Investigating Species Boundaries within the Hard Coral Genus *Goniopora* (Cnidaria, Scleractinia) from the Red Sea Using an Integrative Morphomolecular Approach

Thesis by

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In Partial Fulfillment of the Requirements

For the Degree of

Marine Science

King Abdullah University of Science and Technology, Thuwal, Kingdom of Saudi Arabia

© December, 2015

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ABSTRACT

Investigating Species Boundaries within the Hard Coral Genus *Goniopora* (Cnidaria, Scleractinia) from the Red Sea Using an Integrative Morphomolecular Approach

Tullia Isotta Terraneo

In the present study the species boundaries of the scleractinian coral genus *Goniopora* from the Saudi Arabian Red Sea were investigated. An integrated morpho-molecular approach was used to better clarify the complex scenario derived from traditional classification efforts based on skeletal morphology. Traditional taxonomy of this genus considers skeletal morphology first and polyp morphology as a secondary discriminating character. This leads to potential complication due to plasticity in skeletal features within a species. To address this issue, molecular analyses of evolutionary relationships between nine traditional morphospecies of *Goniopora* from the Red Sea were performed and were used to re-evaluate the informativeness of macromorphological and micromorphological features. Between four and six putative molecular lineages were identified within *Goniopora* samples from the Saudi Arabian Red Sea on the basis of four molecular markers: the mitochondrial intergenic spacer between Cytochrome *b* and the NADH dehydrogenase subunit 2, the entire nuclear ribosomal internal transcribed spacer region, the ATP synthase subunit *β* gene, and a portion of the Calmodulin gene. The results were strongly corroborated by three distinct analyses of species delimitation. Subsequent analyses of micromorphological and microstructural skeletal features identified the presence of distinctive characters in each of the
molecular clades. Unique in vivo morphologies were associated with the genetic-delimited lineages, further supporting the molecular findings. The proposed re-organization of *Goniopora* will resolve several taxonomic problems in this genus while reconciling molecular and morphological evidence. Reliable species-level identification of *Goniopora* spp. can be achieved with polyp morphology under the proposed revision.
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LIST OF ABBREVIATIONS

mtDNA                                       mitochondrial DNA
nDNA                                          nuclear DNA
rDNA                                           ribosomal DNA
COI                                              Cytochrome Oxydase subunit 1
Cytb                                            Cytochrome b
ATP6                                           ATP Synthase subunit 6
ATP8                                           ATP Synthase subunit 8
ATPsβ                                          ATP Synthase subunit β
NAD2                                          NADH dehydrogenase subunit 2
NAD3                                          NADH dehydrogenase subunit 3
NAD4L                                        NADH dehydrogenase subunit 4
NAD5                                          NADH dehydrogenase subunit 5
NAD6                                          NADH dehydrogenase subunit 6
ITS1                                           Internal Transcribed Spacer 1
ITS2                                           Internal Transcribed Spacer 2
CalM                                           Calmodulin
tRNATrp                                       Tryptophan transfer RNA
IGR                                              region spanning between the 3’ end of Cytochrome b and
                                                   the 5’ end NAD2
PCR                                           Polymerase Chain Reaction
BI                                             Bayesian Inference
ML                                           Maximum Likelihood
MP                                           Maximum Parsimony
PPBi                                         Bayesian posterior probability
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<tr>
<td>BT&lt;sub&gt;ML&lt;/sub&gt;</td>
<td>ML bootstrapping support</td>
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<tr>
<td>BT&lt;sub&gt;MP&lt;/sub&gt;</td>
<td>MP bootstrapping support</td>
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<tr>
<td>MCMC</td>
<td>Markov Chains Monte Carlo</td>
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<tr>
<td>AIC</td>
<td>Akaike Information Criterion</td>
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<tr>
<td>ABGD</td>
<td>Automatic Barcoding Gap Discovery</td>
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<tr>
<td>PTP</td>
<td>Poisson Tree Processes</td>
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<tr>
<td>GMYC</td>
<td>Generalized Mixed Yule Coalescent</td>
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1. INTRODUCTION

1.1 The traditional approach to defining species boundaries in corals

Defining species is fundamental to biodiversity studies and, in an era of ongoing biodiversity loss, these definitions are highly relevant to designating biodiversity hotspots, designing conservation schemes, and informing legislation (Mann and Plummer 1992, Karl and Bowen 1999, Agapow et al. 2004). Current estimates of species extinction rates are three to four orders of magnitude above background extinction rates (Barnosky et al. 2011) and therefore there is an urgent need to establish conservation priorities and a better knowledge of global species biodiversity (Brooks et al. 2006). Recent estimates suggest that 86% of existing species on Earth and 91% of species in the ocean still await description (Mora et al. 2011). Coral reefs occupy one third of the world’s tropical waters (Birkenald 1977), and represent one of the most biologically diverse ecosystems on Earth, by some estimates accounting for one third of total marine fish species (Bowen et al. 2013). Scleractinian corals (Cnidaria, Anthozoa) are primary builders of coral reefs (Veron 2000), and understanding the ecology, evolution, and biodiversity of corals is of fundamental importance for preserving these unique ecosystems (Gilmour et al. 2013). The knowledge of species boundaries within the order Scleractinia, as well as a clear understanding of their phylogenetic relationships and evolution, is the baseline for population genetics, physiological, and ecological studies. Nevertheless, coral systematics is currently undergoing a radical reassessment as a result of rapid advances in molecular techniques to address taxonomic questions. At present, we lack a comprehensive understanding of species boundaries within the
order Scleractinia, which remains one of the most challenging taxonomic groups for reliable species delimitation.

Traditional coral taxonomy has been based on macro- and micro-morphological skeletal features (Milne Edwards and Haime 1848, Ogilvie 1897, Vaughan and Wells 1943, Wells 1956). Since the beginning of the 19th century, taxonomists classified extant corals by examining the gross morphology of coral colonies and examining the basic structures that form the aragonite skeletons deposited by these animals, such as the corallites, the columella, and the coenosteum. A few authors introduced polyp morphology as a key feature for Scleractinia classification (Duerden 1902, Matthai 1914), but the most important classifications of the 19th century, by Milne Edwards and Haime (1857) and Ogilvie (1897), were established using macroscopic and microscopic skeletal features.

In the 20th century Vaughan and Wells (1943) and Wells (1956) developed what was subsequently defined the “traditional” hard coral classification system. On the basis of optical microscope observations of skeletal features the authors completely revised the order Scleractinia, recognizing the existence of 5 extant suborders and 33 extant and fossil families, and proposing an evolutionary tree addressing family level relationships within the order (reviewed by Budd 2010).

Nevertheless, the limitations of the traditional approach became apparent as early as 1886, when, in the report from the Challenger Expedition, Quelch highlighted that coral skeletons were affected by within-species morphological variation in response to the environment. Veron and Pichon (1976) first applied the concept of “ecomorphs” to corals, based on the fact that specific ecological conditions were able to determine intraspecific skeletal variations in corals,
acting on the phenotype and/or on the genotype and thus hiding real evolutionary pattern. It has been experimentally demonstrated that several environmental factors can influence coral morphology, such as light, sedimentation, wave action, depth, and salinity (Randal 1976, Miller 1994, Bruno and Edmunds 1997, Todd 2008). Due to high environmental heterogeneity in coral reefs, the presence of several microhabitats can have important impacts in colonies’ growth forms. In such a variable habitat, a high degree of environment-phenotype matching is expected (Lloyd 1984). The amount of morphological plasticity varies among taxa, as well as within the same taxa under different environmental condition (Todd 2008). This extreme variability of skeletal morphology presents a major limitation to making inferences about the evolution of morphological characters traditionally used in coral taxonomy.

Moreover, morphological features in corals may be influenced by convergent evolution and homoplasy, which can lead to incongruence among different phylogenetic reconstructions (van Oppen et al. 2001). Cases of homoplasy of morphological features have been demonstrated to obscure the real relationships between species (Fukami et al. 2004).

1.2 The advent of DNA taxonomy in corals

In the last couple of decades, an increasing number of molecular tools and genetic techniques have emerged and have opened a new era for coral taxonomy. Several molecular phylogenies demonstrated the inconsistency of macromorphological features as a tool for species delimitation in scleractinians (Romano and Palumbi 1996, Romano and Cairns 2000, Chen et al. 2002, Fukami et al. 2004, 2008, Le Goff-Vitry et al. 2004, Kitahara et al. 2010, Huang et al. 2011).
The molecular revolution that started in the 1990s has led to the emergence of a genetic-based system for systematically cataloging metazoan biodiversity. On the basis of comparisons between homologous DNA sequences it is possible to identify species and assign them to higher taxonomic levels (Tautz et al. 2003). Generally, diverging lineages acquire different mutations through time, eventually creating unique signatures that can be indicative and distinctive among different taxa (de Queiroz 1998). In this context, Herbert et al. (2003) proposed a DNA barcoding system for animal life relying upon sequence divergence in the mitochondrial cytochrome c oxidase subunit 1 (COI). Mitochondrial DNA (mtDNA) in animal genomes typically shows an evolution rate 10 times higher compared to nuclear genomes, is non-recombining, and is intronless (Brown et al. 1979, 1982). Moreover, as mtDNA is maternally inherited and haploid, it has a smaller effective population size, leading to a much faster lineage sorting (Birky et al. 1983).

As our knowledge of mtDNA increases, unique properties of mtDNA in different classes of cnidarians have been identified. In the class Anthozoa, in particular, the mtDNA is characterized by slow evolution rates, resulting in very low sequence divergence, and thus mtDNA is not suitable for inferring genus- and species-level relationships (France and Hoover 2001, 2002, Shearer et al. 2002, McFadden et al. 2004, 2006, Hellberg 2006, Huang et al. 2008). Notably, Shearer and Coffroth (2008) demonstrated that intraspecific COI variation in Scleractinia is much lower than in metazoans even at the third codon position, making it impossible to discern hard coral species on the basis of the COI gene. Moreover, other mitochondrial genes commonly used in phylogenetic studies in metazoans, such as 16S rDNA, Cytochrome b (cytb), 12S rDNA, ATP synthase 6 (ATPs6), and NADH dehydrogenase subunits 2, 3, 4, and 6 (NAD2, NAD3, NAD4L,
NAD6) are less divergent between families in anthozoans than between congeneric species in other marine invertebrates (Shearer et al. 2002).

Recent studies identified long highly variable non-coding regions of the mtDNA containing informative sites. The length of these regions is highly variable between different taxa so different regions will be adequate for different organisms, e.g., the putative control region located between ATP8 and COI and an open reading frame located between ATP6 and NAD4 genes can provide high resolution within the pocilloporid genera *Pocillopora* Lamarck, 1816, *Seriatopora* Lamarck, 1816, and *Stylophora* Schweigger, 1820 (Flot and Tillier 2007, Flot et al. 2008, 2011, Schmidt-Roach et al. 2012, Pinzón et al. 2013). Meanwhile, the mitochondrial spacer between COI and 16S-rRNA is powerful in resolving species boundaries in the agariciid genera *Pavona* Lamarck, 1801 and *Leptoseris* Milne Edwards and Haime, 1849 (Luck et al. 2013, Pochon et al. 2015); in the genus *Pachyseris* Milne Edwards and Haime, 1849 (Terraneo et al. 2014); in the merulinid genera *Goniastrea* Milne Edwards and Haime, 1848, *Paragoniastrea* Huang, Benzoni and Budd, 2014, and *Merulina* Ehrenberg, 1834 (Huang 2014); and in the genus *Sclerophyllia* Klunzinger, 1879 (Arrigoni et al. 2015).

Nuclear DNA (nDNA), on the other hand, accumulates mutations in cnidarians at the same rate as in other animals (Hellberg 2006). The nuclear ribosomal DNA (rDNA) internal transcribed spacers ITS1 and ITS2 (ITS region) are the most used markers to infer species level relationships within corals (Hunter et al. 1997, Lopez and Knowlton 1997, Medina et al. 1999, Odorico and Miller 1997, van Oppen et al. 2000, 2002, Diekmann et al. 2001, Chen et al. 2004). rRNA constitutes a multigene family of tandem repeated units. Each unit consists of three highly conserved coding regions, 18S, 5.8S, and 28S, and two internal transcribed spacers (ITS1 and
ITS2) located in-between. In many eukaryotic taxa, rDNA evolves via concerted evolution (Arnheim 1980), a mechanism that homogenizes different ITS repeated units through unequal crossing over and gene conversion (Dover 1982). In many cases, the rate of concerted evolution is enough to homogenize the variation among unit repeats within species, but interspecific divergence can be high (Hillis and Dixon 1991).

Despite its widespread usage, the utility of the ITS region has been long debated in the genus Acropora Oken, 1815, where high sequence divergence (>40% intraspecific p-distance in Acropora spp.) and the presence of pseudogenes obscure real patterns of evolution (van Oppen et al. 2002, Marquez et al. 2003, Vollmer and Palumbi 2004, Chen et al. 2004, Wei et al. 2006). Nevertheless, detailed studies have demonstrated that these features are unique in the genus Acropora, where it has been shown that the ITS2 has the shortest sequence not only among scleractinian corals, but also among any metazoans and eukaryotes measured to date (Odorico and Miller, 1997), as well as a peculiar secondary structure. Conversely, the ITS region has been successfully used for all the other coral taxa, as pointed out between others in Diekmann et al. (2001), Chen et al. (2004), and Benzoni et al. (2007, 2010).

In the past 20 years a number of other nuclear genetic sequences have been used to infer coral phylogenies, such as the coding genes Calmodulin (CalM), ATPase β (ATPs β), β-Tubulin, mini-collagen, Pax-C 46/47 intron (PCI), and the histone cluster h2ab (Hatta et al. 1999, van Oppen et al. 2000, 2001, 2004, Marquez et al. 2002, Vollmer and Palumbi 2002, Fukami et al. 2004, 2008, Wallace et al. 2007, Stefani et al. 2008a, b, Nunes et al. 2008, Forsman et al. 2009, Arrigoni et al. 2014b). Overall, most frequently successful used markers were rDNA and β-tubulin. On the
contrary, histone h2ab have been used up to now only in few species, but its utility may be extended to other genera.

Molecular phylogenies that use only a single tool to assess relationships among corals may run into substantial limitations because of the potential for hybridization (Veron 1995), and gene introgression (Odorico and Miller 1997, Diekmann et al. 2001, van Oppen et al. 2000, 2001). One of the biggest challenges is that possible recent divergence between species (Marquez et al. 2002, de Queiroz 2007) can obscure real relationships within the order. With regards to hybridization, several studies have shown that synchronized spawning among numerous species of hard corals, i.e. mass spawning sensu Willis et al. (1985), occurs in the majority of reef regions, for example in the Great Barrier Reef (Harrison et al. 1984, Babcock 1986), in Okinawa-Japan (Hayashibara et al. 1993), and in the Caribbean (Sanchez et al. 1999). The simultaneous release of huge quantities of sperms and eggs in a limited period of time creates an incomparable opportunity for interspecific hybridization and gene introgression. Extensive introgressive hybridization, i.e. hybrids backcrossing with parental species and transferring genes from one species to another, has been demonstrated to occur in corals (reviewed by Willis et al. (2006)), especially within the genus Acropora (van Oppen et al. 2001, 2002, Vollmer and Palumbi 2002, Richards et al., 2008, Isomura et al. 2013).

Recent divergence between species can explain low diversity between morphologically distinct species (Marquez et al. 2002, de Queiroz 2007). Miller and Benzie (1997) proposed that several species of Platygyra Ehrenberg, 1834, were not different from a molecular point of view because they have not undergone important genetic divergence and developed complete reproductive isolation. Ancestral polymorphisms can be hidden by low rate of molecular
evolution, large population size, and long generation time, as well as short generation time with overlap of generations (van Oppen et al. 2004).

1.3 The modern synthesis: integration of morphological and molecular data

The extensive number of molecular phylogenies produced in recent years has inspired coral taxonomists to search new diagnostic morphological traits to help reconcile the strong genetic evidence. In particular, micromorphological and microstructural skeletal features traditionally used in classification were re-evaluated in light of molecular data, leading the way into the era of reverse taxonomy (Stolarski and Roniewicz, 2001, Cuif and Sorauf 2001, Stolarski 2003, Cuif et al. 2003, Benzoni et al. 2007, Brahim et al. 2010, Budd and Stolarski 2009, 2011, Janiszewska et al. 2011).

The integration of molecular and morphological analyses is revolutionizing our understanding of evolutionary relationships within the Scleractinia, leading to extensive taxonomic revisions at family level (Budd et al. 2012, Kitahara et al. 2012a, 2012b, Huang et al. 2014) and at the genus level (Wallace et al. 2007, Benzoni et al. 2010, Gittenberger et al. 2011, Schmidt-Roach et al. 2014). For instance, Benzoni et al. (2007) and Stefani et al. (2008a, b) used an integrated morpho-molecular approach to demonstrate that the genus Psammocora Dana, 1846 is not monophyletic, and reconstructed a robust molecular phylogeny of the genus, strongly supported by morphological evidence. A combination of genetic and morphological evidences has been successfully used recently for a comprehensive revision and delineation of Pocillopora Lamarck, 1816 species, where high levels of phenotypic plasticity were encrypting species boundaries and precluding the definition of valid taxonomic units (Schmidt-Roach et al. 2014).
Taking into account morphological analyses, morphometric data, and fine-scale skeletal structures analyses, together with molecular and reproductive evidence, and symbiont associations’ data the authors revised species within the genus.

1.4 The genus *Goniopora* de Blainville, 1830

The hard coral genus *Goniopora* de Blainville, 1830 belongs to the family Poritidae Gray, 1842, together with the genera *Porites* Link, 1807, *Stylaraea* Milne Edwards and Haime, 1851, and *Bernardpora* Kithano and Fukami, 2014. It is zooxanthellate, common and widespread from the tropical Indian and Pacific Ocean to the Red Sea, extending also to sub-temperate regions (Klunzinger 1879, Bernard 1903, Veron and Pichon 1986, 2000, Sheppard and Sheppard 1991).

