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The hidden diversity of Saudi Arabian Red Sea octocorals revealed through a morpho-molecular assessment across bathymetric and latitudinal gradients

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Octocorals, a globally distributed class of Cnidaria, inhabit a wide range of environments, from cold to tropical waters and from shallow to deep-sea ecosystems. In the Red Sea, studies on octocoral diversity have mostly been focused on the Gulf of Aqaba and selected families or genera. While these studies have revealed a remarkable richness and diversity of shallow-water species, mesophotic and deep-sea octocoral research remains limited in the region, in particular along the Saudi Arabian coast. Here, we provide a first comprehensive assessment of this group's genetic diversity across the basin's bathymetric and latitudinal gradients. Following six Red Sea oceanographic expeditions and various biodiversity surveys conducted between 2020 to 2023, we analysed a collection of 728 octocoral specimens sampled along 13 degrees of latitude in the Saudi Arabian Red Sea, from shallow-water reefs to deep-sea habitats. We combined morphological identification and sequencing of mitochondrial barcode markers (*mtMutS* and *COI*) to delimit lineages. Our integrated results revealed the occurrence of 26 families and 56 genera in the basin from 3 to 859 m of depth. While the description of new species was beyond the scope of this work, here we provide a reference dataset for octocoral diversity from a biodiversity hotspot, as well as essential insights to inform biodiversity management and planning of conservation measures, particularly relevant for the rapidly developing Saudi Arabian Red Sea coast.

Keywords Integrative taxonomy, Mitochondrial DNA, Marine animal forests, Biodiversity hotspot, Mesophotic coral ecosystems

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The anthozoan class Octocorallia Haeckel, 1866 is a diverse group of cnidarians, commonly known as soft corals, sea fans, and sea pens[1]. They are characterised by the eight-fold symmetry of their polyps and the general lack of a hard calcium carbonate skeleton comparable to that of scleractinians, although they possess calcareous sclerites[2]. The class is globally distributed throughout cold, temperate, and tropical waters and can withstand a variety of environmental conditions from shallow to deep-water ecosystems[3], although the majority of the currently recognised taxa occur below 50 m depth[4,5]. They often grow in dense benthic communities and due to their three-dimensional structure form Marine Animal Forests (MAFs)[6,7], providing food, habitat and shelter to various marine species[4,8].

Despite the essential ecological roles they fulfil, the actual diversity of the Octocorallia remains uncertain, with species boundaries still unclear among most taxa[1,9]. In fact, while traditionally octocoral taxonomy and systematics have relied on morphological characters such as the colony growth forms, the shape and disposition of the polyps, and the morphology of the sclerites[2], integrated studies have highlighted the incongruence between molecular phylogenies and morphological classification, with extensive poly- or paraphyly of the majority of the historically recognised families and genera[9–11].

To address these challenges, integrated morpho-molecular studies are used to clarify octocoral diversity through the sequencing of barcode markers (*e.g.*, *COI*, *mtMutS*, *28S rDNA*[12]) and, more recently, Next-Generation Sequencing (NGS) techniques, such as the target-enrichment of Ultra-Conserved Elements (UCEs) and exons (*i.e.*, highly conserved regions of the genome shared across species[9,13]). These techniques have proven useful in resolving taxonomic ambiguities and have highlighted a need for future research in scantly explored regions and biodiversity hotspots[9] that could harbour unique species and evolutionary patterns[14]. Among such areas, the Red Sea represents a unique biodiversity hotspot, where environmental extremes and a complex geological history have shaped intriguing biodiversity and evolutionary patterns, leading to some of the highest known rates of endemicity for several marine taxa[15–18].

Rich octocoral collections were conducted during historical explorations in the Red Sea (*e.g.*, The "Pola" Expeditions to the Red Sea[19–23]). Since the 1980s, most studies on octocoral diversity and ecology in the Red Sea have focused on the Gulf of Aqaba (*i.e.*, the Eilat coast[24–26]), leading to the description of several new species[27–30]. However, studies on the Saudi Arabian Red Sea coast (hereafter SA Red Sea), extending *circa* 1800 km within and beyond the Gulf of Aqaba[31], remain scarce in comparison. Haverkort-Yeh et al.[32] provided a first integrated assessment of octocoral diversity in the Saudi Arabian region, reporting four families (Alcyoniidae Lamouroux, 1812, Nephtheidae Gray, 1862, Tubiporidae Ehrenberg, 1828 and Xeniidae Ehrenberg, 1828), 13 genera, and 28 species, based on nuclear and mitochondrial markers. However, that study primarily focused on the collection of shallow-water zooxanthellate soft corals, overlooking sea fans, sea pens, and azooxanthellate octocoral taxa. Similarly, literature focusing on the Red Sea octocoral fauna generally only include data collected above 30 m depth[23,33,34].

Studies such as[29,30,35–37] reported and described octocoral taxa in Mesophotic Coral Ecosystems (MCEs; 30–150 m depth[38]) in the basin, but were again mostly restricted to the Gulf of Aqaba and the northern Red Sea, and only three of them provided molecular data[29,30,37]. These studies reported the presence of 21 families, 47 genera and 99 species of octocorals in Red Sea MCEs. Yet, given the Red Sea environmental latitudinal gradients (temperature increasing from north to south and higher salinities and productivity in the southern part of the basin[16,39,40]) and the known shallow-water fauna distribution trends (*e.g.*, scleractinian coral host species and their symbionts more adapted to warmer and saltier conditions occur in the southern area[41–43]), the Red Sea MCEs octocoral diversity described to date might be greatly underestimated and not representative for the whole basin and its bathymetric profile. In fact, in the Saudi Arabian region, the diversity of octocorals at depth is still largely unknown. Isolated studies have documented their presence and/or collected samples in the deep Red Sea[44–46], with specimens identified to family or genus level based on gross colony morphology (*i.e.*, colony growth form and branching pattern), and a single study applying an integrated morpho-molecular approach[47].

The scarcity of published genetic data for octocorals from the Red Sea basin significantly hampers specimen identification and species delimitation, a challenge further compounded by the paucity of comparative material from adjacent regions such as the Gulf of Aden, Arabian Sea, and Persian Gulf. Given that existing surveys have predominantly focused on shallow-water taxa of the Red Sea[22,33,34] and the Persian Gulf[48–50], the marine ecosystems surrounding the Arabian Peninsula remain a critical knowledge gap in efforts to advance our understanding of octocoral diversity across the Indo-Pacific. Recent explorations along the Red Sea bathymetric and latitudinal gradients provided an unprecedented opportunity to collect invertebrate specimens at depth and integrated morpho-molecular approaches allowed better characterisation of their diversity in the basin[41–53]. So far, these efforts led to the formal description of new species from the Red Sea (*e.g.*, black coral, hydrozoan, and crustacean species[54–56]). However, to date, patterns of octocoral molecular diversity and distribution along the Red Sea basin remain unexplored.

The aim of this study is therefore to provide the first comprehensive assessment of octocoral diversity along the latitudinal and bathymetric gradients of the SA Red Sea, with a focus on the so far unexplored mesophotic and deep-water ecosystems while also including new shallow-water collections. Here, we examined a collection of 728 octocorals obtained from six oceanographic expeditions and various biodiversity surveys conducted in the SA Red Sea from 2020 to 2023. Through an integrated morpho-molecular approach, coupling traditional morphological taxonomy with the information from two mitochondrial markers, we identified specimens and investigated their evolutionary relationships. As many aspects of octocoral evolutionary history are still unresolved, this dataset provides a valuable baseline for future research, representing the most comprehensive phylogenetic study on octocorals from the Red Sea region to date and provisioning molecular data from a biodiversity hotspot. Based on these results, we explored the occurrence patterns of the identified octocoral genera to understand their distribution and zonation and ultimately better inform conservation actions for the SA Red Sea.

Results

Morphological results

In total, we examined 728 octocoral specimens from the eastern Red Sea collected from 3.5 to 858.5 m depth and spanning 13 degrees of latitude along the Saudi Arabian Exclusive Economic Zone (Fig. 5). Based on macro- and micromorphological examinations, specimens were assigned to two orders (Malacalcyonacea McFadden, van Ofwegen & Quattrini, 2022 and Scleralcyonacea McFadden, van Ofwegen & Quattrini, 2022), 26 families, and 56 genera, two of which are currently *incertae sedis*. Of the identified taxa, five families and nine genera are new occurrence records for the basin (Table 1, Supplementary Material 1a).

Octocoral genera such as *Acanthomuricea*, *Altumia*, *Briareum*, *Cladiella*, *Heteroxenia*, *Klyxum*, *Lemnalia*, *Muricella*, *Solenocaulon*, and *Sympodium*, known to occur in the Red Sea[32,35,37], were not found in our study, likely due to our sampling extensively focusing on mesophotic and deep-water taxa, while possibly overlooking shallow-water soft coral taxa.

