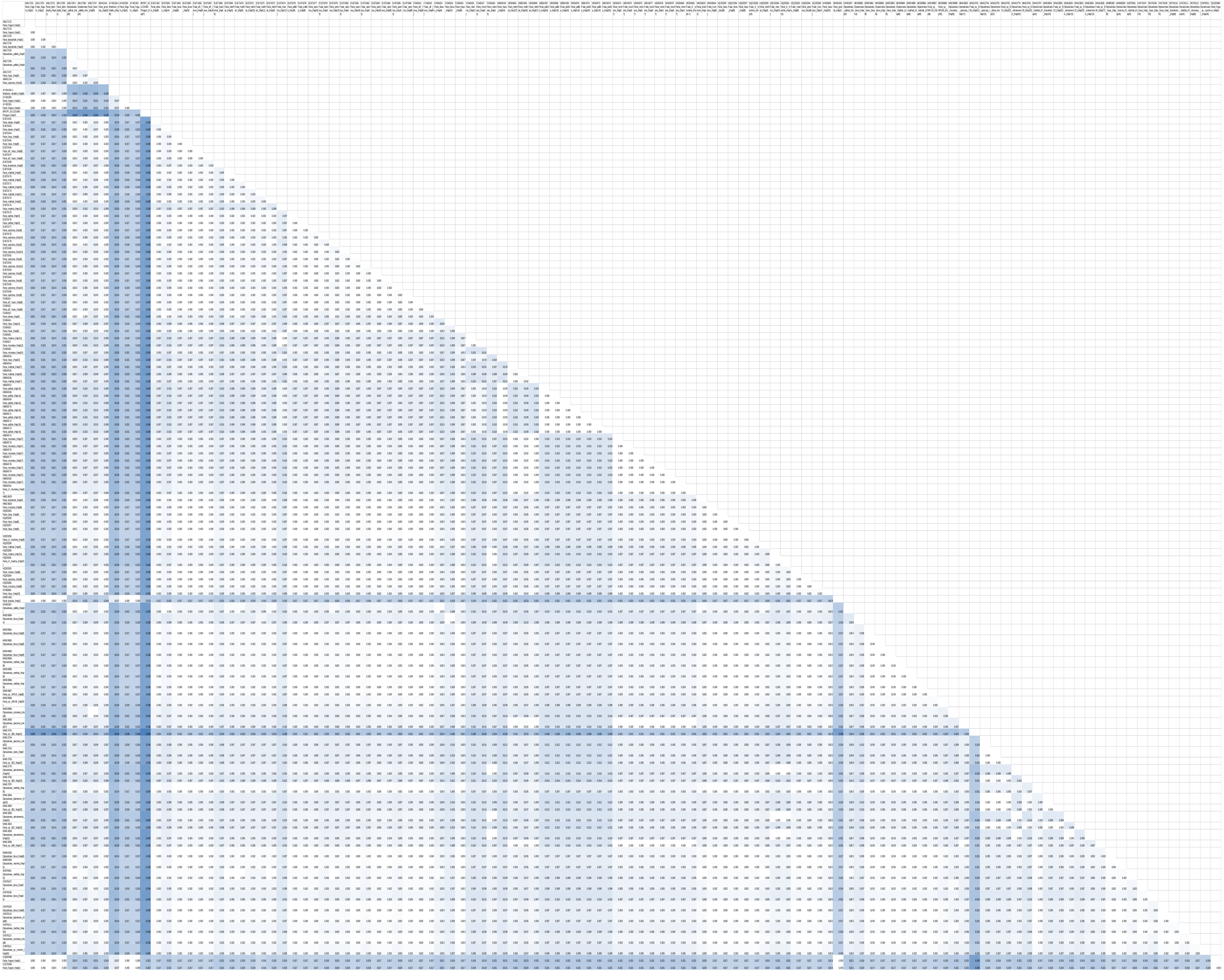
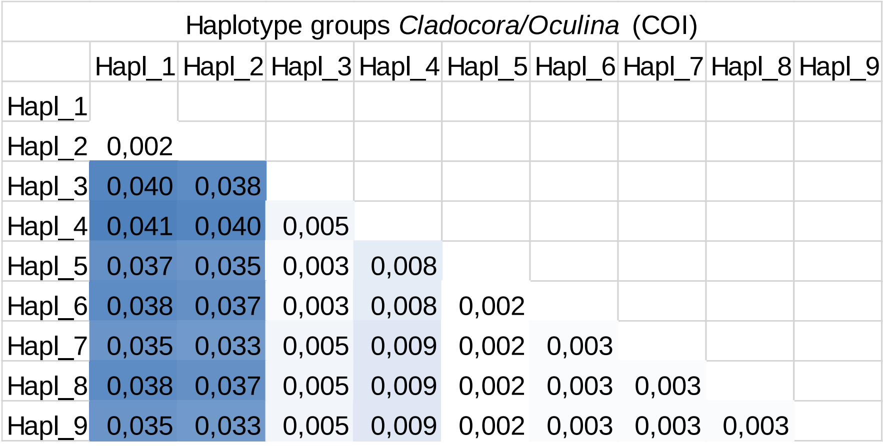


Table S14: Genetic distances (p-distance) values for *Cladocora/Oculina* (COI) within and between haplotype groups and species/subspecies (p-distance: number of nucleotide substitutions per site between DNA sequences. MEGA X)



Haplotype groups *Cladocora/Oculina* (COI)									
	Hapl_1	Hapl_2	Hapl_3	Hapl_4	Hapl_5	Hapl_6	Hapl_7	Hapl_8	Hapl_9
Hapl_1									
Hapl_2	0,002								
Hapl_3	0,040	0,038							
Hapl_4	0,041	0,040	0,005						
Hapl_5	0,037	0,035	0,003	0,008					
Hapl_6	0,038	0,037	0,003	0,008	0,002				
Hapl_7	0,035	0,033	0,005	0,009	0,002	0,003			
Hapl_8	0,038	0,037	0,005	0,009	0,002	0,003	0,003		
Hapl_9	0,035	0,033	0,005	0,009	0,002	0,003	0,003	0,003	

	OQ625384_Dendrogyra_cylindrus_{Hapl_1}	MK309944_Phyllangia_americana_{Hapl_2}	AY451345_Eusmilia_sp._{Hapl_1}	OQ625382_Meandrina_meandrites_{Hapl_1}	AY451359_Solenastrea_bournoni_{Hapl_3}	FJ966870_Solenastrea_hyades_{Hapl_4}	SVL_MP_Psenegalensis_{Hapl_5}	MW032500_Cladocora_caespitosa_{Hapl_5}	MW032501_Cladocora_caespitosa_{Hapl_5}	MW032502_Cladocora_caespitosa_{Hapl_6}	MW032503_Cladocora_caespitosa_{Hapl_5}	MW032504_Cladocora_caespitosa_{Hapl_5}	MW032505_Cladocora_caespitosa_{Hapl_5}	MW032506_Cladocora_caespitosa_{Hapl_5}	MW032507_Cladocora_caespitosa_{Hapl_5}	MW032508_Cladocora_caespitosa_{Hapl_5}	MW032509_Cladocora_caespitosa_{Hapl_5}	MW032510_Cladocora_caespitosa_{Hapl_5}	MW032511_Cladocora_caespitosa_{Hapl_5}	MW032512_Cladocora_caespitosa_{Hapl_5}	MW032513_Cladocora_caespitosa_{Hapl_5}	MW032514_Cladocora_caespitosa_{Hapl_5}	MW032515_Cladocora_caespitosa_{Hapl_5}	MW032516_Cladocora_caespitosa_{Hapl_6}	MW032517_Cladocora_caespitosa_{Hapl_5}	MW032518_Cladocora_caespitosa_{Hapl_5}	MW032519_Cladocora_caespitosa_{Hapl_5}	MW032520_Cladocora_caespitosa_{Hapl_5}	MW032521_Cladocora_caespitosa_{Hapl_5}	MW032522_Cladocora_caespitosa_{Hapl_5}	MW032523_Cladocora_caespitosa_{Hapl_6}	OQ625381_Cladocora_sp._{Hapl_6}	OQ625378_Oculina_cf._varicosa_{Hapl_5}	FJ966871_Oculina_diffusa_{Hapl_5}	OQ625379_Oculina_patagonica_{Hapl_5}	LN614380_Oculina_patagonica_{Hapl_5}	OQ625380_Oculina_robusta_{Hapl_5}	FJ966874_Oculina_robusta_{Hapl_5}	FJ966869_Oculina_robusta_{Hapl_7}	LN614379_Oculina_sp._{Hapl_5}	AY451365_Oculina_sp._{Hapl_5}	OQ625377_Oculina_varicosa_{Hapl_5}	FJ966867_Oculina_varicosa_{Hapl_8}	FJ966875_Oculina_varicosa_{Hapl_5}	FJ966868_Oculina_varicosa_{Hapl_9}	FJ966872_Oculina_varicosa_{Hapl_5}	FJ966873_Oculina_varicosa_{Hapl_5}
OQ625384_Dendrogyra_cylindrus_{Hapl_1}																																															
MK309944_Phyllangia_americana_{Hapl_2}	0,002																																													
AY451345_Eusmilia_sp._{Hapl_1}	0,000	0,002																																											