*Goniopora* has been traditionally described on the basis of morphological features of the skeletons, and the coralla growth form. The genus was first described by Henri M. D. de Blainville (1830); in the 60th tome of his “Dictionnaire des Sciences Naturelles” he describes it as “*Animaux actiniformes, alongés, cylindriques, pourvus d’une couronne de plus de douze tentacules simples et assez longs, contenus dans des loges polygonales, assez irrégulières ou inégales, cannelées assez fortement à l’intérieur, échinulées sur les bords, se réunissant les unes à côté et au-dessus des autres, de manière à former un polypier glomérulé ou encroûtant, adhérent, extrêmement poreux et non fascicule*” [Translated as: “Actiniform, elongated, cylindrical animals provided with a crown of more than 12 simple and enough long tentacles, restrained inside polygonal lodges, that are quite irregular or unequal, heavily grooved in the inside, echinulate on the borders, set against and on top of each other, forming a glomerulus or encrusting skeleton, adherent, highly porous and non-fasciculated.”]
Goniopora colonies are variable in form and shape, displaying massive, columnar, and sometimes even encrusting forms. Corallites present thick porous walls, and calices are filled with trabecular septa joined by synapticulae, i.e., skeletal processes that extend between septa and unite the adjacent. The synapticulae may form one ring or more. Septa vary from 16 to 24, and are normally organized in 3 cycles, but this feature is not always clearly visible. One of the main characteristic of the genus is the presence of the “gonioporoid pattern” of septal fusion, (Bernard in 1903, Veron and Pichon 1982), even though the pattern is at times not discernable. When present, big pali are associated with the second septal cycle. The top of the wall and of the septa presents often granules and spikes. Calices can be shallow or very deep, and most of the time present a columella that, according to the depth of the calice, can be made of a tangle of filaments or be a compacted structure (Bernard 1903, Veron and Pichon 1982, 1986, 2000). In situ, Goniopora has the peculiar characteristic of having long living polyps extended both during day and night time, and this allows the discrimination of the genus with regards to confamiliar genera.

The taxonomic history of the genus indicates problems and mistakes starting nearly 200 years ago with Ehrenberg (1834), who suppressed the long-term validity of the genus, synonymizing it with Astrea Lamark, 1801. Dana (1848) formally resurrected Goniopora, placing it in the family Poritidae. Bernard (1903) published the most comprehensive review of the genus, in his “Catalogue of the Madreporarian Corals”. Despite more than 5 years of study, referring to both Goniopora and Porites, the author states: “I have no hesitation in asserting that in the present state of our knowledge coral species are indeterminable. The long list of names which were steadily growing as I proceeded to designate every apparent different form of Porites and
Goniopora in the old way got completely out of hand”. Indeed, in the attempt of describing corals belonging to the two genera, he abandoned the Linnean system of nomenclature and shifted to a numerical approach mainly based on geographic locality and colony growth form.

Several synonyms were used later on to refer to the genus, such as Litharea de Blainville, 1830, Rhodarea Milne Edwards and Haime, Tichopora Quelch, 1866, Poritipora Veron, 2000, Calathiscus Claereboudt and Al-Amri, 2004, and Machadoporites Nemésio, 2005. Due to the high plasticity of Goniopora’s small skeletal features, the designation of species boundaries was even more confusing. Starting from 1816, in addition to the type species of the genus G. pedunculata Quoy and Gaimard, 1833, more than 50 nominal species of Goniopora were morphologically described, probably overestimating the real diversity of the genus. Veron (2000) proposed that the morphology in situ of Goniopora polyps could be used as a key factor for species delimitation, contributing even more the already taxonomic confusion.

According to the World Register of Marine Species (http://www.marinespecies.org/, WoRMS), 32 extant species are ascribed to Goniopora at the moment, 24 of which are recognized by Veron (2000).

Although since Bernard’s work no major taxonomic revision of the genus has been undertaken, recent molecular analyses tried to clarify our understanding of this complex taxonomic case. Kitano et al. (2013) published a work on the phylogenetic and taxonomic status of the species G. stokesi Milne Edwards and Haime, 1851 from Japan. On the basis of two mtDNA markers, a fragment spacing between NAD5 and the first half of COI, and a region comprising three intergenic regions, tRNATrp and ATPase8, and the complete rDNA ITS region, they investigated the species’ phylogenetic status with regard to four morphologically similar species: G. lobata
Milne Edwards and Haime, 1851, *G. djiboutiensis* Vaughan, 1907, *G. columna* Dana, 1846, and *G. pendulus* Veron, 1985, integrating the genetics with detailed morphological, micromorphological and morphometric analyses of the considered morphological species. The molecular phylogeny resulting from the mtDNA regions showed less resolution than the nuclear marker regarding the position of *G. stokesi* with respect to the similar morphological species. The ITS phylogeny instead revealed that *G. stokesi* was genetically isolated from the other samples.

Subsequently, Kitano et al. (2014) published the most recent morpho-molecular phylogeny of the family Poritidae including samples spanning from Japan to the West Indian Ocean, using three COI barcoding regions and the complete ribosomal ITS. In particular with regards to the genus *Goniopora* they included 15 morphological species, namely *G. albiconus* Veron, 2000, *G. burgosi* Nemenzo, 1955, *G. cellulosa* Veron, 1990, *G. ciliatus* Veron, 2000, *G. columna*, *G. djiboutiensis*, *G. fruticose* Saville-Kent, 1891, *G. lobata*, *G. minor* Crossland, 1952, *G. norfolkensis* Veron and Pichon, 1982, *G. pendulus*, *G. somaliensis* Vaughan, 1907, *G. stokesi*, *G. tenuides* (Quelch, 1886), and *G. stutchburyi* Wells, 1955. The study had important implications at the family and genus level. It revealed fundamental divergence between Indian and Pacific morpho-species of *Goniopora*, such as *G. somaliensis*, suggesting the occurrence of convergent evolution of morphological features between the two original populations. Nevertheless, species level relationships within *Goniopora* remain unclear.

Despite these recent studies, our knowledge of *Goniopora* distribution and biodiversity is limited to specific areas in the Indo-Pacific. In particular, none of the recent morpho-molecular investigations included samples from the Red Sea area. In fact, although the Red Sea is an important region of biodiversity and endemism (Ekman 1953, Briggs 1974, Stehli and Wells
1971, Ormond and Edwards 1987), home to more than 50 genera of hermatypic corals, and was of major interest for early taxonomist (Forskål 1775, Ehrenberg 1834, Klunzinger 1879, Scheer and Pillai 1983, Sheppard and Sheppard 1991), its biodiversity has remained largely understudied. This is especially true since the beginning of the integrated systematics revolution. Moreover, the few recent works regarding this eco-region are mainly based on a small part of the Red Sea, namely the Gulf of Eilat/ Aqaba, which represent less than 2% of the Red Sea area (Berumen et al. 2013). With regards to *Goniopora* in particular, the most recent data of the genus from the Red Sea dates back to Sheppard and Sheppard 1991. The authors identified eight main morphological species of *Goniopora*, namely *G. somaliensis*, *G. djiboutiensis*, *G. tenella* (Quelch, 1886), *G. stokesi*, *G. columna*, *G. tenuidens*, *G. minor*, and *G. savignyi* (Dana, 1846), while Veron (2000) added Red Sea records of *G. lobata*, *G. burgosi*, *G. ciliatus*, *G. pearsoni*, *G. sultani*, and *G. planulata* (Ehrenberg, 1834) thus taking to a total of 14 the number of *Goniopora* morphospecies recorded in the region.

### 1.5 Aims of the work

The main aim of the present study is to clarify the species boundaries within the genus *Goniopora* in the Red Sea, using a combined morpho-molecular approach. In order to clarify the phylogenetic relationships within the genus, 199 samples from the Saudi Arabian Red Sea are genetically characterized using one mtDNA marker (i.e. the intergenic spacer between Cyt*b* and NAD2 - hereafter IGR), one rDNA region (ITS region), and two nuclear genes, ATPsβ and CalM. To provide additional clarification of the boundaries among these challenging taxa, the phylogenies are corroborated with three independent strategies for evaluating putative species with
molecular data. In this study *in situ* morphology, and skeletal macromorphology, and micromorphology are re-evaluated in light of genetic results. Finally, morphological diagnostic characters for species delimitation in *Goniopora* are discussed.
2. MATERIALS AND METHODS

2.1 Collection

A total of 199 *Goniopora* colonies were sampled in 27 different sites along the coast of the Saudi Arabian Red Sea between October 2014 and March 2015 (Fig. 1). Additionally, 11 coral colonies from Djibouti, collected between January and February 2010 during the Tara Oceans Expedition, were also included in the analyses. Digital images of living colonies were taken *in situ* with a Canon Powershot G15 or a Canon Powershot G11 in an Ikelite underwater housing. From each coral colony, a fragment between 10 cm$^3$ and 20 cm$^3$ was collected using a hammer and chisel. To preserve the tissue for molecular analyses, approximately 2 cm$^3$ of each coral specimen sampled in Saudi Arabia was preserved in 95% ethanol while the samples from Djibouti were stored in CHAOS solution (Sargent et al. 1986, Fukami et al. 2004). The rest of the corallum was bleached in a 2% sodium hypochlorite solution for 48 hours to remove soft tissues, rinsed with fresh water, and air dried for morphological analyses. Images of each corallum were taken with a Canon G15 or a Canon G11 digital camera.

2.2 Species identification

Specimens were identified based on skeletal morphology after detailed observation of corallite features using a Leica M80 microscope at the University of Milano-Bicocca, Milan, Italy (UNIMIB, Italy), and a Leica M205 FA stereomicroscope at King Abdullah University of Science and Technology (KAUST, Saudi Arabia). The number of septa, presence of gonioporoid pattern and pali, the number of denticles, calice depth, and columella dimensions, were analyzed with
reference to taxonomic original descriptions, type material, and bibliographic illustrations of species recorded from the Red Sea.

The following original descriptions were analyzed: deBlainville (1830), Dana (1846), Milne-Edwards (1860), Quelch (1886), Bernard (1903), Vaughan (1907), Nemenzo (1955), Veron and Pichon (1982), Veron (2000, 2002).

Museum type material of the following morpho-species was examined: *G. somaliensis*, *G. djiboutiensis*, *G. stokesi*, *G. columna*, *G. tenuidens*, *G. minor* (holotype), *G. savignyi*, and *Goniopora tenuidens* (syntype) from Natural History Museum (NHM), London, UK, collection; *G. somaliensis* and *G. djiboutiensis* holotypes, and *G. stutchburyi* syntype from United States National Museum of Natural History (USNM), Washington, USA; *G. lobata*, *G. gracilis*, *G. stokesi* holotypes from Museum National d’Historie Naturelle (MNHN), Paris, France; *G. albiconus*, *Poritipora paliformis*, *G. ciliata*, and *G. sultani* holotypes from Museum of Tropical Queensland (MTQ), Australia (Fig. 2, a-p) (Table 1). Morpho-species identification was corroborated following Sheer and Pillai (1976), Veron and Pichon (1982), Sheppard and Sheppard (1991), and Veron (2000, 2002).

Veron and Pichon (1982), Nishira and Veron (1985), and Veron (2000) included the morphology of the polyps in addition to skeletal features to support species identification, thus in our study we considered polyp morphology as a potential character for species identification.

All the samples collected in Saudi Arabia were deposited at KAUST, while the samples from Djibouti were deposited at UNIMIB.
Figure 1. Map of the Red Sea showing the sampling sites where *Goniopora* specimens were collected.
<table>
<thead>
<tr>
<th>Genus species</th>
<th>Taxonomic authority</th>
<th>Museum No.</th>
<th>Type status</th>
</tr>
</thead>
<tbody>
<tr>
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<td>Vaughan, 1097</td>
<td>USNM 21989</td>
<td>Holotype</td>
</tr>
<tr>
<td>Goniopora somaliensis</td>
<td>Vaughan, 1097</td>
<td>1991.6.4.45</td>
<td></td>
</tr>
<tr>
<td>Goniopora savignyi</td>
<td>(Dana, 1846)</td>
<td>1991.6.4.53</td>
<td></td>
</tr>
<tr>
<td>Goniopora djiboutiensis</td>
<td>Vaughan, 1097</td>
<td>USNM 21990</td>
<td>Holotype</td>
</tr>
<tr>
<td>Goniopora djiboutiensis</td>
<td>Vaughan, 1097</td>
<td>1991.6.4.46</td>
<td></td>
</tr>
<tr>
<td>Goniopora lobata</td>
<td>Milne Edwards, 1860</td>
<td>MNHN 497</td>
<td>Holotype</td>
</tr>
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<td>Goniopora sultani</td>
<td>Veron, DeVanittier, Turak, 2000</td>
<td>G55838</td>
<td>Holotype</td>
</tr>
<tr>
<td>Goniopora ciliatus</td>
<td>Veron, 2000</td>
<td>G55789</td>
<td>Holotype</td>
</tr>
<tr>
<td>Goniopora stokesi</td>
<td>Milne Edwards &amp; Haime, 1851</td>
<td>MNHN 502</td>
<td>Holotype</td>
</tr>
<tr>
<td>Goniopora albiconus</td>
<td>Veron, 2000</td>
<td>G55850</td>
<td>Holotype</td>
</tr>
<tr>
<td>Goniopora tenuidens</td>
<td>(Quelch, 1886)</td>
<td>1886.12.9.30</td>
<td>Syntype</td>
</tr>
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<td>Goniopora tenuidens</td>
<td>(Quelch, 1886)</td>
<td>1991.6.4.51</td>
<td></td>
</tr>
<tr>
<td>Goniopora minor</td>
<td>Crossland, 1952</td>
<td>1934.5.14.43</td>
<td>Holotype</td>
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<tr>
<td>Goniopora minor</td>
<td>Crossland, 1952</td>
<td>1991.6.4.52</td>
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<td>Goniopora gracilis</td>
<td>Milne Edwards &amp; Haime, 1849</td>
<td>MNHN495</td>
<td>Holotype</td>
</tr>
<tr>
<td>Poritipora paliformis</td>
<td>Veron, 2000</td>
<td>G55857</td>
<td>Holotype</td>
</tr>
</tbody>
</table>
Figure 2. Type specimen skeletal morphology of the *Goniopora* nominal species that were available and examined in this study: (a) USNM 21990 *Goniopora somaliensis* holotype; (b) 1991.6.4.46 *Goniopora somaliensis*; (c) 1991.6.4.53 *Goniopora savignyi*; (d) USNM 21990 *Goniopora djiboutiensis* holotype; (e) 1991.6.4.46 *Goniopora djiboutiensis*; (f) MNHN 497 *Goniopora lobata* holotype; (g) GS5838 *Goniopora sultani* holotype; (h) GS5789 *Goniopora ciliata* holotype; (i) MNHN 502 *Goniopora stokesi* holotype; (j) GS5850 *Goniopora albiconus* holotype; (k) 1886.12.9.304 *Goniopora tenuidens* syntype; (l) 1991.6.4.51 *Goniopora tenuidens*; (m) 1934.5.14.436 *Goniopora minor* holotype; (n) 1991.6.4.52 *Goniopora minor*; (o) MNHN495 *Goniopora gracilis* holotype; GS5857 *Poritipora paliformis* holotype.
2.3 DNA extraction

Total DNA was extracted from samples stored in ethanol using DNAeasy® Tissue kit (Qiagen Inc., Valencia, CA, USA). Samples were dried to remove ethanol and approximately 25mg of tissue was scrubbed from the surface. The extraction method is based on proteolytic cellular lysis through proteinase K, followed by selective binding of the DNA to a siliceous membrane in a spin column and washing with ethanol based buffers to remove contaminants and enzyme inhibitors. DNA was then eluted in a low-salt buffer. DNA was extracted from samples stored in CHAOS (4M Guanidine thiocyanate, 0.5% N-lauroyl sarcosine sodium, 25 mM Tris pH8, 0.1M 2-mercaptoethanol) using a phenol- chloroform-ethanol protocol. In detail: 200 μl of CHAOS solution was added in 2ml tubes with 400μl of phenol- chloroform- isoamyl alcohol 25 : 24 : 1, 200μl of PEB (phenol extraction buffer: 100 mM TrisCl-pH8, 10 mM EDTA, 0.1% SDS). and 0.8 μl of RNase A, and centrifuged at 14000 x g for five minutes. At the end of the centrifuge, three phases were distinguishable in the tube: a phenol phase at the bottom, containing degraded proteins soluble in phenol, an intermediate phase containing degraded proteins not soluble in phenol, and an upper layer with the DNA. Three more phenol- chloroform-isoamyl alcohol washes were made, at the end of which 50 μl of watery phase were added to 1.5 ml tubes with 50 μl of ammonium acetate 7.5 M and 500 μl of 100% ethanol, and stored for one hour at -20°C. The ammonium acetate binds the salts with H⁺ and NH3 ions, while the ethanol precipitates the DNA. Finally two washes with ethanol 80% were done, and the DNA was eluted with 50 μl of TE buffer, preheated at 65°C.

The quantity and quality of the extracted DNA was spectrophotometric estimated, using NanoDrop® 2000C spectrophotometer (Thermo Scientific, Wilmington, DE, USA).
DNA extraction was successful for all the samples stored in ethanol and CHAOS solution. For the samples stored in ethanol, NanoDrop® 2000C spectrophotometer revealed that DNA concentration was very high (around 100 ng/µl), and 260/230 and 260/280 ratios were approximately 2, indicating no contaminations from proteins, phenols, EDTA, and/or carbohydrates. The DNA concentration of samples extracted from CHAOS solution was lower than that obtained from the samples stored in ethanol (around 50ng/ µl). The values of 260/230 ratio were approximately 2 for all the samples, indicating again no contaminations, while 260/280 ratio values were variable between 0.5 and 1.5, underlying the presence of contamination from EDTA and/ or carbohydrates.