New Red Sea octocoral records

Our SA Red Sea dataset revealed the presence of five families namely, Acrossotidae, Aquaumbridae, Carijoidae, Coralliidae, and Parasphaerascleridae, and nine genera namely, *Aquaumbra*, *Calicogorgia*, *Carijoa*, *Cyclomuricea*, *Pacifiphyton*, *Paraminabea*, *Parasphaerasclera*, *Paratelesto*, and *Scleranthelia*, that represent new records for the basin (Fig. 1). These morphological identifications were also confirmed by phylogenetic reconstructions (Fig. 2). The newly recorded genera in the SA Red Sea spanned a broad latitudinal and bathymetric range. Specimens belonging to the family Acrossotidae were found in shallow waters of the central SA Red Sea (Table 1; Figure 1; Supplementary Material 1a). The genera *Aquaumbra, Calicogorgia*, *Carijoa*, *Cyclomuricea*, *Pacifiphyton, Paraminabea* and *Parasphaerasclera* occurred at mesophotic depths (Table 1; Fig. 1; Supplementary Material 1a). The genus *Paratelesto* showed the widest latitudinal distribution, occurring from the northern to southern SA Red Sea at mesophotic depths (Table 1; Fig. 1; Supplementary Material 1a). Lastly, *Scleranthelia*, the deepest-occurring genus among the new records, was found at 403 m depth in the northern SA Red Sea (Table 1; Fig. 1; Supplementary Material 1a). These new records collectively highlight a significant expansion of known octocoral diversity across both the bathymetric and latitudinal gradients of the basin.

Molecular results

We successfully amplified and sequenced the *mtMutS* and *COI* regions for 487 and 554 samples, respectively, for a total of 590 individual specimens. The newly obtained *mtMutS* sequences were combined with 280 sequences previously deposited in GenBank, while *COI* sequences were combined with 186 sequences available in GenBank. The two datasets were concatenated into a final alignment of 2251 bp. Samples that did not amplify or produced unreadable sequences (N = 138) were excluded from the analyses, and their morphological identification is reported in Supplementary Material 1a. At least one specimen for each of the morphologically identified taxa (Table 1) produced readable sequences (Fig. 2; Supplementary Material 2), except for the genera *Anthogorgia* Verrill, 1868 and *Nephthyigorgia* Kükenthal, 1910. Statistical information on the single locus and the final concatenated alignments is reported in Supplementary Material 3.

The topologies obtained from the BI and the ML analyses were mostly concordant for both the single locus and the combined reconstructions (Fig. 2; Supplementary Material 2). Overall, the phylogenetic reconstructions included specimens belonging to 2 orders, 60 families, and 257 genera of octocorals. The newly generated sequences for the Red Sea dataset represented two orders, 24 families, and 54 genera. Specifically, our Red Sea specimens fell into a total of 10 of the 12 major lineages identified by McFadden et al.[9].: two clades in the order Scleralcyonacea (clades S1 and S4) and eight in the order Malacalcyonacea (clades M1-M8) (see McFadden et al.[9] for complete descriptions of orders and clades) (Fig. 2, Supplementary Material 2). The Scleralcyonacea clades S2 and S3 were only constituted by sequences retrieved from GenBank and did not include any of our newly generated Red Sea sequences.

Nevertheless, our phylogenetic reconstruction presented some differences in the relationships found among and within the clades included in the order Malacalcyonacea (Fig. 2, Supplementary Material 2). Specifically, the two genera *Annella* and *Subergorgia*, belonging to the family Subergorgiidae, did not nest in a single M6 lineage in our phylogeny, but fell into two distant clades (Fig. 2a-b, Supplementary Material 2). Similarly, clade M8 was separated into six subclades within the order Malacalcyonacea in our phylogeny (Fig. 2a-b, Supplementary Material 2), and in particular the family Acanthogorgiidae and the genus *Acanthogorgia* were found to be paraphyletic in our study. Moreover, clade M3 was split into two subclades (Fig. 2a-b, Supplementary Material 2). The genera *Bebryce* and *Acanthoptilum*, belonging to the family Acanthogorgiidae and the superfamily Pennatuloidea, respectively, also formed paraphyletic clades (Fig. 2a-c, Supplementary Material 2).

The phylogenetic reconstruction presented here confirmed the identification of the taxonomic assignments based on morphological characters. Moreover, this reconstruction allowed us to identify cryptic specimens, such as those belonging to the family Acrossotidae and the genus *Cyclomuricea*, whose identification was only possible by matching their sequences to previously published records.

Latitudinal and bathymetric octocoral distribution in the Saudi Arabian Red Sea

The central and southern SA Red Sea hosted the highest rates of octocoral diversity in this study, with 67% and 69% of the identified taxa, respectively. Specifically, 96 specimens representing 25 genera were sampled

Family	*Genus*	N	GoA	NSA RS	CSA RS	SSA RS	Depth (m)
Acanthogorgiidae Gray, 1859	*Acanthogorgia* Gray, 1857	34	x	x	x	x	16–718
	Bebryce Philippi, 1842	10		x	x	x	8–494
	Calicogorgia Thomson & Henderson, 1906 *	1	x				135
	Echinomuricea Verrill, 1869	1			x		31
	Menella Gray, 1870	1			x		38
	Muriceides Wright & Studer, 1889	6	x	x	x	x	135–346
	Pseudoparacis Matsumoto & van Ofwegen, 2023	1				x	97
	Pseudothesea Kükenthal, 1919	6	x	x	x		66–118
	Villogorgia Duchassaing & Michelotti, 1860	45	x	x	x	x	73–597
	Acanthogorgiidae sp.	3	x	x			134–495
Acrossotidae Bourne, 1914 *	Acrossotidae sp. *	4			x		8–24
Anthogorgiidae McFadden, van Ofwegen & Quattrini, 2024	*Anthogorgia* Verrill, 1868	1		x			88
Aquaumbridae Breedy, van Ofwegen & Vargas, 2012 *	*Aquaumbra* Breedy, van Ofwegen & Vargas, 2012 *	1				x	115
Astrogorgiidae McFadden, van Ofwegen & Quattrini, 2024	Astrogorgiidae sp.	20	x	x	x	x	100–859
	Astrogorgia Verrill, 1868	16		x	x	x	22–118
Carijoidae McFadden, van Ofwegen & Quattrini, 2024 *	*Carijoa* Müller, 1867 *	1				x	50
Coralliidae Lamouroux, 1812 *	*Paraminabea* Williams & Alderslade, 1999 *	1			x		66
Ellisellidae Gray, 1859	*Ellisella* Gray, 1858	27	x	x	x	x	71–405
	Junceella Valenciennes, 1855	16		x	x	x	12–162
	Nicella Gray, 1870	26	x	x	x	x	93–552
	Verrucella Milne Edwards & Haime, 1857	18	x	x	x	x	72–224
	Viminella Gray, 1870	13	x	x	x	x	87–156
Euplexauridae McFadden, van Ofwegen & Quattrini, 2024	*Euplexaura* Verrill, 1869	15	x	x	x	x	48–348
Incertae sedis	*Scleranthelia* Studer, 1878 *	1		x			403
	Cyclomuricea Nutting, 1908 *	1		x			99
Isididae Lamouroux, 1812	*Rumphella* Bayer, 1955	11		x	x		15–25
Keroeididae Kinoshita, 1910	*Keroeides* Wright & Studer, 1887	8	x	x	x	x	88–621
Lemnaliidae Gray, 1869	*Paralemnalia* Kükenthal, 1913	6			x	x	11–21
	Rhytisma Alderslade, 2000	3	x			x	13–37
Melithaeidae Gray, 1870	*Melithaea* Milne Edwards, 1857	99	x		x	x	3–278
Nephtheidae Gray, 1862	*Dendronephthya* Kükenthal, 1905	30		x	x	x	7–260
	Litophyton Forskål, 1775	8			x	x	8–27
	Pacifiphyton Williams, 1997 *	1				x	125
	Scleronephthya Studer, 1887	7		x	x	x	52–248
	Stereonephthya Kükenthal, 1905	1		x			53
	Umbellulifera Thomson & Dean, 1931	1	x				180
Nephthyigorgiidae McFadden, van Ofwegen & Quattrini, 2024	*Nephthyigorgia* Kükenthal, 1910	1		x			85
Nidaliidae Gray, 1869	*Nidalia* Gray, 1835	4	x		x		89–134
Parasphaerascleridae McFadden & van Ofwegen, 2013 *	*Parasphaerasclera* McFadden & van Ofwegen, 2013 *	2			x	x	75–97
Parisididae Aurivillius, 1931	*Parisis* Verrill, 1864	3	x			x	97–134
Pennatulidae Ehrenberg, 1834	*Pteroeides* Herklots, 1858	4			x		39–47
Sarcophytidae Gray, 1869	*Lobophytum* Marenzeller, 1886	1				x	8
	Sarcophyton Lesson, 1834	10			x	x	8–51
	Sclerophytum Pratt, 1903	34	x	x	x	x	5–68
Siphonogorgiidae Kölliker, 1874	*Chironephthya* Studer, 1887	48	x	x	x	x	78–621
	Siphonogorgia Kölliker, 1874	45	x	x	x	x	32–542
Subergorgiidae Gray, 1859	*Annella* Gray, 1858	10		x	x	x	54–99
	Subergorgia Gray, 1857	7			x	x	10–49
Tubiporidae Ehrenberg, 1828	*Paratelesto* Utinomi, 1958 *	6	x	x		x	73–157
	Tubipora Linnaeus, 1758	69	x	x	x	x	6–38
Veretillidae Herklots, 1858	*Cavernulina* Kükenthal & Broch, 1911	1	x				312
Virgulariidae Verrill, 1868	*Acanthoptilum* Kölliker, 1870	4	x				92–211
	Scytaliopsis Gravier, 1906	9			x		12–43
	Scytalium Herklots, 1858	11	x	x	x	x	71–477
	Virgularia Lamarck, 1816	1				x	477
Continued							

Family	*Genus*	N	GoA	NSA RS	CSA RS	SSA RS	Depth (m)
Xeniidae Ehrenberg, 1828	*Anthelia* Lamarck, 1816	2			x	x	20–29
	Ovabunda Alderslade, 2001	3			x	x	12–31
	Xenia Lamarck, 1816	9		x	x	x	6–44