OQ625382_Meandrina_meandrites_{Hapl_1}	0,000	0,002	0,000																																										
AY451359_Solenastrea_bournoni_{Hapl_3}	0,040	0,038	0,040	0,040																																								
FJ966870_Solenastrea_hyades_{Hapl_4}	0,041	0,040	0,041	0,041	0,005																																							
SVL_MP_Psenegalensis_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008																																					
MW032500_Cladocora_caespitosa_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000																																				
MW032501_Cladocora_caespitosa_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000																																			
MW032502_Cladocora_caespitosa_{Hapl_6}	0,038	0,037	0,038	0,038	0,003	0,008	0,002	0,002	0,002																																		
MW032503_Cladocora_caespitosa_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002																																	
MW032504_Cladocora_caespitosa_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000																																
MW032505_Cladocora_caespitosa_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000																															
MW032506_Cladocora_caespitosa_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000																														
MW032507_Cladocora_caespitosa_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000																													
MW032508_Cladocora_caespitosa_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000																												
MW032509_Cladocora_caespitosa_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000																											
MW032510_Cladocora_caespitosa_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000																										
MW032511_Cladocora_caespitosa_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000																									
MW032512_Cladocora_caespitosa_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000																								
MW032513_Cladocora_caespitosa_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000																							
MW032514_Cladocora_caespitosa_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000																						
MW032515_Cladocora_caespitosa_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000																					
MW032516_Cladocora_caespitosa_{Hapl_6}	0,038	0,037	0,038	0,038	0,003	0,008	0,002	0,002	0,002	0,000	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002																							
MW032517_Cladocora_caespitosa_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,002																						
MW032518_Cladocora_caespitosa_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,000																					
MW032519_Cladocora_caespitosa_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,000	0,000																				