2.4 Amplification, sequencing, and alignment

Four DNA markers were amplified by Polymerase Chain Reaction, one mitochondrial region, and three nuclear genes. The mitochondrial fragment included a region spanning between the 3’ end of Cytochrome b and the 5’ end NAD2 (hereafter IGR). The three nuclear genes included a portion of the ribosomal DNA 18S- ITS1- 5.8S- ITS2-28S (ITS), a Calmodulin intron (CalM), and ATPaseβ gene (ATPSβ). All the amplifications were conducted in a 15 µl PCR volume composed of 0.2 µM of each primer, 1X Multiplex PCR Master Mix (Qiagen Inc., Valencia, CA, USA), and < 0.1ng DNA. The mitochondrial IGR was amplified using primers CSF3 (5’-CAT GTA GAG GGG TCA AAT AGT CC -3’) and CSR3 (5’-CCA GAT GAA AGT GCA CCT AA-3’) (Lin et al. 2011), and the following thermal cycle profile: an initial denaturation at 95°C for 15 min; 35 cycles to 94°C for 1 min, 55.4°C for 1 min, 72°C for 1.30 min; an ending elongation phase at 72°C for 5 min. For the
ITS region primers 1S (5'-GGT ACC CTT TGT ACA CAC CGC CCG TCG CT-3’) and 2SS (5'-GCT TTG GGC AGT CCC AAG CAA CCC GAC TC-3’) were used (Wei et al. 2006). PCR conditions were 95˚C for 15 min; 35 cycles to 94˚C for 1 min, 65˚C for 1.30 min, 72˚C for 1 min; 72˚ for 5 min. The Calmodulin intron was amplified using the primers CalMf (5’-GAG GTT GAT GCT GAT GGT GAG -3’) and CalMr2 (5’-CAG GGA AGT CTA TTG TGC C-3’) (Vollmer and Palumbi 2002) and the following thermal cycle: 95˚C for 15 min; 40 cycles to 94˚C for 30 sec, 45.9˚C for 30 sec, 72˚C for 1 min; 72˚C for 5 min. ATPSβf2 (5’-CGT GAG GGA AAT GAT TTC TAC CAT GAG ATG AT-3’) (Forsman et al. 2010) and ATPSβr2 (5’-CGG GCA CGG GCG CCG GGG GGT TCG TTC AT-3’) (Concepcion et al. 2009) were used to amplify ATPSβ. PCR conditions were: 95˚C for 15 min; 40 cycles at 94˚C for 30 sec, 48˚C for 30 sec, 72˚C for 30 sec; 72˚ for 5 min. A summary of all the primers used in the work is listed in Table2.

The yield of all PCR products was assessed using 1.5% agarose gel in 1 x TAE buffer. PCR reaction success was tested with a 1.5% agarose electrophoresis gel. The sizes of PCR products from the four DNA loci were compared with the 100 bp DNA ladder (Promega, Fitchburg, Wisconsin, USA) and they were in agreement with the expected molecular weights described in the literature where the same primers were employed or designed, i.e. Lin et al. (2011) for IGR, Kitano et al. (2013, 2014) for ITS region, Flot et al. (2008) for ATPSβ, Vollmer and Palumbi (2002) for CalM.

All the amplified markers were than purified using Illustra ExoStar (GE Heathcare, Buckinghamshire, UK) and directly sequenced in forward and reverse directions using an ABI 3730xl DNA Analyzer (Applied Biosystems, Carlsbad, CA, USA).
Forward and reverse sequences were assembled using SeqTrace 0.9.0 (Stucky 2012; available online at [https://code.google.com/p/seqtrace/](https://code.google.com/p/seqtrace/)) or CodonCodeAligner 3.7.0 (Codon Code Corporation, Dedham, MA, USA).

Chromatograms of the three nuclear genes showed intra-individual polymorphisms and double peaks, thereby were statistically analyzed using PHASE (Stephens et al. 2001; available online at [http://stephenslab.uchicago.edu/software.html](http://stephenslab.uchicago.edu/software.html)). In fact, working with nuclear markers for phylogenetic analyses implies dealing with haplotypes of diploid individuals that thus need to be phased, i.e. to identify the alleles that are co-located on the same chromosome (Browning and Browning 2011). The most common method used when the different haplotypes show the same length, is statistical haplotyping using the software PHASE (Stephens et al. 2001). This approach is based on a Bayesian method that allows to use *a priori* expectations about the pattern of haplotypes to be expected in natural populations in order to inform haplotype reconstruction (Stephens et al. 2001). Sequences showing alleles of different length were discarded. Haplotype phase can also be determined by using molecular approaches such as cloning and DGGE, but these are labor intensive, expensive, and may contain inaccuracies (Xu et al. 2002; Bos et al. 2007). SeqPHASE (Flot 2010; available online at [http://seqphase.mpg.de/seqphase/](http://seqphase.mpg.de/seqphase/)) was used to generate PHASE input files from FASTA and convert PHASE output files back into FASTA (Flot et al. 2010).

An additional 136 sequences of *Goniopora* from different localities in the Indian and Pacific Oceans were downloaded from GenBank (Kitano et al. 2013, 2014) and added to the dataset.
Final alignments of the four separated datasets were performed using E-INS-i option in MAFFT 7.130b (Katoh et al. 2002, Katoh and Standley, 2013) under default parameters and manually checked using BioEdit 7.2.5 (Hall 1999).

Table 2. List of primers used for this study

<table>
<thead>
<tr>
<th>Region</th>
<th>Primer</th>
<th>Sequence (5'-3')</th>
<th>Aprox. Size</th>
<th>Reference</th>
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<td>IGR</td>
<td>CSFR</td>
<td>CAT GTA GAG GGG TCA AAT AGT CC</td>
<td>130 bp</td>
<td>Lin et al. 2011</td>
</tr>
<tr>
<td></td>
<td>CSR3</td>
<td>CCA GAT GAA AGT GCA CCT AA</td>
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<td>ITS</td>
<td>1S</td>
<td>GGT ACC CTT TGT ACA CAC CGC CCG TCG CT</td>
<td>1000 bp</td>
<td>Wei et al. 2006</td>
</tr>
<tr>
<td></td>
<td>2SS</td>
<td>GCT TTG GCC GCC AGT CCC AAG CAA CCC GAC TC</td>
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<tr>
<td>ATPsβ</td>
<td>ATPSβf2</td>
<td>CGT GAG GGA AAT GAT TTC TAC CAT GAG ATG AT</td>
<td>200 bp</td>
<td>Forsman et al. 2010</td>
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<td></td>
<td>ATPSβr2</td>
<td>CGG GCA CGG GCG CCG GGG GGT TCG TTC AT</td>
<td></td>
<td>Concepcion et al. 2009</td>
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<tr>
<td>CalM</td>
<td>CalMf</td>
<td>GAG GTT GAT GCT GAT GGT GAG</td>
<td>250 bp</td>
<td>Vollmer and Palumbi 2002</td>
</tr>
<tr>
<td></td>
<td>CalMr</td>
<td>CAG GGA AGT CTA TTG TGC C</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

2.5 Haplotype network and phylogenetic analyses

In order to evaluate the relationships among different haplotypes a median-joining network analyses implemented in Network 4.613 (Bendelt et al. 1999) was applied to the nuclear region ITS, the CalM gene, and ATPsβ gene. This method is based on the assumption that the co-occurrence of alleles in diploid phase can be used to define groups of individuals sharing the same allele pool, hence groups of individuals not sharing any allele can be assumed to belong to different species (Doyle 1995). Following Flot et al. 2010, haplotype networks were converted into haplowebs, i.e., haplotype networks with additional connections between haplotypes co-occurring in heterozygous individuals, using Adobe Illustrator.
Since mitochondrial markers are not recombining, a single haplotype is found in each individual, and haplowebs are not suited to analyze them. Thus, individuals were simply sorted into haplogroups according to their mtDNA haplotype.

Phylogenetic trees were reconstructed for each of the four markers. A sequence of *Porites porites* (Pallas, 1776) was downloaded from GenBank and used as an outgroup for the mitochondrial analyses due to the close relationship of the genus *Porites* Link, 1807 to the genus *Goniopora* (Cairns 2001, Fukami et al. 2008). Following Kithano et al. 2014 a sequence of *Bernardpora stutchburyi* Wells, 1955 was used as outgroup for the ITS phylogenetic reconstruction. The CalM and ATPSβ topologies were rooted using midpoint selection. Indels, invariable, and parsimony informative sites were detected using DnaSp 5.10.1 (Librado and Rozas 2009) and indels where treated as a fifth character in phylogenetic analyses. MEGA 6.0 (Tamura et al. 2011) was used to calculate intra- and inter-pairwise distances and their standard deviations as $p$-distance with 500 bootstrap replicates. Single genes topologies were reconstructed using Bayesian Inference (BI), Maximum Likelihood (ML), and Maximum Parsimony as implemented in MrBayes 3.2 (Ronquist and Huelsenbeck 2003), PAUP* 4.0b10 (Swofford 2003), and PhyML 3.0 (Guindon and Gascuel 2003), respectively. The best-fit substitution model for each locus was determined using Akaike Information Criterion (AIC) as implemented in MrModeltest 2.3 (Nylander 2004) in conjunction with PAUP 4.0b10 (Swofford 2003). IAC suggested the following models as most suitable: AKY+I for IGR, ITS and ATPSβ, and AKY+G for CalM.

Bayesian Inference analysis consisted of four parallel Markov Chains Monte Carlo (MCMC) implemented for 4000000 generations for the mitochondrial IGR, 15000000 generations for the
ITS region, and 4500000 generations for ATPsβ and CalM genes, saving a tree every 1000 generations and discarding the first 2500 trees as burn-in. To determine if the analyses achieved stationarity we visualized log-likelihood scores and model parameter values across each run using Tracer 1.6 (Drummond and Rambaut 2007). Clade support was assessed based on posterior probability.

Maximum Likelihood analyses were reconstructed using the default parameters of 500 bootstrap replicates to verify the robustness of the internal branches of the trees, while Maximum Parsimony was conducted using the TBR branch swapping method with 1000 replications, random addition for 10 replicates, nchuck = 100, chuckscore = 1. Node supports were obtained with 1,000 bootstrap replicates.

2.6 Molecular species delimitation

To determine putative molecular species clusters in our dataset, we used three independent single locus species delimitation approaches, Automatic Barcoding Gap Discovery (ABGD) (Puillandre et al. 2012), Poisson-Tree processes (PTP) (Zhang et al. 2013), and generalized mixed Yule coalescent (GMYC) (Pons et al. 2006, Fujisawa and Barraclough 2013).

All the methods were applied for each dataset because no mitochondrial or nuclear genes have been proposed as a standard barcode for scleractinian corals so far. On one hand, the slow evolution rate of the mitochondrial genome of hard corals does not allow the use of COI as barcoding gene (Huang et al., 2008). On the other hand, although ITS region has been frequently used to infer phylogenetic relationships between closely related species (Wei et al., 2006), its
utility has been criticized in some genera such as *Acropora* due to high intra-individual polymorphisms and the potential presence of ancient lineages (Vollmer and Palumbi, 2004).

ABDG is a tool that determines groups of candidate species directly on the basis of pairwise genetic distances instead of hypothesizing *a priori* species clusters. The algorithm defines a threshold of nucleotide distance below which specimens are considered conspecific and above which they are considered as belonging to different species. A key assumption is that individuals of the same species are more similar molecularly than individuals belonging to different species.

All the alignments were imported in MEGA 6.0 to compute matrix of pairwise genetic distances using the p-distance, the Kimura 2-parameter (K2P) and the Jukes-Cantor (JC69) models. These matrices were further used as input files on the ABGD webpage (http://wwwabi.snv.jussieu.fr/public/abgd/abgdweb.html) and a range of different settings were tested, showing concordant species delimitations results. Therefore, we set parameters as follows: \( P_{\text{min}} = 0.001, P_{\text{max}} = 0.1, \) Steps = 50, \( X = 1.5 \) and Nb bins = 20.

The Poisson tree process model and the generalized Yule-coalescent model are two tree-based species delimitation methods. The PTP method relies on coalescence theory and uses the branch lengths to estimate the average expected substitution number per site between two branching events. Assuming that each substitution has a small probability of generating a speciation event, nucleotide variations between species are expected to be higher than within species (Zhang et al. 2013). This method requires a regular gene tree as input. Following the recommendations by Tang et al. (2014), we adopted the use of model-based gene trees generated with PhyML for PTP analyses. We ran PTP analyses for 400000 MCMC generations,
with thinning value = 100 and burn-in = 0.25. We visually confirmed the convergence of the MCMC chain as recommended by Zhang et al. (2013).

The GMYC approach combines models of stochastic lineage growth (Yule models) with coalescence theory (Pons et al. 2006, Fujisawa and Barraclough 2013). It measures the degree of genetic clustering by detecting a threshold value at the transition of branching patterns that are characteristic of interspecific-level processes versus intraspecific-level processes of molecular evolution. The method starts with an inferred ultrametric gene tree and attempts to model the point on a time calibrated phylogeny where this transition occurs. The ultrametric trees were obtained with BEAST 1.8.2 (Drummond et al. 2012) after removing identical haplotypes. A coalescent tree prior and the heterogeneity of the mutation rate across lineages were set under an uncorrelated lognormal relaxed clock. Analysis was run for 50 million generations, with a sampling frequency of 1000. After checking adequate mixing and convergence of all runs with Tracer 1.6, the first 25% trees were discarded as burn-in and the maximum clade credibility tree was computed using TreeAnnotator 1.8.2 (Drummond et al. 2012). The resulting ultrametric tree was imported into R 3.1.3 (R Core Team 2014) and GMYC analyses were run using the Splits (Ezard et al. 2009) and Ape (Paradis et al. 2004) libraries. Both the single threshold ST-GMYC (Pons et al. 2006) and multiple threshold MT-GMYC (Monaghan et al. 2009) methods were evaluated on all the datasets.

2.7 Morphological analyses

2.7.1 Macromorphological analyses
In situ polyp morphology and skeleton morphology were analyzed in light of molecular results for an analysis of the morphological features of the specimens grouped by genetic markers.

For each voucher specimen, three images were taken with a G15 camera at KAUST, and with a Leica IC80HD camera at UNIMIB. Additionally, skeletal morphology of a subset of 166 specimens included in molecular analyses was analyzed using a Leica M205 FA stereo-microscope. Three 0.73x non-overlapping digital images were shot for each sample using a reference scale.

Skeletal features traditionally used for species identification (Vaughan and Wells 1943, Wells 1956, Budd and Stolarski 2009) were observed, namely the corallites arrangement and shape, the number of septa and septa organization, including the presence of the gonioporoid pattern of fusion, the development of pali and paliformes lobes, and the depth of the calice. Polyp oral disc dimensions and color, stalk and tentacle length, and the shape of tentacle tips were analyzed for each specimen.

2.7.2 Micromorphological analyses

Micromorphology of skeletal structures was investigated using scanning electron microscopy (SEM). For SEM imaging, fragments of coral specimens were ground, mounted on stubs using silver glue, sputter coated using Au–Pd, and examined using a Quanta 200 FEG SEM at KAUST. The presence of the columella and the arrangement of columellar threads, the presence and development of spines and granules on septa, on septal face, on septa fusion points and on corallites fusion points, and the number of denticles were evaluated in each examined specimen.
2.7.3 Morphometric analyses

On the basis of the digital images collection undertaken with Leica M205 FA stereo-microscope with a reference scale, three linear variables were measured on nine different corallites for each colony using ImageJ 1.49 (Rasband 1997): the longest calice diameter (CaD), the longest columella diameter (CoD), and the distance between adjacent centroids (CD) (Fig. 3, a-c). For each character the specimen mean was calculated from nine replicates for each colony.

A principal component analyses (PCA) was performed with the software Primer 5.2.9 (Primer-E Ltd. Plymouth, UK). The biplot of the first two principal components was examined in order to verify whether any distinct group of specimens could be distinguished and if groups matched with a priori morpho-species identifications and/or molecularly defined groups of specimens.
Figure 3. Morphological characters measured in Goniopora specimens: (a) long diameter of calice (CaD); (b) long diameter of columella (CoD); (c) centroids distances (CD).
3. RESULTS

3.1 Species identification

On the basis of morphological skeletal features the 199 collected colonies were assigned to a total of nine different morphospecies. In particular, 46 colonies of *Goniopora somaliensis*, seven of *G. savignyi*, 45 of *G. djiboutiensis*, 43 of *G. lobata*, two of *G. stokesi*, 26 of *G. albiconus*, four of *G. tenuidens*, four of *G. gracilis*, and 22 of *G. minor* were identified. Moreover, *in situ* morphology of the living polyps was compared to that shown in Veron and Pichon (1982), Nishira and Veron (1985), and Veron (2000). The identifications for each specimen and the collection localities are reported in Table 3.

Enetrusting colonies with shallow corallites smaller than three mm in diameter, and small, short polyps were identified as *G. somaliensis*. The collected material, identified based on Vaughan’s (1907) original description and the deposited type specimen (USNM 21989) (Fig. 2, a-b), also matched Veron and Pichon’s (1982) description and pictures of *G. somaliensis* skeletal morphology (pp. 81-82, figs. 148-151, and 154) and *in situ* morphology (p. 144, figs. 297-299). However, specimens in figs. 152-153 (pp. 181-182) in Veron and Pichon (1982) have a different morphology. The skeletal and live polyp morphology of the specimens collected for this study (Fig. 12, a-b-e-f) was consistent with Sheppard and Sheppard’s (1991) (p. 62, fig. 52 a, b, samples 1991.6.4.44, 1991.6.4.45, pl. 40, p. 79) and Veron’s (2000) description and pictures of *G. somaliensis* (p. 358, figs. 1-6). Moreover, the examined material showed morphologic affinities with the holotype of *G. pearsoni* (G55790) (Veron 2002), even though the living morphology of the latter reported by Veron (2000) (p. 365, figs. 4-6) differed from the one of the collected specimens.
Specimens with shallow corallites up to three mm, and polyps of medium length and size were attributed to *G. savignyi* on the basis of Dana’s (1846) original description. The holotype of the species could not be examined. The skeletal morphology of the samples identified as *G. savignyi* (Fig. 2, c) was consistent with Scheer and Pillai’s (1983) (p. 95, pl. 23) and with Sheppard and Sheppard’s (1991) description and pictures of *G. savignyi* (p. 66, fig. 59, sample 1991.6.4.53). Finally, the examined material showed morphologic affinities with Veron’s (2000) skeletal and *in vivo* description and pictures of *G. savignyi* (p. 376, figs. 1-4).