Table 1. Summary of the 728 octocoral specimens collected and identified for this study and their family and genus taxonomic assignment. For each taxon we report the number of specimens collected (N), the geographical occurrence based on our sampling in the Saudi Arabian Red Sea, and their known bathymetric range (Depth) based on the examined collection. GoA = Gulf of Aqaba; NSA RS = northern Saudi Arabian Red Sea; CSA RS = central Saudi Arabian Red Sea; SSA RS = southern Saudi Arabian Red Sea; * = new record for the Red Sea.

from the southern Gulf of Aqaba, 214 colonies belonging to 34 genera were sampled in the northern SA Red Sea, 221 specimens representing 39 genera were collected from the central SA Red Sea, and 197 belonging to 40 genera were sampled in the southern SA Red Sea (Table 1; Figs. 3, 4). Of these, four genera were found exclusively in the Gulf of Aqaba (*Calicogorgia*, *Umbellulifera*, *Cavernulina*, *Acanthoptilum*), five (*Anthogorgia*, *Cyclomuricea*, *Scleranthelia*, *Stereonephthya*, *Nephthyigorgia*) were only sampled in the northern SA Red Sea, six taxa (Acrossotidae, *Echinomuricea*, *Menella*, *Paraminabea*, *Pteroeides*, *Scytaliopsis*) were only found in the central SA Red Sea, and six genera (*Aquaumbra*, *Carijoa*, *Lobophytum*, *Pacifiphyton*, *Pseudoparacis*, *Virgularia*) were only found in the southern SA Red Sea (Fig. 3). An indication of the geographical distribution of each taxon sampled for the present study based on our sampling effort is provided in Table 1 and the coordinates and SA Red Sea area at which each specimen was collected are reported in Supplementary Material 1a.

While a consensus on the depth limit of the photic, mesophotic and aphotic zones has not been reached globally[38], in the Red Sea the mesophotic zone has been defined as extending from 30-150 m based on[38]. Throughout our SA Red Sea collection, octocoral colonies were collected from 3 to 859 m depth, encompassing a bathymetric range of 855 m. The highest levels of octocoral diversity were found in the mesophotic zone. Specifically, 265 colonies representing 24 genera were sampled from the photic zone in shallow waters (< 30 m), 232 specimens belonging to 47 genera were retrieved from the mesophotic zone (between 30 and 150 m), and 231 specimens ascribed to 25 genera extended into the aphotic zone of the deep SA Red Sea (> 150 m) (Fig. 4). In particular, five genera (*Melithaea*, *Dendronephthya*, *Bebryce*, *Junceella*, *Acanthogorgia*) were found to be depth generalists, extending from shallow to deep waters. Along the bathymetric gradient, six taxa, all of which are known to be zooxanthellate, only occurred in shallow waters (Acrossotidae, *Litophyton*, *Lobophytum*, *Paralemnalia*, *Rumphella*, *Anthelia*), 17 were sampled exclusively in the mesophotic zone, and four were only found in the deep SA Red Sea (*Umbellulifera*, *Cavernulina*, *Scleranthelia*, *Virgularia*) (Fig. 4). The collection depth for each specimen included in this study is indicated in Supplementary Material 1a.

Discussion

This study provides the first comprehensive morpho-molecular assessment of the diversity of the class Octocorallia in the SA Red Sea, based on a collection including more than 700 specimens spanning almost the entire latitudinal extension of the SA coast of the basin and a depth gradient of 855 m. For the first time, we report the presence of five families and nine genera never previously recorded in the Red Sea, and we provide an extensive molecular dataset for further assessments of octocoral diversity at all taxonomic levels and comparisons with other biogeographical areas and biodiversity hotspots beyond the Red Sea.

New Red Sea octocoral records

With this study, we expand the known number of octocoral families reported in the Red Sea from 24 to 29 and the number of nominal genera from 63 to 72, thus providing a 12.5% increase of known genus-level octocoral diversity for the basin[1,35,37,60]. In fact, for the first time we recovered specimens belonging to the family Acrossotidae and the genera *Aquaumbra* (family Aquaumbridae), *Calicogorgia* (family Acanthogorgiidae), *Carijoa* (family Carijoidae), *Cyclomuricea* (Octocorallia *incertae sedis*), *Pacifiphyton* (family Nephtheidae), *Paraminabea* (family Coralliidae), *Parasphaerasclera* (family Parasphaerascleridae), *Paratelesto* (family Tubiporidae), and *Scleranthelia* (Octocorallia *incertae sedis*). Moreover, we reported the presence of specimens belonging to the family Acanthogorgiidae, which neither morphologically, nor phylogenetically, correspond to any of the genera described to date. Notably, all of these newly recorded taxa, aside from those belonging to the family Acrossotidae, were collected from mesophotic and deep-water areas of the SA Red Sea, emphasising the importance of oceanographic explorations and biological sampling at depth to document biodiversity and unravel evolutionary patterns[4]. Given the degrees of colony, branching, and polyp variation observed for most of the genera identified in this study, further examination of the specimens included here may also lead to species-level identification of each morphotype and to the discovery of yet undescribed species. However, some octocoral taxa known to occur in the Red Sea, such as the genera *Acanthomuricea*, *Altumia*, *Briareum*, *Cladiella*, *Heteroxenia*, *Klyxum*, *Lemnalia*, *Muricella*, *Solenocaulon*, and *Sympodium*[32,35,37], were not found in our study. This may be due to a bias in our sampling efforts, perhaps overlooking soft coral diversity or rare taxa during shallow-water sampling, compared to previous taxonomic surveys that extensively focused on such groups (*e.g.*, [12,18,32,34]).

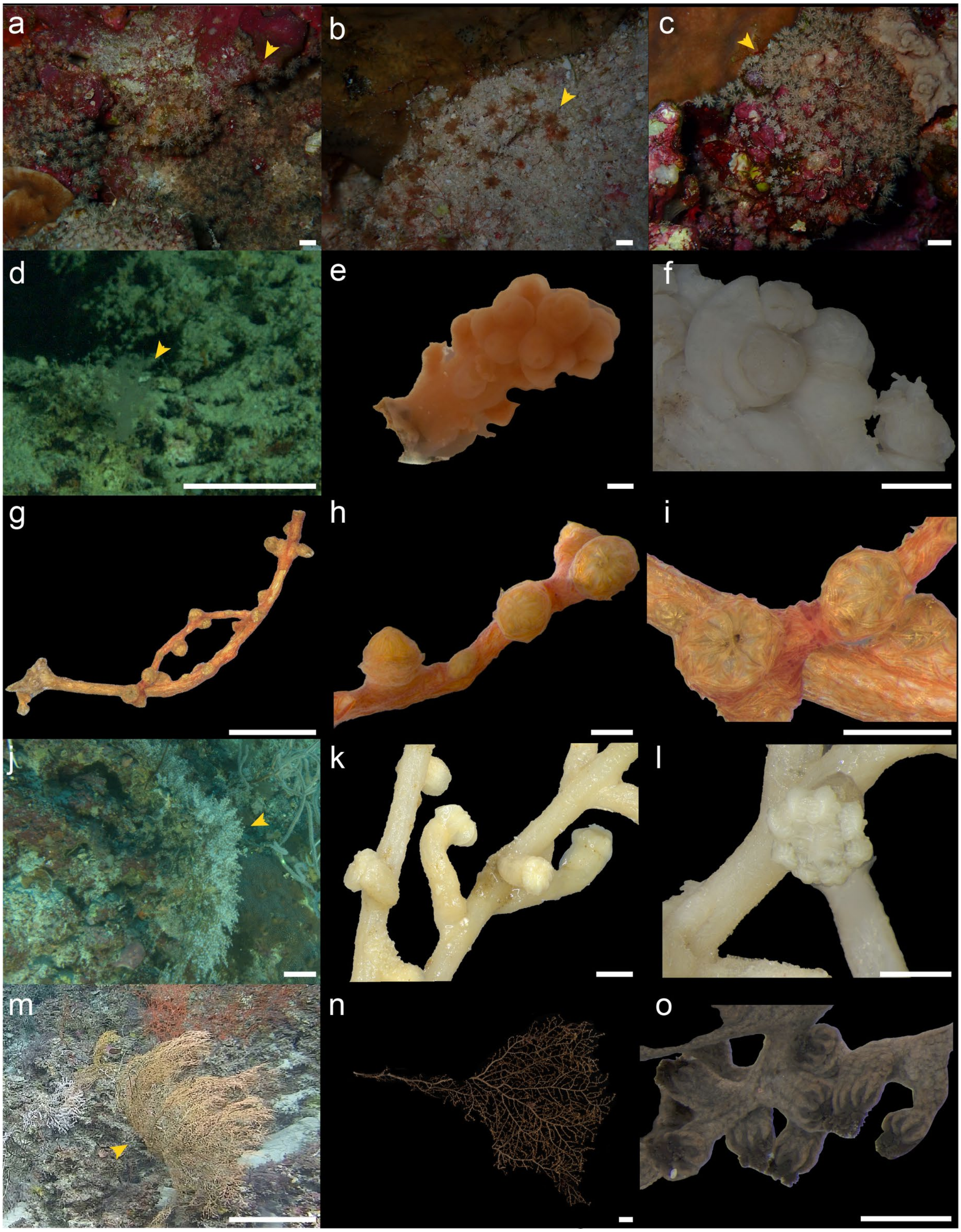

Fig. 1. New octocoral records for the Red Sea. Morphology of the *in situ* or fresh colonies (a-b-c-d-e-j-m-o-p-s-v-y-ab), dry or ethanol-preserved specimens (g-k-n-q-t-w-z-ac), and polyps (f-i-l-o-r-u-x-aa-ad): (**a**-**c**) Acrossotidae sp. indicated by yellow arrowheads (**d**-**f**) *Aquaumbra* sp. NTN0135BIO7 indicated by the yellow arrowhead (**g**-**i**) *Calicogorgia* sp. CHR0044-6H (**j**-**l**) *Carijoa* sp. NTN0134BIO30 indicated by yellow arrowheads (**m**-**o**) *Cyclomuricea* sp. CHR0047-4 (**p**-**r**) *Pacifiphyton* sp. NTN0135BIO16 (**s**-**u**) *Paraminabea* sp. NTN0122BIO16 (**v**-**x**) *Parasphaerasclera* sp. NTN0138BIO15 indicated by the yellow arrowhead (**y**-**aa**) *Paratelesto* sp. CHR0242BIO5B indicated by yellow arrowheads (**ab**-**ad**) *Scleranthelia* sp. NDR0914_3 indicated by yellow arrowheads. Scale bars: d, j, m, v, y: 10 cm; g, n, w, ab: 1 cm; a, b, c, e, f, h, i, k, l, o, p, q, r, s, t, u, x, z, aa, ac, ad: 1 mm.