MW032520_Cladocora_caespitosa_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,000	0,000	0,000																			
MW032521_Cladocora_caespitosa_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000																		
MW032522_Cladocora_caespitosa_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000																	
MW032523_Cladocora_caespitosa_{Hapl_6}	0,038	0,037	0,038	0,038	0,003	0,008	0,002	0,002	0,002	0,000	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,000	0,002	0,002	0,002	0,002	0,002	0,002																	
OQ625381_Cladocora_sp._{Hapl_6}	0,038	0,037	0,038	0,038	0,003	0,008	0,002	0,002	0,002	0,000	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,000	0,002	0,002	0,002	0,002	0,002	0,002	0,000																
OQ625378_Oculina_cf._varicosa_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,002															
FJ966871_Oculina_diffusa_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,002	0,000														
OQ625379_Oculina_patagonica_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,002	0,000	0,000													
LN614380_Oculina_patagonica_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,002	0,000	0,000	0,000												
OQ625380_Oculina_robusta_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,002	0,000	0,000	0,000	0,000											
FJ966874_Oculina_robusta_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,002	0,000	0,000	0,000	0,000	0,000										
FJ966869_Oculina_robusta_{Hapl_7}	0,035	0,033	0,035	0,035	0,005	0,009	0,002	0,002	0,002	0,003	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,003	0,002	0,002	0,002	0,002	0,002	0,002	0,003	0,003	0,002	0,002	0,002	0,002	0,002	0,002									
LN614379_Oculina_sp._{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,002								
AY451365_Oculina_sp._{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,000							
OQ625377_Oculina_varicosa_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,000	0,000						
FJ966867_Oculina_varicosa_{Hapl_8}	0,038	0,037	0,038	0,038	0,005	0,009	0,002	0,002	0,002	0,003	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,003	0,002	0,002	0,002	0,002	0,002	0,002	0,003	0,003	0,002	0,002	0,002	0,002	0,002	0,002	0,003	0,002	0,002	0,002					
FJ966875_Oculina_varicosa_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,002				
FJ966868_Oculina_varicosa_{Hapl_9}	0,035	0,033	0,035	0,035	0,005	0,009	0,002	0,002	0,002	0,003	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,002	0,003	0,002	0,002	0,002	0,002	0,002	0,002	0,003	0,003	0,002	0,002	0,002	0,002	0,002	0,002	0,003	0,002	0,002	0,002	0,003	0,002			
FJ966872_Oculina_varicosa_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,002	0,000	0,002		