Large columnar colonies that presented shallow corallites up to five mm diameter and medium sized polyps were attributed to *G. djiboutiensis* based on Vaughan’s (1907) original description and on the deposited type specimen (USNM 21990) (Fig. 2, d-e). The collected samples matched Veron and Pichon’s (1982) description and pictures of *G. djiboutiensis* (pp. 67-70, figs. 119-124), even though the morphology of the living polyps reported (p. 142, figs. 283-288) showed affinities with the morphology present in other morphospecies, and thus could not be used to discriminate the collected specimens among others. The skeleton morphology of the specimens was consistent with Sheppard and Sheppard’s (1991) description and picture of *G. djiboutiensis* (p. 62, fig. 53, sample 1991.6.4.46) but also shared morphological features with the reported picture of *G. tenella* skeleton (p. 63, fig. 54, sample 1991.6.4.47). Finally, the collected colonies showed affinities with Veron’s (2000) description and pictures of *G. djiboutiensis* morphospecies considering both the skeleton and *in vivo* morphology (p. 351, figs. 3-6). The specimens had similarities with *G. sultani* holotype (G55838) (Veron 2002) and showed affinities with *in situ* morphology of the latter reported by Veron (2000) (p. 355, fig. 4).
Columnar colonies with deep corallites up to five mm diameter, no pali, and medium sized polyps were identified as *G. lobata* on the basis of Milne-Edwards’ (1860) original description and the species holotype (MNHN 497). The collected samples matched Veron and Pichon’s (1982) description and pictures of *G. lobata* skeletons and living polyps (pp. 74-77, figs. 131-138; pp. 142-143, figs. 289-292), and also shared skeletal features and polyps morphology with specimens identified as *G. columna* in the same study (pp. 77-70, figs. 140-147; pp. 143, figs. 293-296). The collected samples showed similarities with Sheppard and Sheppard’s (1991) description and pictures of *G. columna* both in skeletons and in living polyps morphology (p. 66, fig. 56, sample 1991.6.4.50; p. 79, pls. 42-43). The examined material matched with Veron’s (2000) description and pictures of *G. lobata* dried skeletons and living colonies (pp. 354-355, figs. 1-4), and also showed affinities with the ones identified as *G. columna* in the same study (p. 356-357, fig. 1-6). Given the taxonomic confusion occurring in the taxonomic references with respect to *G. lobata* and *G. columna*, the original description of *G. columna* from Dana (1846) was analyzed. Although the *G. columna* description matches the collected morphologies, and pre-dates that of *G. lobata*, the holotype of *G. columna* was not available for analyses, thus it was decided in this study to use *G. lobata* as the identification for the samples which align with *G. lobata* and *G. columna* literature descriptions.

Hemispherical, attached, or free living colonies with deep corallites up to six mm diameters and big and long polyps were identified as *G. stokesi* on the basis of Milne-Edwards and Haime’s (1851) description of *G. stokesi* and holotype analyses (MNHN 502). The collected samples matched Veron and Pichon’s (1982) description and pictures of *G. stokesi* (pp. 70-73, figs. 125-130), but no picture of living colonies is reported. The examined specimens showed affinities
with Sheppard and Sheppard’s (1991) description and skeletal pictures of *G. stokesi* (p. 62, fig. 55 a-b, samples 1991.6.4.48, 1991.6.4.49), and were consistent with Veron’s (2000) description and pictures of *G. stokesi* skeletons and living colonies (pp. 352-353, figs. 1-5). Moreover, the samples shared features with *G. pendulus* (p. 350, figs. 1-2) both in the skeletal morphology and in the size of the living polyps.

Hemispherical or encrusting colonies with corallites of medium depth, up to 3.5 mm in diameters, prominent septa and pali, and big polyps with wide white oral cones were identified as *G. tenuidens* on the basis of Quelch (1886) original description and syntype specimen study (1886.12.9.304). *Goniopora tenuidens* was originally classified as belonging to the genus *Rhodaraea* by Milne Edwards and Haime (1849), but later was moved into the genus *Goniopora* by Bernard (1898). Following his classification of samples by locality, Bernard refers to this morphospecies as *G. moluccas* (p. 266, fig. 7, pl. IV). The collected samples matched Veron and Pichon’s (1982) description and pictures of the skeleton of *G. tenuidens* (pp. 83-86, figs. 55-61) but the morphology *in vivo* of the collected specimens was not consistent with the pictures reported by the authors for *G. tenuidens* (p. 144, figs. 300-303). Sheppard and Sheppard’s (1991) description and pictures of *G. tenuidens* skeletal features (p. 66, fig. 57, sample 1991.6.4.51), and Veron’s (2000) description and picture of *G. tenuidens* (p. 364) resembled the collected specimens skeletal morphology. *In situ* polyps illustrations of *G. tenuidens* (p. 364, figs. 1-6) by Veron (2000) show a different morphology from that of the examined material.

Encrusting colonies with medium depth polygonal corallites, with corallite diameter up to 4.7 mm, and big polyps with wide, white oral cones were identified as *G. albiconus* on the basis of
Veron’s (2002) original description and deposited holotype (G55850). Both skeletal features and *in situ* colony morphology matched Veron’s (2000) pictures of *G. albicus* (p. 361, figs. 1-6).

Encrusting and massive colonies with medium depth small calices, prominent pali forming a crown in the middle of the corallites, and small and short polyps were identified as *G. minor* based on Crossland’s (1952) original description and the deposited holotype (1934.5.14.436).

Veron and Pichon (1982) describe *G. minor* as a synonym of *G. pedunculata*. Their pictures of skeletal and *in situ* morphology (p. 86, figs. 162-168; p. 144, figs. 304-305) did not show affinities with the collected specimens nor with the *G. minor* holotype. The holotype of *G. pedunculata* was not accessible for this study, thus we can not evaluate the synonymy of the two species.

The morphology of the collected specimens was concordant with Sheppard and Sheppard’s (1991) description of *G. minor* and the skeletal picture therein (p. 66, fig. 58, sample 1991.6.4.52). The description and pictures of *G. minor* (p. 365, figs. 1-5) by Veron (2000) present a different morphology. The skeletal morphology of the samples identified as *G. minor* in this study was concordant with Veron’s (2002) description and holotype of *Poritipora paliformis* (G55857). No pictures of living colonies of *P. paliformis* are reported by the author.

Samples were assigned to *G. gracilis* on the basis of the deposited holotype (MNHN495) but no further descriptions of the species were found in the examined literature.
Table 3. List of the material examined in this study. For each specimen code, morphological identification, sampling locality, and molecular markers used for the genetic analyses are listed.

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3.2 Phylogenetic and haplotype network analyses

3.2.1 Mitochondrial DNA markers

A total of 199 *Goniopora* specimens were successfully amplified for the mitochondrial region and used for haplotype network reconstruction and phylogenetic analyses. The final alignment consisted of 1238bp and included 90 variable sites, 40 of which were singleton sites and 50 parsimony informative sites. A total of 91 mutations, considering only synonyms and non-synonyms mutations, were found.

A total of 14 different haplotypes were recovered within the different *Goniopora* morphospecies collected in the Saudi Arabian Red Sea and Djibouti (Appendix 1). Using a median-joining analysis, six well-differentiated clusters, corresponding to six different lineages (clade I to VI hereafter), were resolved with strong statistical support (Fig. 4). Haplotypes that differed by more than five bp were assigned to different groups, and no haplotypes were shared between different clusters. Within each haplogroup the percentage of the different morphological
species clustered in the same lineage is shown and color-coded in Fig. 4. The proportion of each haplotype is represented by different-sized circles (Fig. 4). Cluster I and VI consisted of *G. somaliensis* and *G. savignyi* morphospecies, cluster II contained *G. djiboutiensis* and *G. lobata*, in cluster III included *G. stokesi*, cluster IV consisted of *G. tenuidens* and *G. albiconus*, and cluster V contained *G. minor* and *G. gracilis* morphospecies.

Topologies from BI, ML, and MP analyses were largely congruent, with no contrasting signals (Appendix 2). Only the topology resulting from the Bayesian analysis is shown, with branch support indicated by Bayesian posterior probability (PP\(_{BI}\)), ML bootstrapping support (BT\(_{ML}\)), and MP bootstrapping support (BT\(_{MP}\)). The phylogenetic reconstruction was in agreement with the median-joining network analyses, showing again the presence of six well-differentiated highly supported clades (clade I: PP\(_{BI}\) = 0.94, BT\(_{ML}\) = 97, BT\(_{MP}\) = 99; clade II: PP\(_{BI}\) = 1, BT\(_{ML}\) = 100, BT\(_{MP}\) = ; clade III: PP\(_{BI}\) = 1, BT\(_{ML}\) = 93, BT\(_{MP}\) = 97; clade IV: PP\(_{BI}\) = 0.92, BT\(_{ML}\) = 93, BT\(_{MP}\) = 90; clade V: PP\(_{BI}\) = 0.98, BT\(_{ML}\) = 99, BT\(_{MP}\) = 100; clade VI: PP\(_{BI}\) = 0.87, BT\(_{ML}\) = 95, BT\(_{MP}\) = 99). Average pairwise genetic distances are reported in Appendix 3.

Single-locus species delimitation results from ABGD, PTP, and GMYC approaches are summarized in Fig. 5. The partitions delimited by these three independent methods were mostly congruent and recovered a similar subdivision of sequences in putative lineages. All analyses delimited the following lineages: *G. somaliensis* + *G. savignyi* group, *G. djiboutiensis* + *G. lobata* group, *G. albiconus* + *G. tenuidens* group, *G. minor* + *G. gracilis* group, and the *G. stokesi* group.

In the ABGD analysis, the distribution of pairwise genetic distance using a \(P_{max}\) value = 0.1, regardless of the substitution model used (Jukes-Cantor and Kimura), displayed five to six
lineages (depending on the gap width parameter). For gap width values ranging from 1 to 2% the ABGD analyses inferred six distinct groups, while higher threshold values resulted in five lineages, nesting all specimens identified as *G. somaliensis* and *G. savignyi* into a single group (Fig. 5). The six lineages defined by ABGD approach were also in agreement with the ones proposed by the PTP. Although the PTP identified six main groups (Fig. 5), the mean support value of the partitions was low (0.34 ± 0.2), ranging from 0.75 (*G. stokesi* cluster) to 0.15 (*G. albiconus* and *G. tenuidens* cluster). Concerning the GMYC approach, a lineage-through-time plot based on the BEAST ultrametric tree revealed a sudden increase in branching rate towards the present, likely corresponding to the switch from interspecific to intraspecific branching events (Fig. 5). The likelihood of the null model ($L_0 = 86.72$) was lower than the maximum likelihood of the ST-GMYC model ($L_{\text{single}} = 89.26$, $L_{\text{ratio}} = 5.08$, $p$-value = 0.078) and, according to the latter, the transition from speciation to coalescence resulted in a partition with seven putative species, adding one group to the ones identified by the ABGD. In particular, the GMYC model identified a third lineage within *G. somaliensis* and *G. savignyi* cluster. The MT-GMYC analysis yielded similar results to ST-GMYC and recovered the same seven lineages, according to the lineage-through-time plot and the likelihood function estimated by the software R ($L_0 = 86.72$, $L_{\text{single}} = 89.26$, $L_{\text{ratio}} = 5.08$, $p$-value = 0.078).
Figure 4. Median-joining haplotype network for *Goniopora* from the Red Sea inferred from the mitochondrial intergenic spacer region (IGR). The size of the circles is proportional to the frequencies of specimens sharing the same haplotype. Colors within the circles indicate the morphotypes of the individuals in which each haplotype was detected. Mutations are shown on the branches (numbers refer to positions in the alignments), and haplotype clusters are enclosed in dashed circles.
Figure 5. On the left: coalescent tree inferred from the mitochondrial intergenic spacer region (IGR) for Goniopora from the Red Sea, obtained through BEAST analysis; the tree is being used for representation, but is not intended to be a definitive phylogenetic tree for the genus; On the right: summary of putative species delimitation drawn by median-joining network analyses, ABGD, PTP, sGMYC, mGMYC, phylogeny inferred through Bayesian Inference, and morphology (one column per method).
3.2.2 Nuclear DNA markers

*ITS region*

A total of 195 *Goniopora* samples from the Saudi Arabian Red Sea and Djibouti were successfully amplified for the ribosomal ITS region and used for haplotype network and phylogenetic analyses. An additional 136 *Goniopora* sequences published by Kitano et al. (2013, 2014) were downloaded from Genbank and added to the dataset.

A total of 88 samples collected for this study were homozygotes for the ITS region, and the sequences produced did not show any intraspecific polymorphism. The remaining 107 samples were heterozygotes for the ITS region, and the sequences showed multiple peaks in the electropherograms due to the presence of intra-individual polymorphisms in the variable regions ITS1 and ITS2. Chromatograms showed only double peaks. No triple or quadruple peaks were observed, thus allowing the detection of two main variants for each samples. In particular, 60 sequences showed two haplotypes with only one bp difference (one double peak in the chromatogram), while 47 showed haplotypes of the same length with more than one bp difference. These sequences were analyzed in a Bayesian framework using SeqPHASE in order to infer the most likely haplotypes. No samples presented sequences with haplotypes of different length.

The final alignment consisted of 986 bp and included 251 variable sites, 103 of which were singleton sites and 148 parsimony informative sites. A total of 331 mutations, considering only synonyms and non-synonyms mutations, were found.
A total of 155 different haplotypes were recovered from the ITS region within the different *Goniopora* morphospecies collected in the Saudi Arabian Red Sea, Djibouti, and several other localities in the Indo-Pacific (Appendix 4). Using a median-joining analysis eight well-differentiated clusters corresponding to eight different lineages were resolved with strong statistical support (Fig. 6). Cluster I consisted of *G. somaliensis* and *G. savignyi*, cluster II contained *G. djiboutiensis* and *G. lobata*, in cluster III consisted of *G. stokesi*, cluster IV consisted of *G. tenuidens* and *G. albiconus*, cluster V was composed of *G. minor* and *G. gracilis*, whereas cluster VI identified in the IGR analyses was not recovered in the network reconstruction based on the ITS region. All samples in cluster VI based on IGR were grouped within cluster I using ITS region. Clusters VII, VIII, and IX are only comprised of samples from the Pacific Ocean. In cluster VII were nested samples identified by Kitano et al. (2013, 2014) as *G. cf djiboutiensis*, *G. pendulus*, and *G. cf cellulosa*. Cluster VIII grouped *G. cf fruticosa*, *G. norfolkensis*, and *G. somaliensis* together, while cluster IX consisted of samples identified as *G. tenuidens*.

Topologies from BI, ML, and MP analyses were largely congruent, with no contrasting signals (Appendix 5). The phylogenetic reconstruction was in agreement with the median-joining network analyses, showing again the presence of eight well-differentiated, highly supported clades (clade I: PP$_{BI}$ = 1, BT$_{ML}$ = 99, BT$_{MP}$ = 100; clade II: PP$_{BI}$ = 0.62, BT$_{ML}$ = 84, BT$_{MP}$ = 75; clade III: PP$_{BI}$ = 0.99, BT$_{ML}$ = 99, BT$_{MP}$ = 100; clade IV: PP$_{BI}$ = 1, BT$_{ML}$ = 99, BT$_{MP}$ = 98; clade V: PP$_{BI}$ = 1, BT$_{ML}$ = 93, BT$_{MP}$ = 100; clade VII: PP$_{BI}$ = 0.73, BT$_{ML}$ = 73, BT$_{MP}$ = 100; clade VIII: PP$_{BI}$ = 0.92, BT$_{ML}$ = 73, BT$_{MP}$ = 79; clade IX: PP$_{BI}$ = 1, BT$_{ML}$ = 100, BT$_{MP}$ = 100). Three haplotypes (H85, H86, H87) nested within clade VIII according to the median-joining reconstruction, were nested within clade IV with BI analysis. Average pairwise genetic distances are reported in Appendix 3.
Single-locus species delimitation results from ABGD, PTP, and GMYC approaches are summarized in Fig. 7. In the ABGD analysis, the distribution of pairwise genetic distance using a P values ranging from 0.001 and 0.1, whatever the substitution model used (Jukes-Cantor and Kimura), displayed nine lineages for gap width values ranging from 4 to 5% (Fig. 7). The delimitated candidate lineages correspond to the network clusters (clade from I to IX) with the exception of cluster III comprising \textit{G. stokesi} that was spitted by ABGD analysis into two different groups.

The PTP identified 12 candidate molecular lineages, detecting three distinct groups into clade VIII, and two within clade VII (Fig. 7). Also for the ITS region, the mean support value of the partitions identified by the PTP was low (0.42 ± 0.18). In particular, the presence of a the second lineage within clade VII was scarcely supported (0.074), while the partitions that the analysis identifies within clade VIII had support values close to the mean support value (\textit{i.e.}, 0.296, 0.245, 0.303).