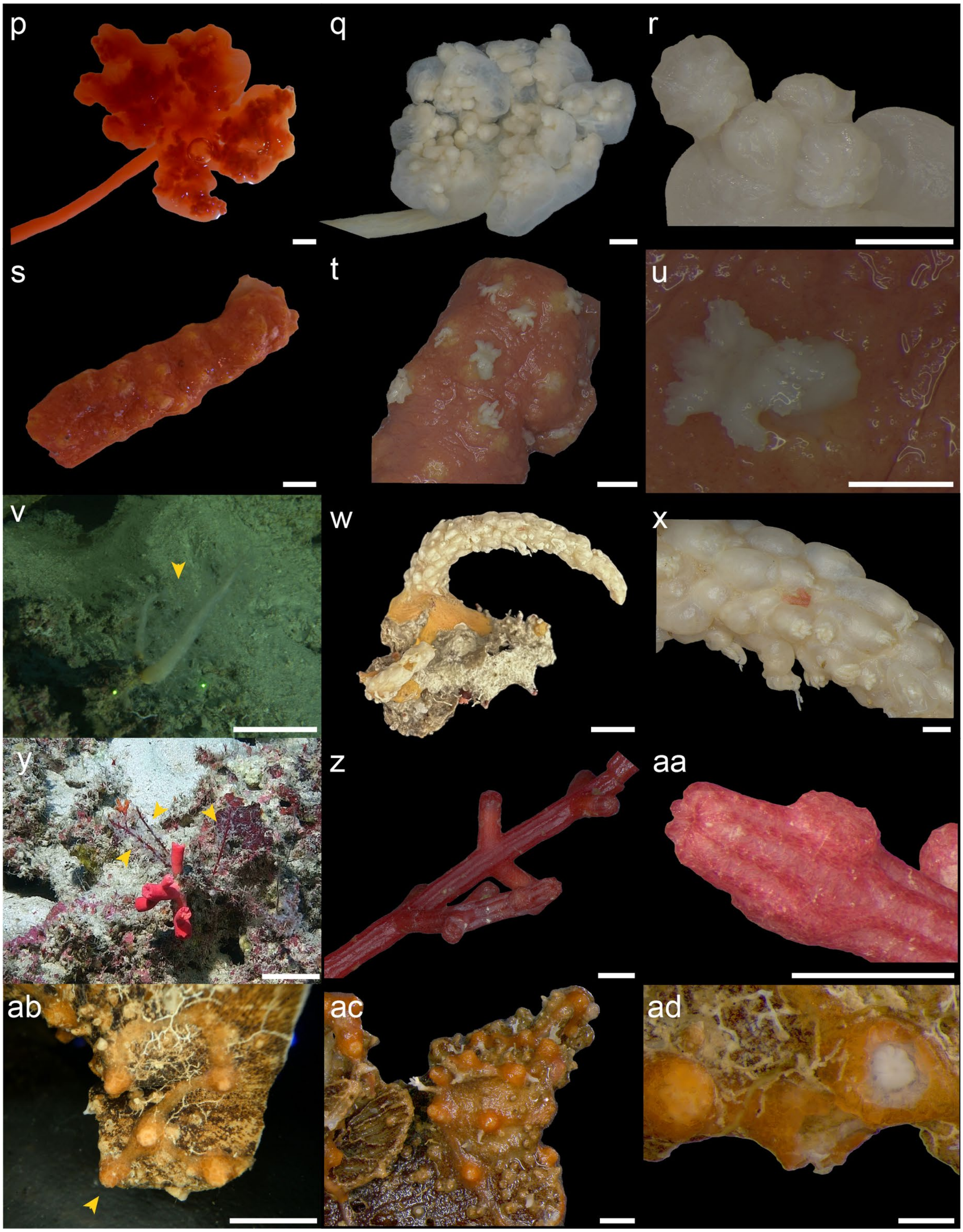

Fig. 1. (continued)

Phylogenetic relationships of Red Sea octocorals in the context of the Octocorallia class systematics

Following an unprecedented sampling effort along the latitudinal and depth extensions of the SA Red Sea, the sequences generated for this study represent the first available molecular data for many mesophotic and deep-sea taxa from the basin. While the phylogenetic trees generated for this study (Fig. 2, Supplementary Material 2) generally reflected the topology of the two major orders, Malacalcyonacea and Scleralcyonacea, some taxa appeared to nest into different clades than expected. However, as discussed by McFadden et al.[9], several of the

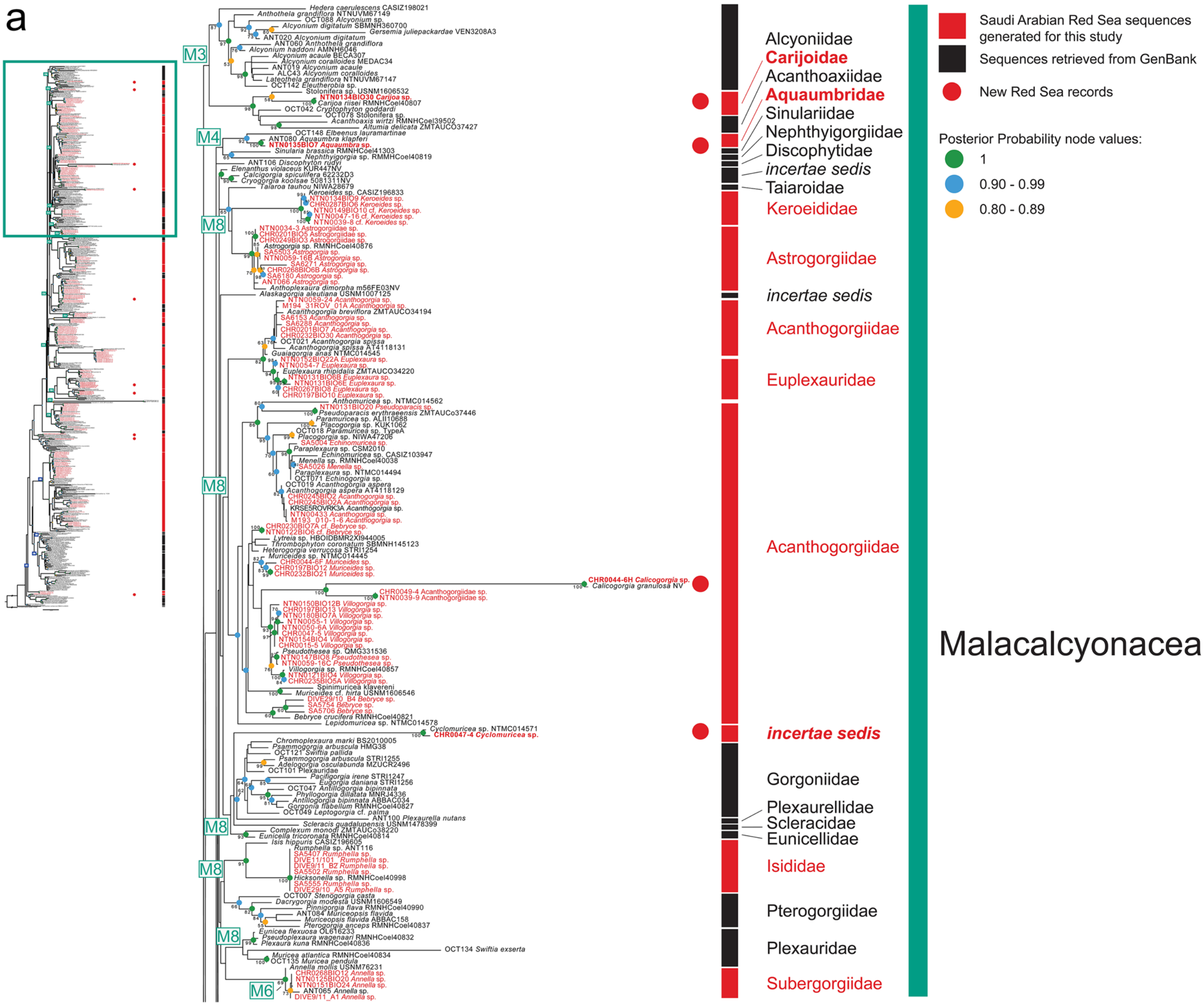

Fig. 2. Bayesian Inference phylogenetic reconstruction of Octocorallia inferred from the concatenation of the mitochondrial gene regions *mtMutS* and *COI*. Node circles correspond to Bayesian posterior probability (≥ 0.8) and node values correspond to Maximum Likelihood bootstrap values (≥ 80). The tree was rooted to *Cornularia pabloi*. Taxa for which new sequences were obtained from our SA Red Sea collection are in red, and red dots next to them indicate new records for the Red Sea. Numbered squares on tree branches indicate clades corresponding to those discussed in[9]. (**a**-**b**) Order Malacalcyonacea (**c**) Order Scleralcyonacea. A selection of the specimens sequenced for this study is presented here for clarity of the figure, the full phylogenetic tree including all the newly generated SA Red Sea sequences for this study is available as Supplementary Material 2.

taxa included in the order Malacalcyonacea have unstable relationships, which may be the reason why some of the subclades included in the order were retrieved throughout the lineage in our tree, for which the phylogenetic reconstruction was only based on mitochondrial markers without constraining it to genomic data[61]. For instance, the fact that the family Acanthogorgiidae and the genus *Acanthogorgia* were found to be paraphyletic in our study is consistent with the results of other analyses performed with traditional mitochondrial markers[47,62]. Although clade M8 is known to be monophyletic based on UCEs and exons data, McFadden et al.[9] also discussed the existence of several subclades therein, which could therefore explain the relationships found in our phylogenetic analyses.