FJ966873_Oculina_varicosa_{Hapl_5}	0,037	0,035	0,037	0,037	0,003	0,008	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,002	0,000	0,002	0,000	

Table S15: List of references used for the table of coral species in Macaronesia (Table 3.3.1)

#	Source
1	Rakka, M., Orejas, C., Sampaio, I., Monteiro, J., Parra, H., & Carreiro-Silva, M. (2017). Reproductive biology of the black coral Antipathella wollastoni (Cnidaria: Antipatharia) in the Azores (NE Atlantic). *Deep Sea Research Part II: Topical Studies in Oceanography, 145*, 131-141.
2	OBIS : dataset_id: 09be818d-531c-4d86-8eba-5db81d42fdba
3	Capel, K. C., López, C., Moltó-Martín, I., Zilberberg, C., Creed, J. C., Knapp, I. S., ... & Kitahara, M. V. (2020). Atlantia, a new genus of Dendrophylliidae (Cnidaria, Anthozoa, Scleractinia) from the eastern Atlantic. PeerJ, 8, e8633.
4	Ocaña, O., Den Hartog, J. C., Brito, A., Moro, L., Herrera, R., Martín, J., ... & Bacallado, J. J. (2015). A survey on Anthozoa and its habitats along the Northwest African coast and some islands: new records, descriptions of new taxa and biogeographical, ecological and taxonomical comments. Part I.
5	Zibrowius, H. (1980). Les Scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. Mémoires de l'Institut océanographique, Monaco.
6	Molodtsova, T. N. (2006). Black corals (Antipatharia: Anthozoa: Cnidaria) of the north-eastern Atlantic. In ‘Biogeography of the Atlantic Seamounts’.(Eds AN Mironov, AV Gebruk, and AJ Southward.) pp. 141–151.
7	Roule, L. (1905). Description des antipathaires et cérianthaires recueillis par S.A.S. le Prince de Monaco dans l'Atlantique nord (1886-1902). *Résultats des Campagnes Scientifiques Accomplies sur son Yacht par Albert I Prince Souverain de Monaco.* XXX: 1-96.
8	Wirtz, P. (2020). *A pictorial catalogue of shallow-water Scleractinia of Madeira Island.* https://www.researchgate.net/publication/344457837_Revised_pictorial_catalogue_of_shallow-water_Scleractinia_of_Madeira_Island
9	Wirtz, P. (2021b). *A pictorial catalogue of the shallow water Alcyonacea (Cnidaria Octocorallia) from Madeira.* https://www.researchgate.net/publication/353637563_A_pictorial_catalogue_of_the_shallow_water_Alcyonacea_Cnidaria_Octocorallia_from_Madeira
10	Wirtz, P. (2022e). *A pictorial catalogue of the shallow water Alcyonacea (Cnidaria Octocorallia) from the Azores.* https://www.researchgate.net/publication/361548286_A_pictorial_catalogue_of_the_shallow_water_Alcyonacea_Cnidaria_Octocorallia_from_the_Azores

11	Wirtz, P. (2022d). *A pictorial catalogue of the shallow water Scleractinia (Cnidaria, Anthozoa) of the Azores.* https://www.researchgate.net/publication/362790690_A_pictorial_catalogue_of_the_shallow_water_Scleractinia_Cnidaria_Anthozoa_of_the_Azores
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