The GMYC predicted a higher number of molecular lineages in comparison with the results of the other species delimitation methods. The likelihood of the null model (L_o = 1430.251) was lower than the maximum likelihood of the ST-GMYC model (L_{single} = 1441.05, L_{ratio} = 21.59, p-value = 2.042) and, according to the latter, the transition from speciation to coalescence resulted in a partition with 14 putative species, adding six groups to the ones identified by the ABGD. In particular, the GMYC model detected four lineages within clade II, two lineages within clade III, two lineages within clade V, and two lineages within clade VIII. The MT-GMYC analysis yielded similar results to ST-GMYC and recovered again the same 14 effective lineages,
according to the lineage-through-time plot and the likelihood function estimated by the software R \((L_0 = 1430.251, L_{\text{single}} = 1445.639, L_{\text{ratio}} = 30.77, p\text{-value} = 2.074)\).
Figure 6. Median joining haplweb for Goniopora from the Red Sea, Japan, and Malaysia, inferred from the ITS region. The size of the circles is proportional to the frequencies of specimens sharing the same haplotype. Colors within the circles indicate the morphotypes of the individuals in which each haplotype was detected. Colored curves connect haplotypes that co-occur in at least one individual. The black solid circles are indicative of mutations that differentiate each haplotype, and haplotype clusters are enclosed in dashed circles.
Figure 7. On the left: coalescent tree inferred from ITS region for *Goniopora* from the Red Sea, obtained through BEAST analysis; the tree is being used for representation, but is not intended to be a definitive phylogenetic tree for the genus; On the right: summary of putative species delimitation drawn by median-joining network analyses, ABGD, PTP, sGMYC, mGMYC, phylogeny inferred trough Bayesian Inference, and morphology (one column per method).
A total of 175 sequences of *Goniopora* from the Saudi Arabian Red Sea and Djibouti were successfully amplified for ATPsβ gene and used for haplotype network and phylogenetic analyses. Of these, 109 samples were homozygotes for the amplified gene, showing one single haplotype, 37 samples were heterozygotes for ATPsβ and presented two haplotypes with one bp difference, and the remaining 29 samples showed two haplotypes with more than one bp difference. No samples presented haplotypes of different length.

The final alignment consisted of 695bp and included 41 variable sites. A total of 48 mutations, considering only synonyms and non-synonyms mutations, were found.

From the dataset, 24 different haplotypes were identified (Appendix 6). Using a median-joining analysis five well-differentiated clusters corresponding to five different lineages were resolved with strong statistical support (Fig. 8). Cluster I consisted of *G. somaliensis* and *G. savignyi*, cluster II was comprised of *G. djiboutiensis* and *G. lobata*, cluster III contained *G. stokesi*, cluster IV consisted of *G. tenuidens* and *G. albiconus*, and cluster V was comprised of *G. minor* and *G. gracilis*. As recovered using the ITS region, all the samples that nested in cluster VI in the IGR network were now grouped in cluster I.

Topologies from BI, ML, and MP analyses were largely congruent, with no contrasting signals (Appendix 7). The phylogenetic reconstruction was in agreement with the median-joining network analyses, showing again the presence of five well differentiated highly supported clades (clade I: PP_{BI} = 0.98, BT_{ML} = 82, BT_{MP} = 100; clade II: PP_{BI} = 1, BT_{ML} = 90, BT_{MP} = 100; clade III: PP_{BI} = 1, BT_{ML} = 97, BT_{MP} = 100; clade IV: PP_{BI} = 0.98, BT_{ML} = 86, BT_{MP} = 86; clade V: PP_{BI} = 1, BT_{ML} = 97, BT_{MP} = 100). Average pairwise genetic distances are reported in Appendix 3.
Single-locus species delimitation results from ABGD, PTP, and GMYC approaches are summarized in Fig. 8. The partitions delimitated by these three independent methods were mostly congruent and recovered a similar subdivision of sequences in putative lineages. All analyses delimitated the following candidate entities: *G. somaliensis* + *G. savignyi* group, *G. djiboutiensis* + *G. lobata* group, *G. albiconus* + *G. tenuidens* group, *G. minor* + *G. gracilis* group, and the *G. stokesi* group. In the ABGD analysis, the distribution of pairwise genetic distance using a $P_{\text{max}}$ value = 0.1, whatever the substitution model used (Jukes-Cantor and Kimura), displayed five lineages for gap width values ranging from 7 to 10% (Fig. 9). These five lineages defined by ABGD approach were also in agreement with the ones proposed by the PTP. Although the PTP identified the five main groups (Fig. 9), the mean support value of the partitions was low (0.491 ± 0.25), ranging from 0.93 (*G. stokesi* cluster) to 0.19 (*G. somaliensis* + *G. savignyi* cluster). Concerning the GMYC approach, a lineage-through-time plot based on the BEAST ultrametric tree revealed a sudden increase in branching rate towards the present, likely corresponding to the switch from interspecific to intraspecific branching events (Fig. 9). The likelihood of the null model ($L_0 = 129.94$) was lower than the maximum likelihood of the ST-GMYC model ($L_{\text{single}} = 134.61$, $L_{\text{ratio}} = 9.34$, $p$-value = 0.009) and, according to the latter, the transition from speciation to coalescence resulted in a partition with five putative lineages. The MT-GMYC analysis yielded similar results with respect to ST-GMYC and recovered six effective lineages, according to the lineage-through-time plot and the likelihood function estimated by the software R ($L_0 = 129.43$, $L_{\text{single}} = 134.75$, $L_{\text{ratio}} = 9.62$, $p$-value = 0.008), adding one further lineage within clade IV.
Figure 8. Median joining haplomega for *Goniopora* from the Red Sea inferred from ATPβ. The size of the circles is proportional to the frequencies of specimens sharing the same haplotype. Colors within the circles indicate the morphotypes of the individuals in which each haplotype was detected. Colored curves connect haplotypes that co-occur in at least one individual. Mutations are shown on the branches (numbers refer to positions in the alignments), and haplotype clusters are enclosed in dashed circles.
Figure 9. On the left: coalescent tree inferred from ATPsβ for *Goniopora* from the Red Sea, obtained through BEAST analysis; the tree is being used for representation, but is not intended to be a definitive phylogenetic tree for the genus; On the right: summary of putative species delimitation drawn by median-joining network analyses, ABGD, PTP, sGMYC, mGMYC, phylogeny inferred through Bayesian Inference, and morphology (one column per method).
A total of 184 samples were successfully amplified for the CalM gene and used for haplotype network and phylogenetic analyses. Of these, 76 samples were homozygotes for the amplified gene, showing one single haplotype, 70 samples were heterozygotes for CalM and presented two haplotypes with 1bp difference, and the remaining 38 samples showed two haplotypes with more than 1bp difference. Again, no samples presented haplotypes of different length.

The final alignment consisted of 254bp and included 60 polymorphic sites, 55 of which were parsimony informative and five singleton sites. A total of 68 mutations, considering only synonyms and non-synonyms mutations, were found.

From the dataset 39 different haplotypes were identified (Appendix 8). Using a median-joining analysis four well-differentiated clusters corresponding to four different lineages were resolved with strong statistical support. Cluster I consisted of G. somaliensis and G. savignyi, cluster II was comprised of G. djiboutiensis and G. lobata, cluster IV consisted of G. tenuidens and G. albiconus, and cluster V was comprised of G. minor and G. gracilis. Finally, in disagreement with the three previous analyzed molecular markers, all the samples of G. stokesi nesting in cluster III were now grouped within cluster II.

Topologies from BI, ML, and MP analyses were largely congruent, with no contrasting signals (Appendix 9). The phylogenetic reconstruction was in agreement with the median-joining network analyses, showing again the presence of four well differentiated highly supported clades (clade I: PP\(_{BI}\) = 1, BT\(_{ML}\) = 86, BT\(_{MP}\) = 97; clade II: PP\(_{BI}\) = 1, BT\(_{ML}\) = 86, BT\(_{MP}\) = 100; clade IV: PP\(_{BI}\) = 1, BT\(_{ML}\) = 99, BT\(_{MP}\) = 100; clade V: PP\(_{BI}\) = 1, BT\(_{ML}\) = 100, BT\(_{MP}\) = 100). Average pairwise genetic distances are reported in Appendix 3.
Single-locus species delimitation results from ABGD, PTP, and GMYC approaches are summarized in Fig. 10. The partitions delimited by these three independent methods were mostly congruent and recovered a similar subdivision of sequences in putative lineages. All analyses delimitated the following candidate entities: *G. somaliensis* + *G. savignyi* group, *G. djiboutiensis* + *G. lobata* group, *G. albiconus* + *G. tenuidens* group, *G. minor* + *G. gracilis* + *G. stokesi* group. In the ABGD analysis, the distribution of pairwise genetic distance using a P value ranging from 0.01 to 0.1, whatever the substitution model used (Jukes-Cantor and Kimura), displayed four lineages for gap width values ranging from 2 to 4% (Fig. 11). These four lineages defined by ABGD approach were also in agreement with the ones proposed by the PTP, even though the lineage subdivision presented no statistical support. The GMYC predicted a higher number of molecular lineages in comparison with the results of the other species delimitation methods. The likelihood of the null model ($L_0 = 261.67$) was lower than the maximum likelihood of the ST-GMYC model ($L_{single} = 266.283$, $L_{ratio} = 9.225$, $p$-value = 0.0099) and, according to the latter, the transition from speciation to coalescence resulted in a partition with six putative lineages, adding two groups to the ones identified by the ABGD. In particular, the GMYC model detected two distinct lineages within clade I and within clade II. The MT-GMYC analysis yielded similar results with respect to ST-GMYC but recovered a higher number of lineages. According to the lineage-through-time plot and the likelihood function estimated by the software R ($L_0 = 1430.251$, $L_{single} = 1445.639$, $L_{ratio} = 30.77$, $p$-value = 2.074), seven separated genetic groups are present. The analysis detected four different lineages within clade II, while all the samples belonging to *G. somaliensis* and *G. savignyi* are nested in clade I, contrary to the results from the ST-GMYC approach.
Figure 10. Median joining haploweb for Goniopora from the Red Sea, inferred from CalM. The size of the circles is proportional to the frequencies of specimens sharing the same haplotype. Colors within the circles indicate the morphotypes of the individuals in which each haplotype was detected. Colored curves connect haplotypes that co-occur in at least one individual. Mutations are shown on the branches (numbers refer to positions in the alignments), and haplotype clusters are enclosed in dashed circles.
Figure 11. On the left: coalescent tree inferred from CalM for Goniopora from the Red Sea, obtained through BEAST analysis; the tree is being used for representation, but is not intended to be a definitive phylogenetic tree for the genus; On the right: summary of putative species delimitation drawn by median-joining network analyses, ABGD, PTP, sGMYC, mGMYC, phylogeny inferred through Bayesian Inference, and morphology (one column per method).
3.3 Morphological analyses

3.3.1 Macromorphological analyses

Polyp morphology

*In vivo* polyp morphology of 199 *Goniopora* specimens was investigated in light of morphospecies identifications and molecular results. In particular, for each coral colony the stalk and tentacle length, the shape of tentacle tips, and the oral disc dimension and color were evaluated. A summary of polyp morphological data is given in Table 4.

The morphology of the polyps was variable between and within the morphospecies and the molecular clades, and could not always be properly evaluated because of the different degree of retraction of the polyps *in situ*. Based on their length, stalks were assigned to four different categories: very short stalks (< 1 cm), short stalks (between 1 and 5 cm), medium stalks (between 5 and 10 cm), and long stalks (> 10 cm). Tentacles were divided into three classes of length: short tentacles (< 3 mm), medium tentacles (between 3 and 5 mm), and long tentacles (> 5 mm). The tips of the tentacles showed two main morphologies, pointed and bulbous. Oral discs were white in most of the cases, but the central part could show a pink or blue coloration. Finally, based on the major diameter, the oral discs could be assigned to three main classes: small oral discs (< 3 mm), medium oral discs (between 3 and 5 mm), and large oral discs (> 5 mm).

Samples assigned to *G. somaliensis* and *G. savignyi* in clade I showed stalks of different length. In the majority of the samples identified as *G. somaliensis* the stalks were observed an extension of up to 5 cm, while all the samples identified as *G. savignyi* presented stalks longer than 5 cm,
when fully extended. Similarly, the length of the tentacles and the dimension of the oral disc were smaller in *G. somaliensis* (< 3 mm for both variables) compared to *G. savignyi* (up to 5 mm for both variables). Tentacle tips were pointed in all the samples nested within clade I, and oral cones, *i.e.* the area surrounding the mouth, always white (Fig. 12, a-d). All the specimens grouped within clade II and identified as *G. djiboutiensis* and *G. lobata* had a similar morphology of the polyps *in situ*. In general, when fully extended stalks and tentacles were always of medium length, and oral discs presented medium dimensions. Tentacle tips were pointed or bulbous, and oral discs were normally white or white with pink/blue mouths (Fig. 13, a-d). *Goniopora stokesi* (clade III) showed long stalks and long pointed tentacles (> 10 cm, > 5 mm respectively), and presented white oral discs of medium size (Fig. 14, a-b). Samples nested within clade IV, assigned to *G. albiconus* and *G. tenuidens*, presented stalks and tentacles of medium length, and always had peculiar big white oral discs (Fig. 15, a-d). Finally, samples identified as *G. minor* and *G. gracilis* shared the same *in situ* morphology of the polyps, presenting stalks shorter than 1 cm, pointed tentacles shorter than 3 mm, and white small oral cones (Fig. 15, a-d).
Table 4 Summary of morphological variables analyzed for each Goniopora specimen from the Red Sea, with reference to each morphospecies, and each molecular defined clade

<table>
<thead>
<tr>
<th></th>
<th>CLADE I</th>
<th>CLADE II</th>
<th>CLADE III</th>
<th>CLADE IV</th>
<th>CLADE V</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>G. somaliensis</td>
<td>G. savignyi</td>
<td>G. djiboutiensis</td>
<td>G. stokesi</td>
<td>G. albiconus</td>
</tr>
<tr>
<td>POLYPS</td>
<td>&lt; 3mm</td>
<td>3-5mm</td>
<td>3-5mm</td>
<td>&gt; 5mm</td>
<td>&gt; 5mm</td>
</tr>
<tr>
<td>ORAL DISC</td>
<td>white</td>
<td>white</td>
<td>white, white and pink/blue</td>
<td>white</td>
<td>white, white and pink/blue</td>
</tr>
<tr>
<td>ORAL DISC</td>
<td>0-5cm</td>
<td>0-10cm</td>
<td>&gt; 10cm</td>
<td>&gt; 10cm</td>
<td>0-10cm</td>
</tr>
<tr>
<td>STALK LENGTH</td>
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<td>3-5mm</td>
<td>3-5mm</td>
<td>&gt; 5mm</td>
<td>&gt; 5mm</td>
</tr>
<tr>
<td>TENTACLE LENGTH</td>
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<td>pointed</td>
<td>pointed, bulbous</td>
<td>pointed</td>
<td>pointed, bulbous</td>
</tr>
<tr>
<td>MACROMORPHOLOGY</td>
<td>CALICE DIAMETER</td>
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<td>2.7-3.25</td>
<td>3.488-5.146</td>
<td>3.107-5.052</td>
</tr>
<tr>
<td>NUMBER OF SEPTA</td>
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<td>24</td>
<td>20-26</td>
<td>16-24</td>
<td>20-24</td>
</tr>
<tr>
<td>GONIOPOROID PATTERN</td>
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<td>yes</td>
<td>yes</td>
<td>yes</td>
<td>yes</td>
</tr>
<tr>
<td>NUMBER OF PALI</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>no</td>
<td>no</td>
</tr>
<tr>
<td>DEPTH OF CALICE</td>
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<td>shallow</td>
<td>deep</td>
<td>deep</td>
</tr>
<tr>
<td>MICROMORPHOLOGY</td>
<td>TIPS OF COLUMELLAR THREADS</td>
<td>spines</td>
<td>spines</td>
<td>single spines</td>
<td>single spines</td>
</tr>
<tr>
<td></td>
<td>COLUMELLA</td>
<td>single process</td>
<td>multiple process</td>
<td>single process</td>
<td>multiple process</td>
</tr>
<tr>
<td>NUMBER OF DENTICLES</td>
<td>1, 2</td>
<td>1, 2</td>
<td>2, 3</td>
<td>1, 2</td>
<td>1</td>
</tr>
</tbody>
</table>
Figure 12. Polyps and skeleton characters of Goniopora morphospecies clustered within clade I. *In vivo* morphology (a-b, c-d), corallites structures (e-f, g-h), and micromorphology (i-j, k-l) of *Goniopora somaliensis* (SA1691), and *Goniopora savignyi* (SA1431).
Figure 13. Polyps and skeleton characters of *Goniopora* morphospecies clustered within clade II. *In vivo* morphology (a-b, c-d), corallites structures (e-f, g-h), and micromorphology (i-j, k-l) of *Goniopora djiboutiensis* (SA1740), and *Goniopora lobata* (SA1396).
Figure 14. Polyps and skeleton characters of *Goniopora* morphospecies clustered within clade III. *In vivo* morphology (a-b), corallites structures (c-d), and micromorphology (e-f) of *Goniopora stokesi* (BU039).
Figure 15. Polyps and skeleton characters of *Goniopora* morphospecies clustered within clade IV. *In vivo* morphology (a-b, c-d), coralites structures (e-f, g-h), and micromorphology (i-j, k-l) of *Goniopora albiconus* (SA1631), and *Goniopora tenuidens* (SA1627).
Figure 16. Polyps and skeleton characters of *Goniopora* morphospecies clustered within clade V. *In vivo* morphology (a-b, c-d), corallites structures (e-f, g-h), and micromorphology (i-j, k-l) of *Goniopora minor* (SA1597), and *Goniopora gracilis* (SA1804).
Skeletal structures

Macromorphological skeletal structures of *Goniopora* specimens were analyzed in light of morphospecies identifications and molecular results. A summary of macromorphological skeletal data is given in Table 4.