Molecular insights from a biodiversity hotspot

Although it was not possible to fully compare the patterns of SA Red Sea octocoral molecular diversity with other biogeographic regions, such as the Atlantic or Pacific Oceans, for all the taxa included in this study, due to a lack of sequencing data, specimens of the genus *Melithaea* collected from the basin showed an interesting geographic signal when compared with specimens collected from Réunion Island (South Western Indian Ocean) (Supplementary Material 2). In fact, the material from the two regions grouped in two distinct and sister clades, confirming the existence of region-specific lineages[63]. These observations are in line with the findings of recent studies on the biogeography of Indo-Pacific soft corals, highlighting distinct and endemic lineages in the Red

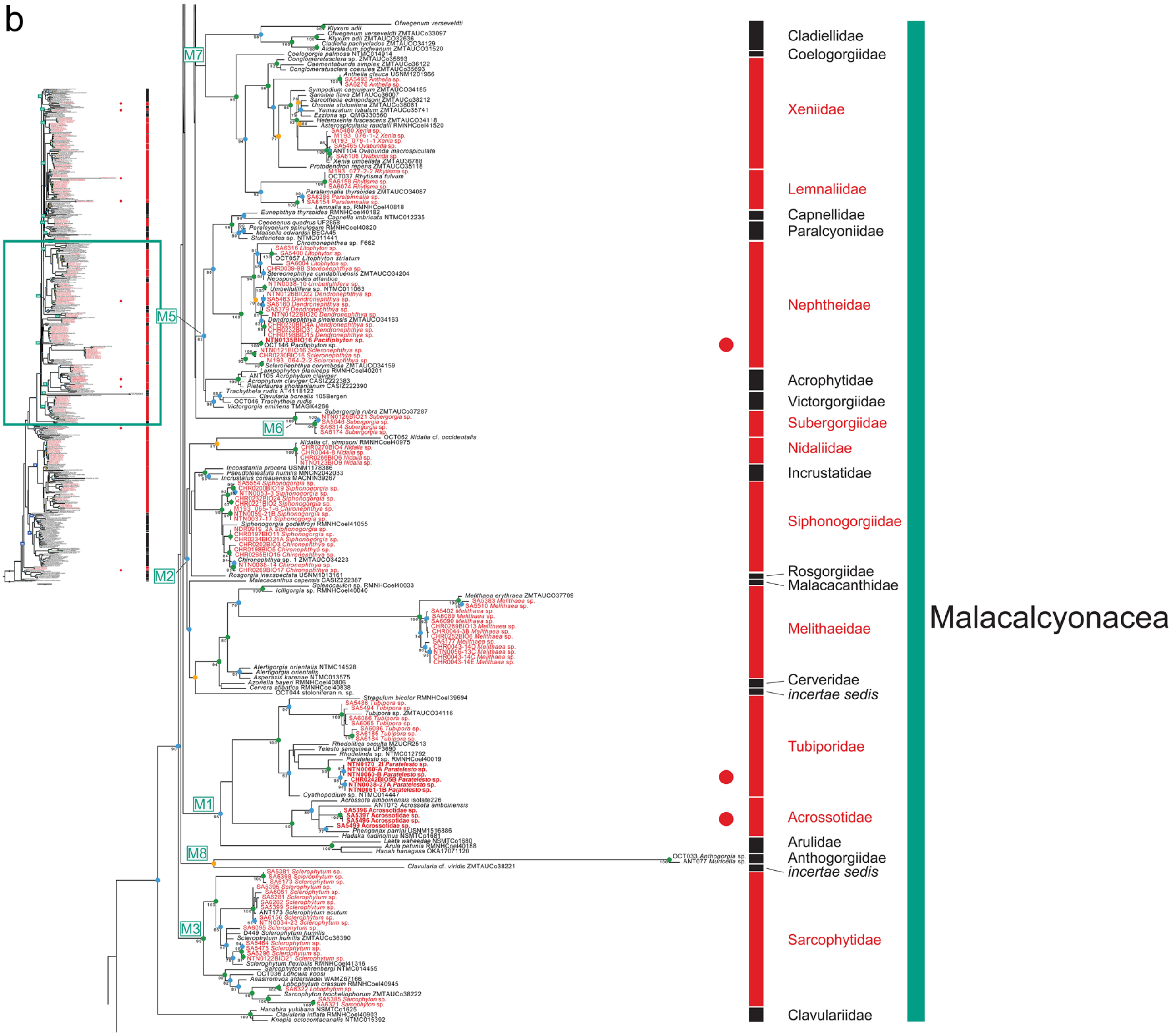

Fig. 2. (continued)

Sea and South Western Indian Ocean[18]. Although the investigation of these patterns is beyond the scope of this study, our specimens provide an opportunity to perform similar analyses for other families, such as the Ellisellidae, for which biogeography has been recognised as a potentially important systematic character but could not be fully addressed due to a lack of molecular data for specimens collected from the Red Sea[64]. Similarly, it has been reported that the diversity of octocoral assemblages may change across bathymetric ranges[5]. The depth gradient encompassed in the SA Red Sea by our specimens therefore warrants further analyses of the distribution of the reported lineages, to explore the potential occurrence of depth-specific lineages that may be found when thoroughly investigating abundant and diverse octocoral taxa in the basin and beyond (*e.g.*, the families Acanthogorgiidae, Ellisellidae, Melithaeidae, Siphonogorgiidae).

In addition to providing baseline genetic data for the octocoral class from the SA Red Sea, this study further highlights the value of integrative taxonomy to identify octocorals at the family and genus levels, even without molecular reference studies considering the same biogeographic area for many taxa. The topological differences in our trees and the instability of some clades, together with uncertainties on the actual number of species included in many octocoral genera due to a lack of variation in mitochondrial markers, also confirm the need of more advanced and informative techniques, such as genomics, when trying to address deeper evolutionary questions within and among nodes of the Octocorallia tree[65]. Accordingly, the levels of diversity presented in this study may be underestimated, and further studies addressing specific evolutionary questions within and among octocoral families and genera are needed to fully elucidate octocoral diversity in the Red Sea.

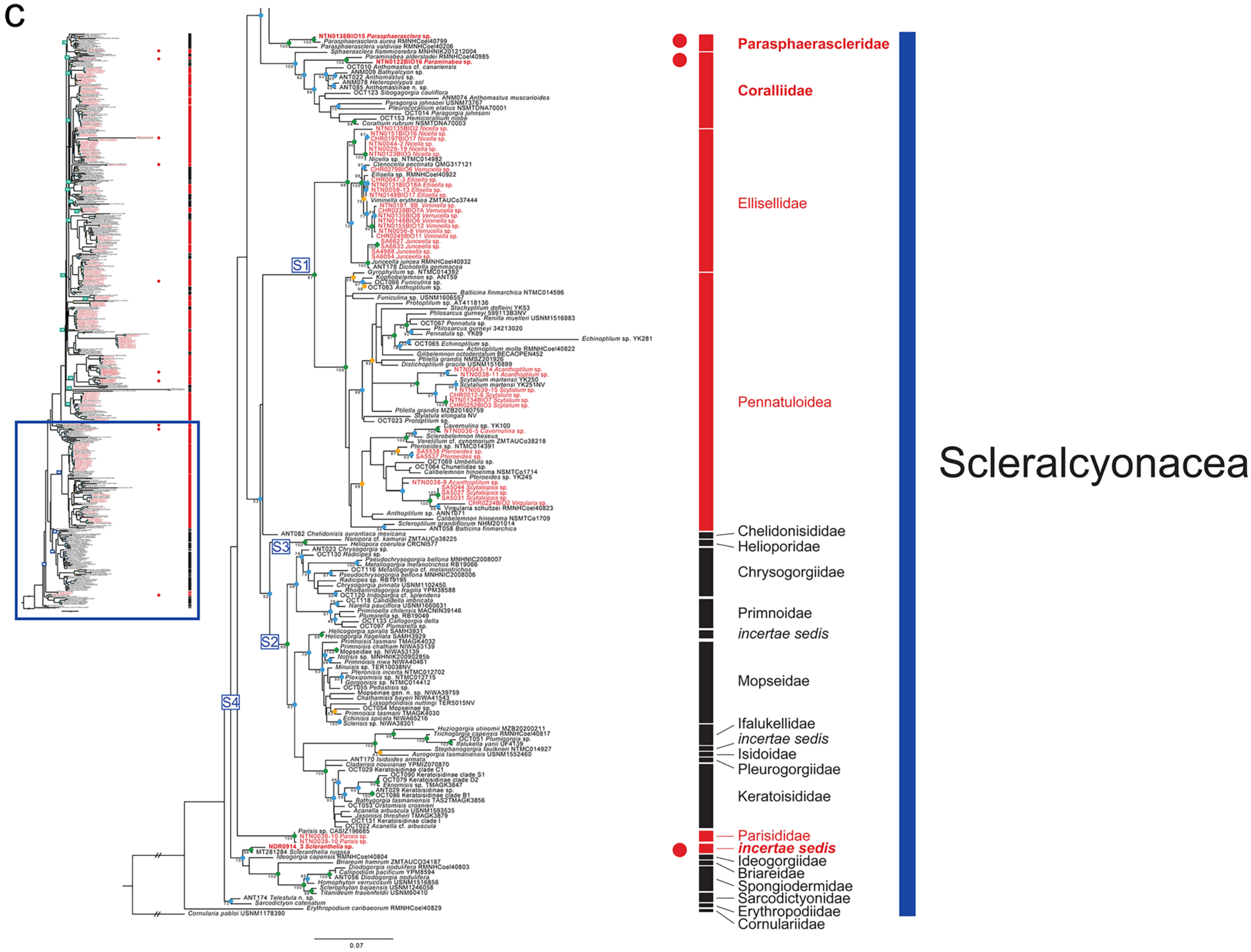

Fig. 2. (continued)

Octocorallia bathymetric and latitudinal distribution in the Saudi Arabian Red Sea

The depth zonation observed in the occurrence of octocoral taxa in the SA Red Sea could be due to the environmental conditions existing in the basin driving the evolution of these organisms[16]. The presence of genera such as *Acanthogorgia*, *Bebryce*, *Dendronephthya*, *Junceella* and *Melithaea* across extensive depth ranges from shallow to deep waters in our dataset (Fig. 4) indicates their ecological versatility and ability to withstand a variety of environmental conditions[1]. In contrast, the confinement of certain taxa to specific depth zones (*e.g.*, Acrossotidae and *Rumphella* in shallow waters, *Nidalia*, *Parisis* and *Pseudothesea* in MCEs, and *Scleranthelia*, *Umbellulifera* and *Virgularia* in the deep-sea) suggests niche specialization[66]. Partitioning of octocoral diversity across different bathymetric zones could also be driven by factors such as light availability for zooxanthellate taxa such as the members of the families Sarcophytidae and Xeniidae. As such, it is interesting to note that, based on our dataset, the zooxanthellate genera *Sclerophytum* and *Xenia* were found not only in shallow-waters, but also extended into the upper mesophotic (Table 1, Fig. 4), confirming the patterns reported by[37] for the Gulf of Aqaba. The mesophotic zone, in particular, exhibited the highest diversity of octocoral genera, a trend similar to the one previously reported in the Red Sea for other cnidarians such as black corals[53]. This observation suggests the role of MCEs as a critical habitat for octocoral biodiversity in the basin, as also reported for the Gulf of Aqaba[36] and for other regions beyond the Red Sea, such as the central Indian Ocean[67]. As[5] highlighted that mesophotic ecosystems may have prompted the evolution and diversification of several octocoral lineages, our findings raise questions about the role of these areas for octocoral diversification and community structure in the Red Sea, a basin characterised by extreme environmental conditions all along its bathymetric range[16,44]. In fact, taxa such as the genera *Pacifiphyton, Parasphaerasclera,* and *Paratelesto* were found to occur deeper in our dataset than expected for other areas of the world[68], which may be a result of the Red Sea water clarity, high temperatures, and oligotrophy shaping octocoral distribution in the basin. Accordingly, a more extensive molecular investigation may help document depth-specific lineages occurring in our dataset, and identification to the species level may provide further insights into the zonation of these organisms in the SA Red Sea, highlighting patterns of species distribution and zonation within each of the identified genera.

Overall, we found that only 15 of the genera we recorded occurred all along the latitudinal gradient of the SA Red Sea sampled in our study. The higher octocoral diversity shown by our results in the central and southern SA

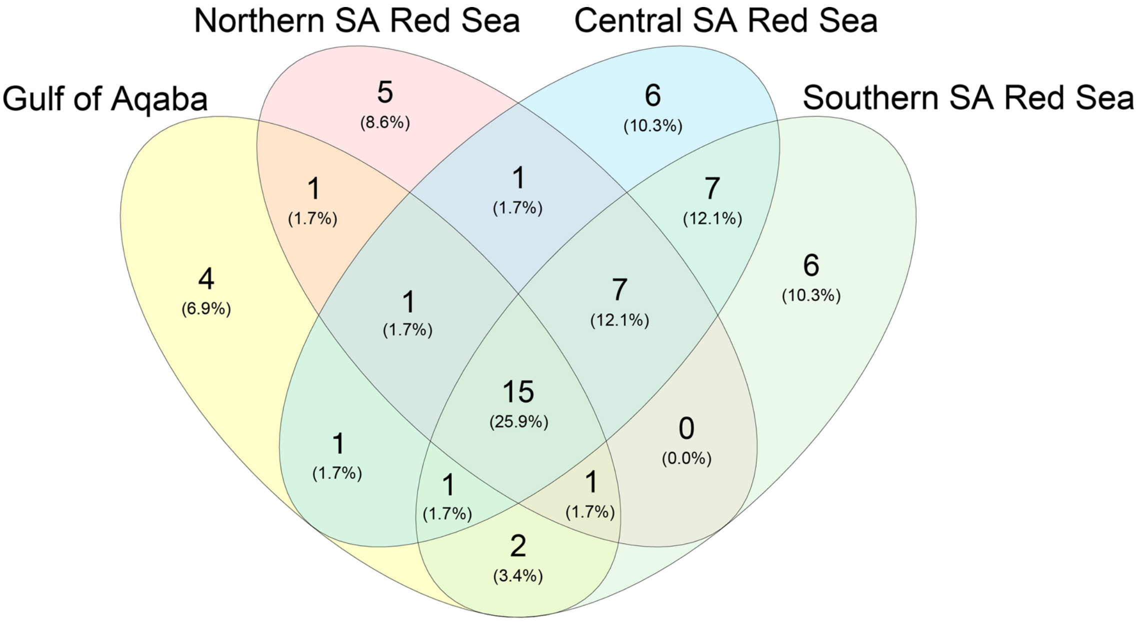

Fig. 3. Venn diagram showing the distribution of the octocoral genera occurring across the SA Red Sea as identified in this study: yellow represents the Gulf of Aqaba, pink the northern SA Red Sea, blue the central SA Red Sea, and green the southern SA Red Sea. The figure was created with the package *ggvenn*[57] in RStudio v4.3.0[58].

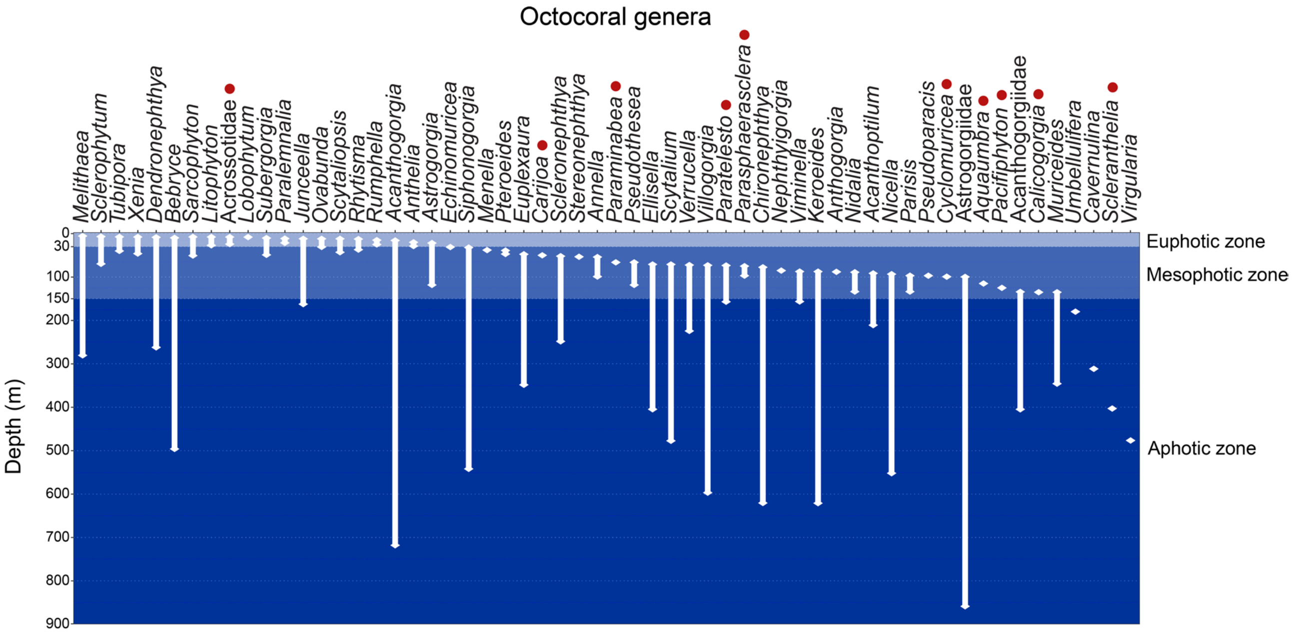

Fig. 4. Bathymetric distribution ranges of the octocoral taxa identified in our SA Red Sea dataset. Vertical double-headed arrows indicate the depth range encompassed for each taxon considering the minimum and maximum depth at which specimens were collected in this study. Red dots indicate new records for the Red Sea. Depth limits for the mesophotic zone are based on[38]. The figure was created with the package *ggplot2*[59] in RStudio v4.3.0[58].