In general, specimens nested within clade I and identified as *G. somaliensis* showed the smallest calices and columellae (CaD 1.72 - 2.71 mm; CoD 1.25 - 1.45 mm) among all the collected samples. The specimens had between 20 and 24 septa, and presented the gonioporoid pattern of fusion, five main pali, and shallow calices. *Goniopora savignyi*, also in clade I, had bigger calices and columellae (CaD 2.72 - 3.25 mm; CoD 1.47 - 1.84 mm) compared to *G. somaliensis*. All the specimens presented 24 septa, gonioporoid pattern of fusion, five main pali, and shallow calices (Fig. 12, e-h).

Specimens in clade II and identified as *G. djiboutiensis* presented large big calices and columellae (CaD 3.49 - 5.15 mm; CoD 1.99 - 2.62 mm) and up to 26 septa. All the specimens presented the gonioporoid pattern of fusion, five pali, and shallow calices. In *G. lobata*, the dimensions of calices and columellae were similar to the ones of *G. djiboutiensis* (CaD 3.11 - 5.05 mm; CoD 1.53 - 2.61 mm) but the number of septa ranged from a minimum of 16 to a maximum of 24. The gonioporoid pattern of fusion was visible in almost all the cases, but no pali could be clearly identified (Fig. 13, e-h). The calices were always deeper compared to the ones in *G. djiboutiensis*.

Specimens belonging to *G. stokesi* and grouped in clade III had the largest calices and columellae among all the analyzed samples (CaD 4.08 - 6.07 mm; CoD 2.09 - 3.61 mm). The number of septa
was variable between 20 and 24 and the gonioporoid pattern of fusion was always clearly visible (Fig. 14, c-d). No pali could be easily recognized and calices were always very deep.

The samples in clade IV identified as *G. albiconus* had CaD variable between a minimum of 2.97 mm to a maximum of 4.75 mm, and CoD varied between 1.52 mm to 2.36 mm. In all *G. albiconus* samples, 24 septa arranged in a gonioporoid pattern, and five pali were distinguishable. Calices were deeper in comparison to *G. somaliensis*, *G. savignyi*, and *G. djiboutiensis*, but shallower than calices of *G. lobata* and *G. stokesi* samples, thus we referred to them as being of medium depth. The skeletal morphology of the other samples grouped within clade IV and belonging to *G. tenuidens* presented smaller calices and columellae, and a reduced number of septa compared to *G. albiconus* specimens (Fig. 15, e-h). In fact, in *G. tenuidens* CaD varied between a minimum of 2.46 mm to a maximum of 3.46 mm, CoD between 1.33 mm and 2.01 mm, and the number of septa was reduced to 16 - 20. In these specimens the gonioporoid pattern was visible and 5 pali could be identified. Calices showed a medium depth.

Specimens belonging to molecular clade V showed small calices and columellae and a reduced number of septa in comparison with all the other samples. In particular in *G. minor*, CaD ranged between a minimum of 1.86 mm to a maximum of 2.96 mm, CoD between 1.02 mm and 1.88 mm, and the number of septa was always 12. No gonioporoid pattern of fusion was visible, and four structures similar to pali were distinguishable in the specimens in some cases, although in the majority of them these structures were fused forming a crown. The depth of the calices was medium. Finally, specimens identified as *G. gracilis* had calices and columellae larger than the ones of *G. minor* (CaD 2.07 - 3.38 mm; CoD 1.46 - 1.90 mm) and a higher number of septa (14 - 20). Also in these samples, the septal gonioporoid pattern of fusion was not visible, but instead
of having a fused crown, five main pali were distinguishable. Calices were always of medium depth (Fig. 16, e-h).

3.3.2 Micromorphological analyses

The skeletal morphology of one specimen (SA1571) grouped in clade III as well as a subset of four samples for each of the other identified morphospecies belonging to molecular clade I, II, IV, and V were analyzed using SEM. A summary of micromorphological skeletal data is given in Table 4.

Within the same molecular clade, samples showed peculiar micromorphological and microstructural features. In particular, the micro-ornamentation and the arrangement of the columella were consistent within each molecular clade, with the exception of clade II, while the number of denticles was more variable between the morphospecies.

In clade I, all the analyzed specimens belonging to both *G. somaliensis* and *G. savignyi* presented highly developed spines on the septa, on the septal face, and on the tips of columellar threads. The columella was always organized in a single process and one or two rows of denticles were found on the septa (Fig. 12, i-l).

Samples nested within clade II identified as *G. djiboutiensis* and *G. lobata* showed a similar micro-ornamentation to the one of samples in clade I, but instead of having multiple spines on the septa, on septal face, and on the tips of columellar threads as in *G. somaliensis* and *G. savignyi*, single spines ornamented the skeletons of samples within clade II. Specimens identified as *G. djiboutiensis* presented columellae organized in multiple processes, while
columellae of *G. lobata* specimens were always present as a single process. Also the number of denticles on the septa was different between the two morphospecies, in particular in *G. djiboutiensis* there were two or three rows of denticles, while in *G. lobata* there were only one or two rows of denticles (Fig. 13, i-j).

*Goniopora stokesi* specimens within clade III showed structures similar to paddles on the tips of columellar threads instead of presenting spines. The rest of the skeleton was smooth. The columella was organized in a multiple process, and there was only one row of denticles (Fig. 14, e-f)

Within clade IV, all the samples belonging to both *G. albiconus* and *G. tenuidens* shared the same micromorphological traits. In particular, the micro-ornamentation on the septa, on the septal face, and on the tips of columellar threads, presented poorly developed single spines. The columella was always organized as a single process, and one or two rows of denticles ornamented the top of the septa in both the morphospecies (Fig. 15, i-j).

Finally, specimens nested within clade V, identified as *G. minor* and *G. gracils*, presented leafy structures similar to paddles on the tips of the columellar threads. The columella was composed of multiples processes and one single row of denticles was present on the upper side of the septa (Fig. 16, i-j).

### 3.3.3 Morphometric analyses

Three morphometric variables (CaD, CoD, CD) were scored from 166 specimens for a total of 1496 corallites. The three assessed morphological characters presented an overlapping pattern
between the morphospecies, except for *G. stokesi* which is morphologically different from the other taxa based on CaD, CoD, and CD (Fig. 17, a). In particular, on one hand all the variables were overlapping between *G. djiboutiensis*, *G. lobata*, *G. albiconus*, and *G. tenuidens* morphospecies. On the other hand, all the variables were overlapping between *G. somaliensis*, *G. savignyi*, *G. minor*, and *G. gracilis*. The morphological characters presented a similar overlapping pattern between the five main molecular clades, except for clade III. In particular, the morphological features overlapped between clade II and IV, and between clade I and V (Fig. 17 b).

A PCA biplot of the morphometric data is shown is Fig. 18. The first two variables accounted for 98.26% of the total variance. Principal component 1 (PC1) was highly correlated with all the variables examined ($r > 0.9$ for each variable). PC2 was also highly correlated with all the variables ($r > 0.89$). No clearly separated groups of specimens were visible in the PCA plot, but applying the plots to the morphospecies and to the five molecular clades, three main groups were distinguishable. In particular, the specimens belonging to *G. somaliensis* and *G. savignyi*, and those belonging to *G. minor* and *G. fragilis*, were clearly separated from *G. djiboutiensis* and *G. lobata*, and *G. albiconus* and *G. tenuidens*. Moreover, *G. stokesi* specimens formed a cluster of their own (Fig.18 b). Similarly, specimens belonging to clades I and V were clearly separated from samples belonging to clades II and IV. Moreover, samples belonging to clade III formed a separated group, not overlapping with any of the others (Fig. 18 a).
Figure 17. Box plots of morphometric variables examined for (a) each morphospecies of *Goniopora*, and (b) for each molecular defined clade of *Goniopora*; CaD: long diameter of calice; CoD: long diameter of columella; CD: centroids distances. Colors indicate (a) morphospecies and (b) genetic lineages labelled at the top and at the bottom.
Figure 18. Results from principal component analyses of morphometric data from *Goniopora*. (a) Grouping by clades in the ITS region tree, (b) grouping by morphospecies. (a) The group in orange represents clade I, the group in blue represents clade II, the group in green represents clade III, the group in light blue represents clade IV, and the group in pink represents clade V. (b) The group in yellow represents *G. somaliensis*, the group in orange represents *G. savignyi*, the group in blue represents *G. djiboutiensis*, the group in light green represents *G. lobata*, the group in green represents *G. stokesi*, the group in light blue represents *G. albiconus*, the group in red represents *G. tenuidens*, the group in pink represents *G. minor*, and the group in purple represents *G. gracilis*. 
4. DISCUSSION

4.1 Morpho-molecular evidence as a tool to evaluate species delimitation

A re-evaluation of morphological and micromorphological features in light of molecular results has been successfully used to better clarify the relationships within the genus *Pocillopora* (Pinzón et al. 2012, 2013, Schmidt-Roach et al. 2012, 2013, 2014), in the genus *Stylophora* (Flot et al. 2011), in the genus *Porites* (Forsman et al. 2009, 2015, Prada et al. 2014), within *Montipora* (Forman et al. 2010), in the genus *Psammocora* (Benzoni et al. 2007, 2009), and in the genus *Seriatopora* (Flot et al. 2008). This work represents a further example of how the integration between morphological and molecular data can provide new insights into scleractinian taxonomy and phylogeny, which is otherwise usually hidden by misleading plastic morphological features of the colonies.

In this study addressing re-evaluation of morphological and micromorphological features in the genus *Goniopora*, haplotype network results from the mitochondrial marker (IGR) and three nuclear regions (ITS region, ATPsβ, CalM) suggest the presence of five molecular lineages of *Goniopora* within the Saudi Arabian Red Sea (clades I to V). Each molecularly defined lineage is comprised of at least two traditional known morphospecies, with the exception of clade III. Results from the ITS region evidenced the presence of three additional molecular lineages within the genus *Goniopora* (clades VII to IX). These three clades are comprised only of samples from Japan (with the exception of one sample from Malaysia nested within clade VII, i.e., PEN29). The identifications of samples belonging to clade VII, VIII, and IX are based on Kitano et al. (2013, 2014). Further morphological identification would be necessary to confirm the attribution of the
samples to the above mentioned morphospecies. In particular, when referring to specimens that are nested by the ITS region analyses in the present work within clade VII, and identified as *G. djiboutiensis*, *G. pendulus*, and *G. cellulosa*, the authors state that these may all represent morphological variations of *G. pendulus*, showing no significant differences in the morphological variables of the corallites and of the polyps.

The molecular results of the present study are highly corroborated by molecular species delimitation approaches ABGD, PTP, and GMYC, which supported the presence of five main putative species of *Goniopora* in the Saudi Arabian Red Sea. Although DNA taxonomy techniques have been proven to be a fast, objective, and rigorous means to assess biodiversity (Fontaneto et al. 2015), it is important that these molecular analyses are always corroborated with integrative taxonomic analyses to more accurately delimit the species (Dayrat 2005, Roe and Sperling 2007, Schlick-Steiner et al. 2010, Schwarzfeld and Sperling 2014). This is particularly true when dealing with organisms such as corals, where large population sizes and dispersal abilities make them prone to incomplete lineage sorting, and their breeding strategies provide high chances for hybridization (Frank and Modaky 2002). Results from macromorphological, micromorphological, and morphometric analyses of the Red Sea specimens, evaluated in light of molecular results, suggest a complex scenario for each of the five identified molecular clades.

In clade I, macromorphological analyses and morphometric analyses evidenced the presence of two different morphospecies, defined on the basis of the diameter of calices and columellae, and on the number of septa. Nonetheless, a reevaluation of micromorphological and microstructural analyses revealed the presence of shared features between the morphospecies nested within the clade. Further comparisons of all the samples clustered in clade I with *G.*
savignyi specimen number 1991.6.4.53, identified by C. Sheppard and deposited at NHM (Fig. 2, c) highlighted further similarities between the skeletal morphology of G. somaliensis and G. savignyi, suggesting that they may represent morphological variation of a single entity. Unfortunately, the holotype of G. savignyi was not accessible, thus this scenario remains hypothetical and further analyses are needed to better clarify the species boundaries between G. somaliensis and G. savignyi.

According to macromorphological and micromorphological results clade II is comprised of two distinct entities. However, PCA results based on the examined variables could not discriminate the two different morphospecies, which present overlapping CaD, CoD, and CD. With the exception of a shared micro-ornamentation, the two identified morphologies differ in the arrangement of the columella, and in the number of denticles present on the upper side of the primary septa. Nonetheless, according to Kitano et al. 2013 some of the samples identified as G. djiboutiensis in their study and nested within clade II according to the ITS marker in the present work, showed deeper calices compared to the other samples of G. djiboutiensis, mostly at the top of the colony, as well as a reduced number of pali, and smaller columellae. Similarly, some specimens identified by Kitano et al. (2013) as G. lobata presented pronounced pali and wider columellae. These considerations may suggest the presence of intermediate morphologies between G. djiboutiensis and G. lobata. A detailed analysis of the morphology of these samples would be necessary in order to further discuss the morphological variability of the samples nested within clade II. Nonetheless, our molecular and morphological analyses allowed a re-evaluation of the identity of the specimen identified by Kithano et al. (2013) as G. ciliata, (BA076) which is G. lobata. Moreover, a detailed comparison of our specimens with the
holotype of *G. ciliata* (G55789) and Veron’s (2002) original description of the species, suggest that *G. ciliata* may represent a morphological variation of *G. lobata*. In the original description the author also uses the morphology of the polyps as a diagnostic feature to identify the species. *In situ* morphology of *G. ciliata* in comparison with *G. lobata* will be addressed later in the discussion. Similarly, detailed morphological comparison of material identified as *G. djiboutiensis* with the holotype of *G. sultani* and Veron’s (2002) original description, may suggest that *G. sultani* is a morphological variant of *G. djiboutiensis*. Moreover, in the original description the author himself recognized the similarity of *G. sultani* to *G. lobata*, although he stated that the former is characterized by bigger corallites compared to the latter, which also does not present septal deltas, and has smaller columellae. A comparison between the morphologies of *G. djiboutiensis*, *G. lobata*, *G. ciliata*, and *G. sultani* is given in Fig. 2.

All the samples grouped by the molecular markers within clade III are identified as *G. stokesi*. Skeletal macromorphological and micromorphological analyses showed common features in all the analyzed samples. This represents the only case in the present study for which all the analyzed morphological and molecular characters agreed in discriminating one single lineage. Macromorphological and morphometric analyses of the skeletons suggest that two lineages are grouped within clade IV, defined on the basis of the dimensions of calices and columellae, the number of septa, and the arrangement of septa. Nevertheless, detailed micromorphological analyses highlighted a common micro-ornamentation in all the specimens clustered in clade IV. Finally samples nested within clade V can be separated into two different lineages based on the macromorphological and morphometric analyses of the skeletons. Nevertheless, some of the analyzed specimens presented in the same colony both the morphologies, suggesting that the
two morphospecies could represent the two extremes of a single plastic entity. Moreover, scanning electron microscopy results evidenced a common micro-ornamentation in all the specimens clustered into clade V. Kitano et al. (2014) propose that *P. paliformis* as described by Veron (2000) should be regarded as *G. pedunculata* on the basis of the skeletal morphology and molecular analyses. Morpho-molecular results of the present work confirm this idea, but as the holotype of *G. pedunculata* is lost and could not be analysed, we maintain *G. minor* in our identifications, and suggest that *P. paliformis* should be considered a junior synonym of *G. minor*.

4.2 *In situ* morphology of the polyps as a diagnostic character for species boundaries definition in *Goniopora*

Veron and Pichon (1982), Veron (1986), Nishira and Veron (1995), and Veron (2000) propose that *in situ* morphology of the polyps in *Goniopora* can be used as a diagnostic character to assess species boundaries within the genus. In particular Veron and Pichon (1982) state that: “Most *Goniopora* and *Alveopora* species have distinctive growth forms and large polyps which remain extended during the day. This allows many to be identified *in situ* and all to be separated into probable species units *in situ*” (Veron and Pichon 1982, p. 1), and Veron (1986) describing *Goniopora* states: “Different species have polyps of different shapes and colors, which allow them to be identified under water” (Veron 1986, p. 57). Based on this idea, the morphology of the living polyps was added to the morphological analyses in the present study and evaluated for each traditionally identified morphospecies. Furthermore, it was reevaluated in light of molecular results for each of the molecular identified lineages.
All the *G. somaliensis* in clade I showed small polyps, with short stalks and short pointed tentacles. The color was generally pale brown and the oral disc of the polyps white. Polyps of *G. savignyi* were very similar those of *G. somaliensis*, but they differed greatly in dimensions, being always larger and presenting stalks up to twofold longer. Considering the skeletal variability between the two morphospecies, differing in particular by the dimensions of the calices a variability of the polyps dimension is an additional morphological character confirming these differences. In this study, the polyp morphology of *G. somaliensis* and *G. savignyi* seemed consistent for all the specimens and unique compared to that of the other examined morphospecies. The polyp morphology of the two morphospecies nested in clade I was similar, but different with regards to the polyp dimensions. As the holotype of *G. savignyi* was not accessible for this study, no conclusion can be drawn with regards to this molecular clade in reference to the two different *in situ* morphologies, which could represent either two different morphotypes of the same lineage, or two distinct lineages.

All the samples nested within clade II showed similar *in situ* polyps morphologies. Both *G. djiboutiensis* and *G. lobata* had long stalks and long pointed or bulbous tentacles, with medium sized white oral discs, sometimes characterized by distinctive pink or blue mouths. Moreover, these features are consistent with Veron’s (2000) description and *in vivo* pictures of *G. sultani* and *G. ciliata* (p. 355, fig. 4, pp. 372-373, figs. 1-5). From the morpho-molecular results of this work, we can state that the polyp morphology in this case is concordant with molecular results, and could help to identify in the field samples nested within clade II. However, living polyps are not useful to distinguish between the different morphological species in the same clade.
Samples nested within clade III had a peculiar morphology in the field. They presented polyps with very long stalks and tentacles. A distinctive brown coloration was shared between all the colonies, which also had polyps with white oral discs of medium dimensions. Nevertheless, these morphological features are shared by *G. pendulus in vivo* pictures reported by Veron (2000) (p. 350, figs. 1-2). The polyp morphology of the samples nested within clade III is identical to the morphology of *G. pendulus* specimen (OT30) reported by Kitano et al. (2013) (p. 8 fig. 4, A). We included this specimen and others identified by Kitano et al. (2013) as *G. pendulus* in the analyses of the ITS region and they all are nested in clade VII. In this case thus in vivo polyp morphology could not be used to discriminate between distinct lineages.

All the samples in clade IV identified as *G. albiconus* and *G. tenuidens* show a common polyp morphology, distinct from the other analyzed specimens *in situ* thanks to the presence of white large oral cones in the polyps. This is a unique feature of the samples nested within this molecular clade, but according to our results no living traits can be used to discriminate between the two morphospecies nested in clade IV. The analyses of two samples (BA002, DJ074) identified by Kitano et al. (2013) as *G. albiconus* on the base of the *in vivo* morphology of polyps provided a further prove that the morphology of the polyps of *G. albiconus* and *G. tenuidens* is identical, although the skeletons are not. Both BA002 and DJ074 are deposited at UNIMIB, and the macromorphology of these specimens was re-evaluated in light of the molecular and morphological results of the present study. Although the samples shared the same *in vivo* morphology with all the specimens identified as *G. albiconus* in the present study and in the literature (Veron 2000), the macromorphology of their skeletons suggest that they are instead *G. tenuides*. This consideration is also supported by the comparison with *G. tenuides*
and *G. albiconus* original descriptions and their holotypes (Quelch (1886), 1886.12.9.304 and Veron, 2002, G55850, respectively)

Finally, all the specimens clustered within clade V shared a distinctive identical morphology of the polyps. *In situ* all the collected samples presented small polyps, with very reduced stalks, small white oral cones, and short pointed tentacles. This result corroborates the idea that *G. minor* and *G. gracilis* form a single lineage. Besides the general dimensions of the polyps shared with *G. somaliensis* (which can be easily discriminated by the presence of short stalks) no further feature was in common with any of the other identified living morphologies.

To conclude, although the polyp morphology seems not useful in discriminating among morphologically defined species, it may be a diagnostic character to differentiate between molecularly defined lineages of *Goniopora* in the Red Sea. Integrating these results with the micromorphological and molecular results, the most likely scenario is that the nine morphospecies of *Goniopora* in the Saudi Arabian Red Sea identified based on morphological features actually belong to five main separate evolutionary lineages and that within four of these the range of morphological variation encompasses that of different traditionally described taxa. Nevertheless, the reported results are based only on samples from the Saudi Arabian Red Sea and Djibouti, thus further specimens from different localities in the Red Sea and in the Indian and Pacific Oceans should be added to the dataset before drawing general conclusions in a formal genus revision. In corals, cases of convergent evolution of morphological characters are common (van Oppen et al. 2001) and homoplasy has been demonstrated to obscure the real relationships among species (Fukami et al. 2004). At the same time, incomplete lineage sorting
(mostly in recently diverged lineages) and hybridization can obscure real evolutionary relationships (Vollmer and Palumbi 2002, Combosh and Palumbi 2015).

4.3 Molecular insights

The four molecular markers used in the present work resolved the same putative lineages within the analyzed samples of *Goniopora* (clades I to V), although showing minor differences.

With regards to the mitochondrial DNA, the amplified region (IGR) showed high levels of sequence variations, and provided high resolution into the genus *Goniopora*, resolving 6 main molecular lineages (clade I to VI) congruent with the lineages identified by the nuclear markers, with the exception of clade VI highlighted only by the mitochondrial region. These results represent a further demonstration that, even though the mitochondrial DNA of scleractinian corals has slow evolution rates with resulting low levels of variations between species (France and Haoover 2001, 2002, Shearer et al. 2002, McFadden et al. 2004, 2006, Hellberg 2006, Huang et al. 2008), some non-coding regions peculiar to corals can prove useful to resolve boundaries at species level. The utility of these IGRs in fact has been already proven in different scleractinian genera such as *Pocillopora*, *Seriatopora*, *Stylophora* (Flot and Tillier 2007, Flot et al. 2008, 2011, Schmidt-Roach et al. 2012, Pinzón et al. 2013), and in the genera *Pavona*, *Leptoseris*, and *Pachyseris* among others (Luck et al. 2013, Pochon et al. 2015, Terraneo et al. 2014). Kitano et al. (2013) used the mitochondrial region between the end of NAD5 and the first half of COI, comprising three IGRs, tRNA<sub>Tp</sub>, and ATPs8, to infer the phylogenetic position of the species *G. stokesi*. Nevertheless, the chosen region did not show levels of variation suitable for this purpose, and could not distinguish the species from the other congeners. This can be
explained by the fact that on a total of 1640 bp analyzed by Kitano et al. (2013), 702 bp belonged to the slow evolving COI region, 457 bp to NAD5 gene, 69 bp to the tRNA\textsuperscript{Trp} gene, and 215 bp belonged to ATPs\textsubscript{8} gene. Only a total of 197 bp belonged to the three variable IGRs. In particular, 40 bp belonged to the IGR between NAD5 and tRNA\textsuperscript{Trp}, 33 to the IGR between tRNA\textsuperscript{Trp} and ATPs\textsubscript{8}, and 124 to the IGR between ATPs\textsubscript{8} and COI. The IGR chosen in the present study (nested between the end of Cytb and the beginning of NAD2) is the longest IGR present in the mitochondrial genome of \textit{Goniopora}, and accounts for 1200 bp.

The three used nuclear markers, ITS region, ATPs\textsubscript{β} and CalM, led to the same results, identifying five main evolutionary distinct lineages within the analyzed samples from the Red Sea, with the exception of CalM which only discriminated four lineages. Previous works successfully used rDNA for low-level taxonomic comparisons, especially thanks to the presence of the two high variable internal transcribed spacer regions, ITS\textsubscript{1} and ITS\textsubscript{2}, which have fewer functional constraints than the ribosomal genes (Lopez and Knowlton 1997, Odorico and Miller 1997, Medina et al. 1999, Fukami et al. 2000, van Oppen et al. 2000, 2002, Diekmann et al. 2001, Marquez et al. 2003, Vollmer and Palumbi 2004, Chen et al. 2004, Forsman et al. 2005, 2009, 2010, 2015, Wei et al. 2006, Benzoni et al. 2007, 2010, 2011, 2012 a, b, 2014, Stefani et al. 2008, 2011, Arrigoni et al. 2012, 2014 a, b). Moreover, the ITS region was recently used also by Kitano et al. (2013, 2014) to assess species level relationships into the genus \textit{Goniopora}. Although in these last two papers some of the \textit{Goniopora} lineages remained unresolved using the ITS region, the results may probably be related to misinterpretations of the morphological data, which could not be fully re-assessed in the present study, rather than because of the unsuitability of the chosen marker. ATPs\textsubscript{β} gene was used by Flot et al. (2008) and by Forsman et al. (2010) in
the attempt to disentangle the complex situation within Hawaiian samples of the genus *Pocillopora* from one side and of the genus *Montipora* from the other. Nonetheless, the marker resulted in less resolution in comparison to mitochondrial genes in *Pocillopora*, and unsuitable in resolving species boundaries within *Montipora*. Nevertheless, within the genus *Goniopora* results from ATPsβ analyses were in agreement with the other molecular markers analyzed. Analyses of a portion of the CalM gene resulted in four main distinct lineages within *Goniopora* samples from the Red Sea, not showing one molecular clade that was revealed by all the other amplified markers. In particular, samples of clade III were nested within clade II by the CalM results. Different hypotheses can be proposed to explain this discrepancy. Calmodulin for example is one of the calcium binding proteins that are highly conserved in their protein and gene structure (Yuasa et al. 1999) and, therefore, this could emerge in low levels of gene sequence variation that can thus hide real evolutionary relationships. Alternatively, considering that *G. stokesi* colonies harbored two alleles of CalM gene of which one was exclusive to the species and the other one was the most common allele shared also by *G. djiboutiensis* and *G. lobata*, it is likely that the latter allele might represent a retention of a shared ancestral allele resulting in an unresolved phylogeny (Degnan and Rosenberg 2009). Another possible explanation might be an incomplete lineage sorting due to a deceleration in the evolutionary rate of CalM gene within the lineage leading to these two clades and this phenomenon is known to cause discrepancies in comparative phylogeny (Maddison and Knowles 2006). Molecular results are corroborated by species delimitation analyses, ABGD, PTP, and GMYC, which endorse the presence of five putative species of *Goniopora* from the Saudi Arabian Red Sea and Djibouti. Although showing similar results when delimiting species, the three analyses
differed in resolution. However, this is expected since the three methods rely on different criteria and inputs (Fontaneto et al. 2010), and, moreover, it has been demonstrated that their performance depends on several factors, such as the variability of sequenced molecular locus, the number of analyzed species, the population size, and the speciation rate (Tang et al. 2014, Dellicour and Flot 2015). For example, haplowebs outperform sGMYC and mGMYC when dealing with three to six-species datasets (Dellicour and Flot 2015) because the latter two approaches usually exceed the total number of putative entities when compared to all the other algorithms (Talavera et al. 2013). Moreover, despite both GMYC and PTP are both tree-based methods, the former one is more sensitive because of lower consistency due to differences among gene trees introduced by smoothing step and, furthermore, unresolved nodes have a greater effects on GMYC estimates than to PTP ones (Tang et al. 2014). Even if the development of these molecular tools was above all targeted to disentangle species diversity of meiofauna and other poorly studied taxa (Fontaneto 2014, Fontaneto et al. 2015), these approaches seem to be powerful also for hard corals in which the great and ambiguous variability of skeleton features related to both environment and genotype has challenged the taxonomy for centuries.

The advent of next-generation sequencing tools (NGS) has revolutionized our understanding of evolutionary processes and provided practical applications into phylogenomics and species delimitation (Davey et al. 2011). Therefore, it is important to highlight that the four used molecular markers represent only a small portion of the entire genome of Goniopora and we cannot exclude the presence of further genetic divergence in other regions of the nuclear genome that would explain the different morphologies of the skeletons. Nevertheless this
hypothesis seems to be unlikely considering the general concordance between different independent mitochondrial and nuclear loci.

4.4 General considerations about the relevance of *Goniopora* as a case study

The present study represents a stepping stone for a better understanding of *Goniopora* species boundaries and this may provide major implications in different fields, from conservation and evolution, to biogeography and ecology. Huang and Roy (2013) recently showed that the loss of phylogenetic diversity in reef corals is dependent on the nature of extinction threats, especially bleaching, *i.e.* loss of dinoflagellate symbionts and/or symbiont pigmentation from the holobiont (Hoegh-Guldberg and Smith 1989, Brown 1997), and diseases, *i.e.* impairment of vital functions from normal state of health caused by pathogens and/or environmental stressors (Harvell et al. 1999, Rosenberg and Loya 2004), but also tree shape. Therefore, establishing evolutionary relationships between coral taxa and their evolutionary distinctiveness is essential for conservation strategies as the extinction of species can lead to larger loss of phylogenetic diversity (Huang 2012, Huang and Roy 2013, 2015, Forest et al. 2015). This is particularly important when dealing with a genus such as *Goniopora*, characterized by a broad distribution, and able to form big colonies in a variety of different habitats, two factors that ensure to the genus a place among the major framework builders of coral reefs.

Nevertheless given the integrated molecular and morphological results emerging from the present work, the diversity of *Goniopora* in the Red Sea seems to be lower than previously thought. From the 14 species described from the Red Sea in the literature (Sheppard and Sheppard 1991, Veron 2000) only 5 lineages have been detected in this study. However it must
be taken into account that only a small part of the Red Sea has been investigated in this work, and future studies in other regions of the Red Sea, such as south from the Farasan Islands, and along the western coast of the Red Sea, will be necessary to provide a more precise overview about the real diversity of the genus in the region. This might be particularly important given the presence of peculiar latitudinal ecoregions in the Red Sea (Ormond et al. 1984, Sheppard 1985, Sheppard and Sheppard 1991), often characterized by different coral reef composition, both in terms of species diversity and richness. There is emerging evidence for example that the environmental shift between the Farasan Banks and the Farasan Islands may represent an important biogeographic barrier, with corals, fish, and sponges species showing marked genetic structure correlated with environmental gradients (such as temperature, salinity, or productivity) between these habitats (Nanninga et al. 2014, Giles et al. 2015, Terraneo et al. 2014).

Finally, it should be not overlooked that, being characterized by attractive long polyps extended during day time, *Goniopora* is among the corals of major interest in the aquarium market. In fact many corals such as the genus *Blastomussa* Wells, 1961 are popular in the aquarium trade because of their brightly colored fleshy polyp mantle (Veron, 2000) and are therefore increasingly targeted by commercial harvesting (Green and Shirley 1999, Lilley 2001). Nevertheless the lack of knowledge about *Goniopora* species rendered the success of keeping colonies alive in captivity for a period of time longer than one year very unlikely. A deeper knowledge of *Goniopora* species will allow aquarists to provide a better feeding regime and general care more suited for each specimen, thus increasing the chances of survival of the colonies.
5. CONCLUSIONS

In the present study the species boundaries within the genus *Goniopora* in the Saudi Arabian Red Sea and Djibouti were clarified using a combined morpho-molecular approach.

This work represents a stepping stone in understanding the actual evolutionary relationships within *Goniopora*, which, although being widespread in the Indo-Pacific, remained largely understudied, with the exception of two recent works by Kitano et al. (2013, 2014) that investigated the phylogenetic relationships of several species of *Goniopora*. Nevertheless, this is the first work that investigated the biodiversity of the genus using molecular tools within an under-explored region such as the Red Sea (Berumen et al. 2013), where corals and many other organisms are being investigated for the first time combining morpho-molecular data (DiBattista 2013, DiBattista and Randall 2013, Terraneo et al. 2014, Arrigoni et al. 2015, Giles et al. 2015, Robitzch et al. 2015).

In this work, a multi locus genetic approach provided the basis for re-evaluating morphological evolutionary informative features and to assess the phylogenetic relationships of nine traditional species of *Goniopora*. Moreover, the work highlighted the utility of molecular species delimitation analyses in complex groups of organisms such as hard corals (Pons et al. 2006, Puillandre et al. 2012, Fontaneto 2014, Tang et al. 2014, Fontaneto et al. 2015).

Nevertheless, additional studies comparing genetic and morphological variability in different geographic areas in the Red Sea, as well as in the Indian and Pacific Oceans, will be necessary to better understand species boundaries within the genus and to undertake taxonomic decisions.
Appendix 1. List of Goniopora haplotypes defined with the IGR region.

H 1: 1 [DJ004]
H 2: 2 [SA1624 SA1890]
H 4: 4 [SA1431 SA1598 SA1881 SA1884]
H 5: 4 [SA1718 SA1857 SA1886 SA1985]
H 10: 2 [SA1571 SA1572]
H 12: 9 [DJ294 SA1416 SA1709 SA1715 SA1862 SA1864 SA1865 SA2013 SA2014]

H 14: 6  [SA1396 SA1417 SA1670 SA1738 SA1982 SA2020]
Appendix 2. Phylogeny reconstruction of *Goniopora* from the Red Sea based on Bayesian inference (BI) analysis of the mitochondrial IGR. Bayesians posterior probability (left) higher than 0.7, ML bootstrap values (middle) higher than 70, and MP bootstrap values (right) higher than 50, are displayed on the nodes.
Appendix 3. Matrix of mean genetic distances within and between molecular identified clades. Standard errors are in italic script. Numbers on the diagonal represent mean genetic distance intra-clade and standard errors.