Red Sea compared to the northern region (Fig. 3) is in contrast with the biodiversity trends previously reported for scleractinian corals, fish, and sponges, which were reported to have levels of diversity gradually decreasing from the northern to the southern areas of the basin[16]. In fact, previous assessments of marine fauna in the basin found that environmental gradients could explain the distribution of the Red Sea reef communities[16,69]. However, such studies only considered shallow-water taxa, while the sampling presented here encompassed the bathymetric gradient of the SA Red Sea. Therefore, these discrepancies may be due to the increased sampling effort in the mesophotic and aphotic zone, where octocoral communities are known to thrive[5–7].

Nevertheless, common octocoral taxa, such as those belonging to the Scleralcyonacea clade S2 (*e.g.*, the families Chrysogorgiidae, Keratoisididae, Primnoidae), known to be conspicuous and deep-water specialists in other oceans[70,71], were not found in our surveys. This may be due to a combination of geographic, ecological and environmental factors driving biodiversity patterns in the Red Sea[15]. For instance, the Bab al Mandab Strait may act as a physical barrier due to its relatively shallow sill (about 137 m), which may limit the exchange of deep-water fauna between the Red Sea and the Gulf of Aden and Indo-West Pacific. Moreover, taxa belonging to the Octocorallia clade S2 may be adapted to cold temperatures and low salinities as well as stable conditions in other oceans, and their thresholds of physiological tolerance may be exceeded in the deep Red Sea, preventing their colonization and survival. Finally, adapted and endemic Red Sea taxa may dominate deep environments in the basin, potentially outcompeting other colonisers and limiting their establishment.

The future of Octocorallia research in the Red Sea

The results of our current assessment warrant future investigations into octocoral evolutionary relationships in the Red Sea and beyond at all taxonomic levels. Moreover, this study provides a collection of specimens that can be used in future studies to address specific evolutionary questions and re-evaluate the rate of species-level endemism for octocorals in the basin. As for other marine invertebrates such as Scleractinia (Cnidaria, Anthozoa), mitochondrial markers often are not variable enough to distinguish species for many of the currently recognised families and genera[12,73,74]. Nevertheless, the combination of such markers with the sequencing of nuclear genes has proven useful to differentiate species in cnidarian groups[75–77]. Therefore, NGS and the target-enrichment of UCEs and exon loci[9,13] or genome skimming[62] approaches in many instances may help clarify the evolutionary history of taxa across the octocoral tree and disentangle species boundaries (as seen, for instance, for the family Keratoisididae Gray, 1870[78] and the genus *Alcyonium*[13]). The application of these techniques may also help elucidate the actual trends of octocoral diversity in the Red Sea, assessing their level of endemism and understanding if they follow the same patterns found by previous studies for scleractinian corals and fish in the region[15,16,79]. Since molecular data are not available to date for a majority of nominal octocoral species, it is also challenging to estimate species' geographic ranges and endemism rates. In fact, while studies have analysed these patterns for some soft coral families (*e.g.*, Lemnaliidae, Nephtheidae, Sarcophytidae, Xeniidae) in the Indo-Pacific region and found an endemism hotspot in the Red Sea, they also warned that given the low phylogenetic resolution provided by mitochondrial markers, results may be overlooking the actual levels of diversity and distribution of these families[18]. Nevertheless, species level identification within most octocoral families and genera is still challenging given the need for updated morphological descriptions and revision for many of the currently recognised taxa[9]. The combination of extensive surveys in understudied areas, sequencing of museum specimens representing the type material of the currently accepted nominal species (when available) as well as their re-description, and application of novel genomic approaches may therefore allow not only the refinement of species boundaries, but also the definition of more accurate biogeographical patterns and hotspots of endemism for octocoral taxa[78,80,81].

Implications for conservation in the Saudi Arabian Red Sea

Coral reefs, MAFs, MCEs and deep-water coral communities are increasingly being threatened by climate change and anthropogenic activities and have therefore been classified as Vulnerable Marine Ecosystems (VMEs)[82]. Thus, knowledge on the diversity and distribution of the benthic organisms forming VMEs is of fundamental importance. Given the rapid coastal development that is ongoing in the Saudi Arabian Red Sea, this study also provides a reference to inform conservation priorities. As highlighted by the levels of diversity found in this study and the zonation observed for specific taxa, conservation efforts should therefore consider the unique ecological roles and habitat requirements of both depth generalist and specialist octocoral taxa[5], and the fundamental importance of protecting mesophotic and deep-sea habitats[4,6], which host often overlooked octocoral diversity. Datasets such as the one here reported, integrating spatial and molecular data, are also an important reference for planning conservation actions, providing pathways for predicting and modelling the presence of benthic habitats in biodiversity hotspots, and informing the development of Marine Protected Areas (MPAs)[83].

Conclusions

Overall, the dataset presented here provides an assessment of octocoral diversity in the Saudi Arabian Red Sea at the genus level, including, for the first time to our knowledge, mesophotic and deep-sea taxa, with detailed location and depth data and a barcode sequence associated to each specimen. This study thus represents a way forward to understand the diversity, distribution, and evolution of the class Octocorallia in a biodiversity hotspot such as the Red Sea. The particular focus on previously unexplored areas on the Saudi Arabian coast of the basin and on the mesophotic and deep-sea octocoral communities inhabiting it, also highlights the potential for new species discovery and the importance of continued exploration in these areas. The findings from our work emphasize the need for targeted studies addressing octocoral diversity at all taxonomic levels and surveys encompassing all biogeographic areas. Accordingly, future research should focus on comprehensive surveys across various depth zones and integrate morphological, molecular, and ecological data to enhance our understanding of octocoral diversity and distribution and ultimately develop more effective conservation policies to ensure the persistence of these vital marine organisms.

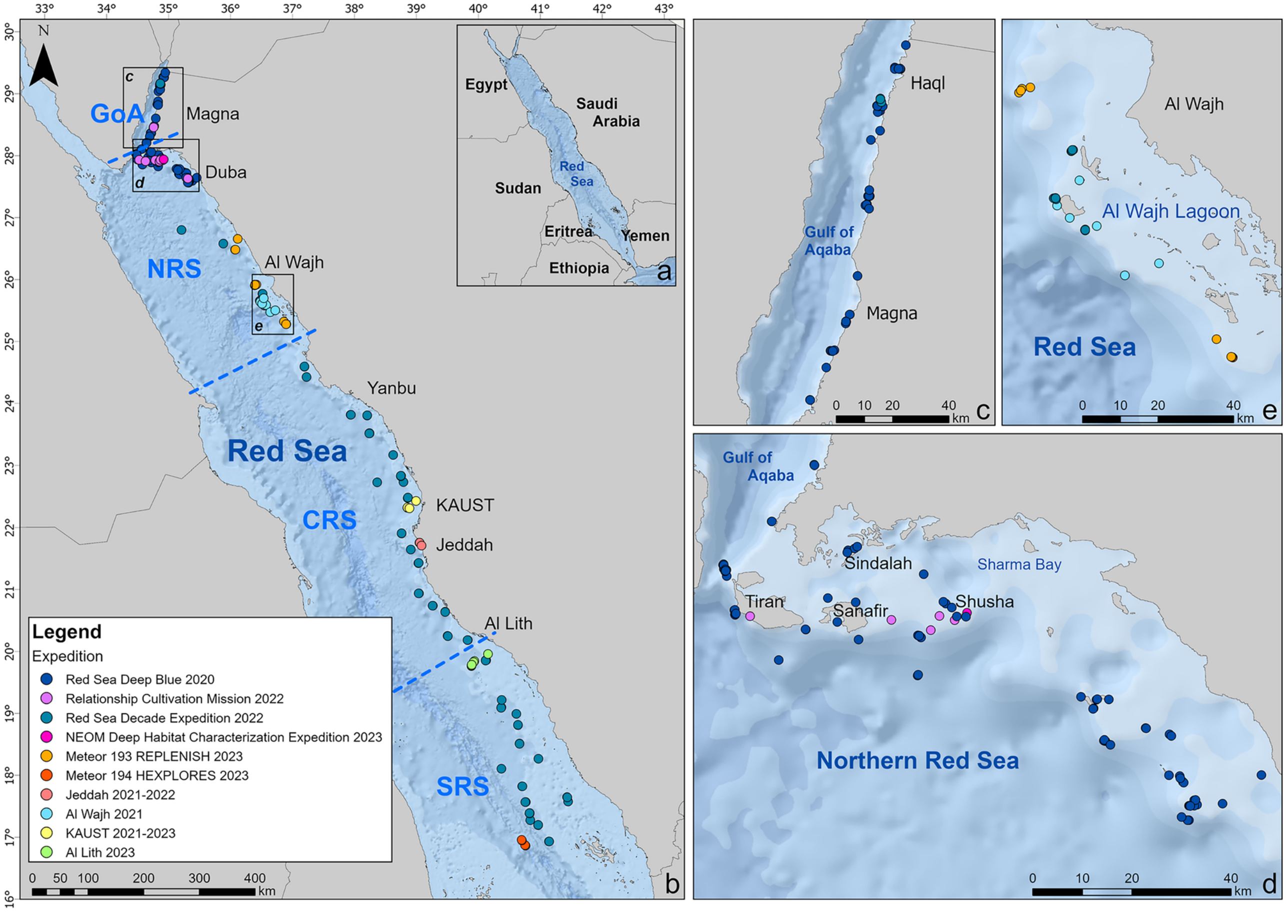

Fig. 5.. Maps showing (**a**) the Red Sea and (**b**) the sampling effort performed across 13 degrees of latitude in the basin during six major oceanographic expeditions and several SCUBA diving surveys. Focus areas showing: (**c**) sampling sites in the Gulf of Aqaba, (**d**) sampling sites in the northern SA Red Sea, (**e**) sampling sites in the Al Wajh Lagoon. Dashed lines in (**b**) denote limits for the Gulf of Aqaba (GoA), northern Red Sea (NRS), central Red Sea (CRS), and southern Red Sea (SRS), based on Raitsos et al.[39] and Cerutti et al.[84]. Maps were created using Esri ArcGIS® Pro software v3.4.0[85].