<table>
<thead>
<tr>
<th></th>
<th>Clade I</th>
<th>Clade II</th>
<th>Clade III</th>
<th>Clade IV</th>
<th>Clade V</th>
<th>Clade VI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clade I</td>
<td>0.003 ± 0.001</td>
<td>0.005</td>
<td>0.003</td>
<td>0.004</td>
<td>0.004</td>
<td>0.003</td>
</tr>
<tr>
<td>Clade II</td>
<td>0.02</td>
<td>0.001 ± 0.001</td>
<td>0.004</td>
<td>0.004</td>
<td>0.005</td>
<td>0.005</td>
</tr>
<tr>
<td>Clade III</td>
<td>0.013</td>
<td>0.016</td>
<td>0.002</td>
<td>0.003</td>
<td>0.004</td>
<td></td>
</tr>
<tr>
<td>Clade IV</td>
<td>0.014</td>
<td>0.02</td>
<td>0.006</td>
<td>0.004 ± 0.001</td>
<td>0.003</td>
<td>0.004</td>
</tr>
<tr>
<td>Clade V</td>
<td>0.015</td>
<td>0.021</td>
<td>0.014</td>
<td>0.012</td>
<td>0.003 ± 0.001</td>
<td>0.004</td>
</tr>
<tr>
<td>Clade VI</td>
<td>0.012</td>
<td>0.025</td>
<td>0.017</td>
<td>0.017</td>
<td>0.018</td>
<td>0.001 ± 0.001</td>
</tr>
</tbody>
</table>

(a) ITS region

<table>
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<tr>
<th></th>
<th>Clade I</th>
<th>Clade II</th>
<th>Clade III</th>
<th>Clade IV</th>
<th>Clade V</th>
<th>Clade VII</th>
<th>Clade VIII</th>
<th>Clade IX</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clade I</td>
<td>0.0014 ± 0.002</td>
<td>0.01</td>
<td>0.01</td>
<td>0.014</td>
<td>0.01</td>
<td>0.01</td>
<td>0.01</td>
<td>0.011</td>
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<tr>
<td>Clade II</td>
<td>0.053</td>
<td>0.0049 ± 0.001</td>
<td>0.006</td>
<td>0.006</td>
<td>0.012</td>
<td>0.005</td>
<td>0.005</td>
<td>0.006</td>
</tr>
<tr>
<td>Clade III</td>
<td>0.064</td>
<td>0.03</td>
<td>0.0072 ± 0.001</td>
<td>0.006</td>
<td>0.013</td>
<td>0.006</td>
<td>0.006</td>
<td>0.006</td>
</tr>
<tr>
<td>Clade IV</td>
<td>0.061</td>
<td>0.029</td>
<td>0.036</td>
<td>0.0042 ± 0.001</td>
<td>0.013</td>
<td>0.006</td>
<td>0.006</td>
<td>0.006</td>
</tr>
<tr>
<td>Clade V</td>
<td>0.089</td>
<td>0.073</td>
<td>0.082</td>
<td>0.086</td>
<td>0.0038 ± 0.001</td>
<td>0.013</td>
<td>0.013</td>
<td>0.013</td>
</tr>
<tr>
<td>Clade VII</td>
<td>0.061</td>
<td>0.026</td>
<td>0.032</td>
<td>0.03</td>
<td>0.082</td>
<td>0.0042 ± 0.001</td>
<td>0.005</td>
<td>0.006</td>
</tr>
<tr>
<td>Clade VIII</td>
<td>0.057</td>
<td>0.024</td>
<td>0.033</td>
<td>0.014</td>
<td>0.083</td>
<td>0.026</td>
<td>0.004 ± 0.001</td>
<td>0.007</td>
</tr>
<tr>
<td>Clade IX</td>
<td>0.066</td>
<td>0.031</td>
<td>0.033</td>
<td>0.034</td>
<td>0.077</td>
<td>0.033</td>
<td>0.033</td>
<td>0.0013 ± 0.001</td>
</tr>
</tbody>
</table>

(c) ATPsβ
(d) CalM

<table>
<thead>
<tr>
<th></th>
<th>Clade I</th>
<th>Clade II</th>
<th>Clade IV</th>
<th>Clade V</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clade I</td>
<td>0.003 ± 0.002</td>
<td>0.018</td>
<td>0.022</td>
<td>0.028</td>
</tr>
<tr>
<td>Clade II</td>
<td>0.036</td>
<td>0.002 ± 0.001</td>
<td>0.015</td>
<td>0.031</td>
</tr>
<tr>
<td>Clade IV</td>
<td>0.052</td>
<td>0.035</td>
<td>0.001 ± 0.001</td>
<td>0.033</td>
</tr>
<tr>
<td>Clade V</td>
<td>0.078</td>
<td>0.088</td>
<td>0.104</td>
<td>0.003 ± 0.002</td>
</tr>
</tbody>
</table>
Appendix 4. List of Goniopora haplotypes defined with the ITS region.

H 1: 2  [AD068Xa  SA1857]
H 2: 1  [AD068Xb]
H 3: 3  [BA032Xa  BA070Xa  BA099]
H 4: 2  [BA032Xb  BA070Xb]
H 5: 52  [BA078Xa  DJ004  DJ321  MU139Xa  SA1434  SA1438a  SA1483Xa  SA1567  SA1601  SA1602a  SA1624Xa  SA1629  SA1688  SA1689Xa  SA1692Xb  SA1710  SA1803a  SA1828Xa  SA1860Xb  SA1861Xa  SA1881Xa  SA1884Xa  SA1886  SA1890Xb  SA1985Xb  SA1992Xb  SA1998Xb  SA2005Xb  BA078Xb  DJ073  SA1392Xb  SA1441a  SA1483Xb  SA1568Xb  SA1598Xa  SA1598Xb  SA1624Xb  SA1628Xb  SA1633Xb  SA1689Xb  SA1691  SA1718Xa  SA1794  SA1795  SA1799Xb  SA1800Xb  SA1861Xb  SA1990  SA1999Xb  SA1599a  SA1602b  SA1686b]
H 6: 3  [MY100  DJ019Xb  DJ198Xb]
H 7: 2  [SA1707  SA1441b]
H 8: 1  [SA1802b]
H 9: 1  [MU139Xb]
H 10: 4  [SA1431b  SA1828Xb  SA1881Xb  SA1884Xb]
H 11: 1  [SA1431a]
H 12: 3  [SA1802a  SA1803b  SA1981b]
H 13: 1  [SA1438b]
H 14: 1  [SA1599b]
H 15: 1  [SA1718Xb]
H 16: 1  [SA1981a]
H 17: 18  [DJ019Xa  DJ198Xa  SA1389  SA1392Xa  SA1568Xa  SA1628Xa  SA1633Xa  SA1799Xa  SA1800Xa  SA1989  SA1999Xa  SA1692Xa  SA1860Xa  SA1890Xa  SA1985Xa  SA1992Xa  SA1998Xa  SA2005Xa]
H 18: 1  [SA1993]
H 19: 3  [AK18Xa AK18Xb TN40Xa]
H 20: 5  [AM26Xb AM48 MO36Xa MO36Xb OT29Xa]
H 21: 1  [KS31b]
H 22: 1  [TN115b]
H 23: 3  [KS28b KS57b YO10Xb]
H 24: 2  [TN113a TN113b]
H 25: 2  [TN55Xa TN55Xb]
H 26: 16  [AM30 AM75Xa AM89 AO58 IR13Xa IR22Xa KS28a KS31a KS57a MO53 MO63Xa OU2 SR62a SR62b TN95a TN95b]
H 27: 3  [AM74 KS51 KS9a]
H 28: 1  [KS9b]
H 29: 1  [TN115a]
H 30: 16  [AM26Xa SR14a SR14b DJ323 IR13Xb IR42b IS20a KK16 OU21a OU28Xa OU7 SA1563a SR23Xa SR24 SR44a TN40Xb]
H 31: 2  [IR3 OU21b]
H 32: 1  [IR67b]
H 33: 3  [IS19 SS35a SS35b]
H 34: 15  [IR42a KK60b SA1396a SA1482a SA1536a SA1632a SA1738a SA1773a SA1826a SA1885a SA1983a SA1984 SA1991a SA1994a SA2004a]
H 35: 1  [SA1432a]
H 36: 3  [SA1566b SA1978b SA2007b]
H 37: 3  [SA1537a SA1888a SA1977a]
H 38: 1  [SA1714a]
H 39: 3  [IR67a IS20b KK60a]
H 40: 5  [IR22Xb MO40Xa OU28Xb SR23Xb YO10Xa]
| H 41: 2 | [MO40Xb MO63Xb] |
| H 42: 1 | [SR44b] |
| H 43: 4 | [MO16 OT29Xb YO1a YO1b] |
| H 44: 1 | [SA1540a] |
| H 45: 1 | [SA1565a] |
| H 46: 2 | [SA1566a SA1596a] |
| H 47: 1 | [SA1621a] |
| H 48: 1 | [SA1772b] |
| H 49: 1 | [SA1430a] |
| H 50: 1 | [SA1891] |
| H 51: 1 | [AM75Xb] |
| H 53: 1 | [SA1414] |
| H 54: 1 | [SA1415a] |
| H 55: 1 | [SA1486] |
| H 56: 1 | [SA1562] |
| H 57: 2 | [SA1994b SA2004b] |
| H 58: 1 | [SA1717b] |
| H 59: 1 | [SA1395Xa] |
H 60: 1  [SA1415b]
H 61: 2  [SA1529Xb SA1866Xb]
H 62: 1  [SA1531Xb]
H 63: 3  [SA1621b SA1693Xb SA1829a]
H 64: 2  [SA1797Xb SA1829b]
H 65: 1  [SA1798b]
H 66: 1  [SA1398Xa]
H 67: 1  [SA1440a]
H 68: 1  [SA1539]
H 69: 1  [SA1432b]
H 70: 2  [SA1570 SA2007a]
H 71: 1  [SA1847b]
H 72: 1  [SA1831b]
H 73: 1  [SA1685a]
H 74: 1  [SA1796b]
H 75: 1  [SA1883a]
H 76: 1  [SA1796a]
H 77: 2  [OT30 OU33]
H 78: 2  [AK2a TR1b]
H 79: 2  [AK2b AK8b]
H 80: 2  [IS7b TR1a]
H 81: 2  [KK53b TN12b]
H 82: 1  [AK8a]
H 83: 6 [AO28a IS7a AO87 TN12a TR4a TR4b]
H 84: 1 [KK53a]
H 85: 1 [AO28b]
H 86: 3 [IR61Xa TR85a TR85b]
H 87: 3 [IR61Xb KK50 OU29]
H 89: 2 [SA1391Xb SA2010Xa]
H 90: 3 [SA1399b SA1600b SA2010Xb]
H 91: 1 [SA1429Xa]
H 92: 2 [SA1429Xb SA1988b]
H 93: 1 [SA1711Xb]
H 94: 1 [SA1894Xb]
H 95: 1 [SA1987a]
H 96: 1 [SA1987b]
H 97: 1 [SA1631b]
H 98: 1 [DJ074]
H 99: 2 [PEN9 SA1631a]
H 100: 1 [SA1390Xb]
H 101: 2 [SA1997Xb SA2001Xb]
H 102: 1 [SA2006Xb]
H 103: 3 [SA1980a SA2000a SA2019a]
H 104: 1 [SA1980b]
H 105: 2 [SA1634b SA1684b]
H 106: 3 [BU034 BU039a BU063a]
H 107: 4 [BU039b BU063b SA1571 SA1572Xb]
H 108: 1 [SA1572Xa]
H 109: 1 [OU43]
H 110: 4 [OU12 OU14 OU22 OU26]
H 111: 1 [OU20]
H 112: 1 [OU24]
H 113: 3 [NK1 OU19 OU41Xa]
H 114: 1 [OU17]
H 115: 1 [OU41Xb]
H 116: 3 [IR27Xa IR27Xb IR65]
H 117: 5 [KK11Xa OT14Xa OT14Xb TN41Xb TN42Xa]
H 118: 1 [KK11Xb]
H 119: 1 [TN41Xa]
H 120: 1 [TN42Xb]
H 121: 4 [KK22a KK4a TN11a TN11b]
H 122: 1 [PEN29Xa]
H 123: 1 [PEN29Xb]
H 124: 1 [KK22b]
H 125: 1 [TN29Xa]
H 126: 1 [MO23a]
H 127: 1 [KK27a]
H 128: 1  [KK27b]
H 129: 1  [MO23b]
H 130: 1  [KK4b]
H 131: 1  [OT19]
H 132: 1  [OT27]
H 133: 1  [OT24Xa]
H 134: 1  [OT24Xb]
H 135: 1  [TN54b]
H 136: 1  [TN54a]
H 137: 1  [OT31]
H 138: 3  [TN29Xb TN2a TN2b]
H 139: 4  [AM85 KK28Xa OT15Xa OT18Xa]
H 140: 2  [IS18 KK28Xb]
H 141: 3  [KS15 OT15Xb OT18Xb]
H 142: 2  [TN53a TN53b]
H 143: 7  [AO135 IS27 IS3Xa IS48 IS4Xa MI6 MY029]
H 144: 2  [IS3Xb IS4Xb]
H 145: 1  [IR34]
H 146: 16  [DJ142 DJ294 SA1416 SA1597b SA1625Xb SA1635Xa SA1636 SA1637b SA1709Xb SA1865 SA1880 SA1887 SA2011 SA2014b SA2015b SA2017Xa]
H 147: 9  [SA1437 SA1533Xb SA1625Xa SA1709Xa SA1801 SA1804Xb SA1862 SA1864 SA2012a]
H 148: 4  [SA1533Xa SA1597a SA1804Xa SA1863a]
H 149: 1  [SA1637a]
H 150: 1  [SA1715]
H 151: 2  [SA1863b SA2012b]
H 152: 1  [SA2017Xb]
H 153: 1  [SA1635Xb]
H 154: 2  [SA2014a SA2015a]
H 155: 1  [SA2013]
Appendix 5. Phylogeny reconstruction of Goniopora from the Red Sea based on Bayesian inference (BI) analysis of the ITS region. Bayesians posterior probability (left) higher than 0.7, ML bootstrap values (middle) higher than 70, and MP bootstrap values (right) higher than 50, are displayed on the nodes.
Appendix 6. List of *Goniopora* haplotypes defined with ATPsβ.


H 2: 11  [SA1599b SA1624Xb SA1567a SA1599a SA1707b SA1710a SA1794Xb SA1795a SA1881Xb SA1993a SA2005b]

H 3: 3  [SA1691Xb SA2005a SA1707a]

H 4: 1  [SA1884a]

H 5: 5  [SA1799b SA1992b SA1389b SA1688 SA1718a]

H 6: 1  [SA1981b]

H 7: 3  [SA1628 SA1998b SA1633b]

H 8: 2  [DJ019b SA1686b]

H 9: 2  [SA1718b SA1886b]

H 10: 1  [SA1800b]

H 11: 1  [SA1800a]


H 13: 1  [SA1690Xb]

H 14: 7  [DJ073Xb SA1390Xb SA1433Xb SA1600Xb SA1684Xb SA1687Xb SA1711Xb]

H 15: 2  [SA1571 SA1572]

H 16: 13  [DJ142 SA1615 SA1625 SA1635 SA1636 SA1637 SA1801 SA1804 SA1833 SA1856Xb SA1862 SA1864 SA1865]

H 17: 2  [SA2011 SA2017]
H 18: 7 [SA2014Xb SA1533 SA1709 SA1856Xa SA1880 SA1887 SA2014Xa]

H 19: 1 [SA2013]

H 20: 25 [DJ048a SA1381 SA1396a SA1397b SA1417Xb SA1419Xb SA1430Xb SA1436Xb SA1442Xb SA1485Xb SA1530b SA1531a SA1535a SA1536Xb SA1539Xb SA1562b SA1564Xb SA1595Xb SA1685b SA1832Xb SA1983a SA1994Xb SA2004a SA2007Xb SA2009b]


H 22: 2 [SA1486b SA1540b]

H 23: 2 [SA1540a SA1693]

H 24: 6 [SA1712b SA1738Xb SA1885b SA1888Xb SA1891 SA2021b]
Appendix 7. Phylogeny reconstruction of *Goniopora* from the Red Sea based on Bayesian inference (BI) analysis of ATPsβ. Bayesians posterior probability (left) higher than 0.7, ML bootstrap values (middle) higher than 70, and MP bootstrap values (right) higher than 50, are displayed on the nodes.
Appendix 8. List of Goniopora haplotypes defined with CalM.


H 3: 4 [DJ073b SA1389b SA1601b SA1992b]


H 5: 11 [DJ142 DJ294 SA1625 SA1636a SA1636 SA1801 SA1862a SA1887 SA2012 SA2013a SA2014a]

H 6: 64 [DJ295b DJ323 SA1395b SA1396b SA1398a SA1400a SA1414 SA1417a SA1420b SA1428b SA1430b SA1436b SA1439b SA1440b SA1481a SA1485b SA1486b SA1529b SA1531 SA1536b SA1537b SA1538 SA1539a SA1540 SA1541a SA1565b SA1566 SA1571a SA1572a SA1595b SA1596a SA1621a SA1626b SA1632b SA1670a SA1670b SA1693a SA1712b SA1714b SA1716 SA1717a SA1741 SA1772b SA1773a SA1796b SA1829a SA1831 SA1853b SA1883 SA1885 SA1888a SA1889 SA1892a SA1892b SA1893 SA1986a SA1994 SA2004 SA2007b SA2018b SA2024 SA1442a SA1535b]

H 7: 5 [SA1398b SA1417b SA1481b SA1891a SA1986b]

H 8: 3 [SA1399a SA1627a SA1684a]

H 9: 1 [SA1400b]

H 10: 4 [SA1415a SA1420a SA1439a SA1826a]

H 11: 3 [SA1415b SA2009b SA1535a]

H 12: 12 [SA1416a SA1437a SA1533a SA1635a SA1637a SA1862b SA1863a SA1865a SA2011a SA2013b SA2014b SA2017a]
H 13: 7 [SA1416b SA1635b SA1863b SA1864b SA1865b SA2011b SA2012b]
H 14: 1 [SA1431a]
H 15: 1 [SA1431b]
H 16: 2 [SA1434a SA1567a]
H 17: 1 [SA1435a]
H 18: 2 [SA1435b SA1482b]
H 19: 9 [SA1437b SA1597 SA1637b SA1709a SA1715 SA1864a SA1880 SA2012a SA2015]
H 20: 5 [SA1438b SA1602a SA1628b SA1985b SA1999b]
H 21: 6 [SA1482a SA1539b SA1569b SA1570b SA1693b SA1798b]
H 22: 2 [SA1483b SA1981a]
H 23: 2 [SA1533b SA2017b]
H 24: 8 [SA1541b SA1596b SA1621b SA1797b SA1827a SA1830a SA1978b SA1991b]
H 25: 2 [SA1571b SA1572b]
H 26: 4 [SA1598b SA1718b SA1800b SA1860b]
H 27: 4 [SA1600 SA1634 SA1987 SA1988a]
H 28: 5 [SA1602b SA1629b SA1633b SA1799b SA1802b]
H 29: 1 [SA1633a]
H 30: 2 [SA1636b SA1709b]
H 31: 6 [SA1686b SA1718a SA1794b SA1828b SA1860a SA1884b]
H 32: 2 [SA1689a SA1890a]
H 33: 2 [SA1717b SA1773b]
H 34: 5 [SA1826b SA1827b SA1830b SA1888b SA1891b]
H 35: 1 [SA1829b]
H 36: 1 [SA1981b]
H 37: 1 [SA1442b]
H 38: 1 [SA1989a]
H 39: 1 [SA1984a]
Appendix 9. Phylogeny reconstruction of Goniopora from the Red Sea based on Bayesian inference (BI) analysis of CalM. Bayesians posterior probability (left) higher than 0.7, ML bootstrap values (middle) higher than 70, and MP bootstrap values (right) higher than 50, are displayed on the nodes.
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