Materials and methods

Sampling

Octocoral specimens were collected along 13 degrees of latitude in the Saudi Arabian Red Sea during six oceanographic expeditions and various biodiversity surveys conducted between 2020 and 2023, from shallow (< 30 m), mesophotic (from 30 to 150 m) and deep-water (> 150 m) ecosystems (Fig. 5). Four expeditions were carried out aboard the M/V *OceanXplorer* (USA), namely, the Red Sea Deep Blue (RSDB) from October to November 2020, the Red Sea Decade (RSDE) from February to June 2022, the Relationships Cultivation (RC) in June 2022, and the NEOM Deep Habitat Characterization in October 2023. Two expeditions were carried out aboard the R/V *Meteor* (Germany), namely, the M193 REPLENISH from September to October 2023 and the M194 HEXPLORES from October to November 2023. Finally, octocoral colonies in shallow waters were collected by SCUBA diving between 0 and 30 m in the Saudi Arabian Red Sea between September 2021 and September 2023.

Sampling aboard the M/V *OceanXplorer* occurred through an Argus Mariner XL108 remotely operated vehicle (ROV) and two Triton 3300/3 submersibles, as well as through SCUBA diving during the Red Sea Deep Blue 2020 expedition. Sampling aboard the R/V *Meteor* during the M193 REPLENISH expedition was performed with a MARUM-Squid light work-class ROV (SAAB Seaeye, UK)[86], and with the ROV KIEL 6000 (FMCTI/Schilling Robotics LLC, CA, USA) during the M194 HEXPLORES expedition[87]. Technical details of the ROVs, cameras, and sampling equipment are reported in Supplementary Material 4.

Sampling for the present study was undertaken in accordance with the policies and procedures of the King Abdullah University of Science and Technology (KAUST, Saudi Arabia). Permission relevant for KAUST to undertake this research and sampling was obtained from the applicable governmental agencies in the Kingdom of Saudi Arabia.

For each octocoral specimen collected below 30 m, high-definition (HD) videos were recorded with the cameras mounted on ROVs and submersibles, and images were extracted from the videos using the software Adobe Premiere Pro v22.6.2 (Adobe Inc., USA). Octocoral colonies were collected with knives or pliers while

SCUBA diving and *in situ* pictures of live colonies were taken with a Canon PowerShot SX260 HS or an Olympus Tough TG-6 Waterproof camera in a PT-059 Underwater Housing. The sampled colonies were processed aboard the research vessels during the RSDB 2020, RSDE 2022, RC 2022, REPLENISH 2023 and HEXPLORES 2023 expeditions, or immediately upon return to shore when collected during single-day sampling trips. Samples were assigned a unique specimen code and processed immediately after collection. For octocorals presenting an axis, the apical part (~ 10 cm) of a branch for each colony was preserved in 99% ethanol for subsequent DNA extraction and molecular analyses, while the rest of the colony was air-dried out of direct sunlight for 24 hours. For soft corals, full colonies were fixed in 99% ethanol.

Morphological analyses and identification

All collected specimens were transported to King Abdullah University of Science and Technology (KAUST, Thuwal, Saudi Arabia). When available, the whole dry colony was photographed using a Nikon D7500 camera equipped with a Nikkor 18-55 mm lens, and macro-morphological characters were examined at the Red Sea Research Center Laboratory at KAUST. Dry skeletons and ethanol-preserved specimens were inspected with a Motic SMZ-171 stereomicroscope (Motic, Hong Kong), and imaged using a Leica M205 A stereomicroscope equipped with a Leica DMC 5004 camera (Leica Microsystems, Wetzlar, Germany) to examine skeletal features, including the presence of an axis, the polyp morphology and the disposition of the sclerites on the axis and polyps. Specimens included in this study were identified to genus level following original descriptions and taxonomic revisions (*e.g.*[2,9,35,60,88,89],). The dry colonies and ethanol-preserved samples are stored at KAUST.

DNA extraction, amplification, and sequencing

DNA was extracted from 728 ethanol-preserved specimens. Specifically, one polyp was sub-sampled from each individual octocoral for genomic DNA extraction using a DNeasy® Blood and Tissue kit (Qiagen Inc., Hilden, Germany) and following the manufacturer's protocol. Quality and quantity of the extracted DNA were checked using a NanoDrop® 2000c spectrophotometer (Thermo Fisher Scientific, Wilmington, USA) and quantified using a Qubit 4 Fluorometer (Thermo Fisher Scientific, Wilmington, USA). Raw DNA is stored at KAUST (Thuwal, Saudi Arabia).

Two mitochondrial loci, *mtMutS* and *COI*, were amplified through polymerase chain reaction (PCR) using the primer pairs ND42599F/mut3458R[90,91], mut2761F/mut3270R[60], and COII8068F/COIOctR[12,92]. Details of the PCR primer sequences, PCR thermal profiles run for amplifications, and target size of the amplicons are reported in Supplementary Material 5. All PCR reactions were performed in a final volume of 15 µL obtained with 1.2 µL of raw DNA diluted 1:50, 1.5 µL of each primer 2 µM, 3.3 µL of H_2O and 7.5 µL of Multiplex PCR Master Mix (Qiagen, Hilden, Germany).

Success of PCR amplifications was tested using a QIAxcel Advanced System (Qiagen Inc., Hilden, Germany). PCR products were then enzymatically purified by adding 2 µL of Illustra™ ExoProStar™ (Global Life Sciences Solutions Operations UK Ltd, Buckinghamshire, UK) to 5 µL of amplified DNA in a final volume of 7 µL and incubated for 15 min at 37 °C and for 15 min at 80°C. The purified products of the *mtMutS* and *COI* amplifications were directly sequenced in both forward and reverse directions using an ABI 3730xl DNA analyzer (Applied Biosystems, Massachusetts, USA) at KAUST BioScience Core Lab (Thuwal, Saudi Arabia).

Phylogenetic analyses

Chromatograms were manually inspected, and forward and reverse reads were assembled, edited, and trimmed, using Geneious® v2023.0.1 (Biomatters Ltd., Auckland, New Zealand). Previously deposited sequences available on GenBank (https://www.ncbi.nml.nih.gov/genbank/) and representing specimens belonging to the class Octocorallia (Supplementary Material 1b) were aligned to the newly produced sequences using MAFFT v7.490[93] through the E-INS-i settings. Alignments were manually inspected and edited using the software AliView v1.28[94]. All newly produced sequences were deposited in GenBank (https://www.ncbi.nml.nih.gov/genbank/) (Accession numbers are listed in Supplementary Material 1a). The alignments were checked using MEGA v11 (Ref[95].; Supplementary Material 3). Evolutionary models were selected using jModelTest2[96] on CIPRES[97], under the Akaike Information Criterion (AIC), which selected the model GTR+I+G for both markers. The *mtMutS* and *COI* alignments were concatenated using Geneious® v2023.0.1. Phylogenetic trees were then inferred using both Maximum Likelihood (ML) with RAxML-HPC2 on XSEDE v8[98] and Bayesian Inference (BI) through MrBayes on XSEDE v3.2.7a[99] on the CIPRES portal. Maximum Likelihood analyses were run using the default parameters and 1,000 bootstraps replicates. For Bayesian analyses, two independent runs for four Monte Carlo Markov chains (MCMC) were conducted for 10 million generations, with trees sampled every 1000th generation, and burn-in set to 25%. ML and BI analyses were performed on both the single marker and concatenated alignments (Fig. 3; Supplementary Material 2). Phylogenetic trees were plotted using FigTree v1.4.4[100] and rooted to a sequence representing the octocoral species *Cornularia pabloi* McFadden & van Ofwegen, 2012 based on previously published Octocorallia phylogenies[9].

Data availability

The genetic data generated during and/or analysed during the current study are available from the NCBI GenBank database (https://www.ncbi.nml.nih.gov/genbank/): the accession numbers are listed in Supplementary Material 1a. Further data generated and/or analysed during the current study are included in this published article and its supplementary information files.

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Author contributions

L.M., F.B., T.I.T., C.S.M., and G.C. designed the research. L.M., F.B., T.I.T., G.C., F.M., S.Vim., S.Vic., S.J.P., and J.D.R. collected samples. L.M., C.S.M., and G.C. performed morphological analyses and specimens' identification. L.M. performed molecular work, analysed the data, prepared figures 1-5, and wrote the original manuscript with feedback from F.B., T.I.T, and C.S.M. F.M. prepared figure 6. F.B, T.I.T., C.S.M., and G.C. provided supervision. F.B., C.M.D. F.M.Z., N.A., and H.W. acquired funds for research vessel operations, sampling expeditions and ROV scientific operations. F.B. acquired funds for samples processing and analyses at KAUST. All authors have read and agreed to the published version of the manuscript.

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Declarations

Competing interests

The authors declare no competing interests.

Additional information

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