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The first record of ring sea anemones from the Saudi Arabian Red Sea mesophotic zone

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Abstract

Ring sea anemones (Cnidaria, Actiniaria) engage in symbiotic associations with octocorals by attaching to their branches and surrounding them with tissue junctions, causing a significant reduction of the host's coenenchyme. They have previously been reported from the North Atlantic, Western Indian, and Pacific Oceans, from 30 m to aphotic depths, colonising species of sea fans and sea pens in potentially parasitic relationships. Here, we report the first record of ring sea anemones from the Saudi Arabian Red Sea mesophotic waters, living on an octocoral host of the family Ellisellidae at 97 m depth. Through morphological and phylogenetic analyses based on the sequencing of the 12S small subunit rRNA region, we confirmed the identification of these ring sea anemones as *Peronanthus* sp. (Actiniaria, Amphianthidae). While expanding our knowledge on the geographic range of this genus, this finding emphasises the importance of explorations of coral-associated fauna at mesophotic depths, to better understand their diversity, their relationships with their hosts, and their potential ecological roles within these ecosystems.

Introduction

Symbiotic relationships among marine organisms are widespread and diverse (Gittenberger and Gittenberger 2011; Rouzé *et al.*, 2017), and a wide array of associations has been described in the literature, from shallow to deep waters, involving two or multiple organisms (Brown *et al.*, 2025; Hoeksema 2017; Maggiorni *et al.*, 2022a; Mercier and Hamel 2008). For instance, in shallow-water tropical reefs, coral-associated fauna represents most of the invertebrate diversity (Montano 2022), with the highest levels found for crustaceans and molluscs (Stella *et al.*, 2011). Such interactions are fundamental for the survival of benthic communities, promoting productivity (Rodríguez-Troncoso *et al.*, 2019), structural complexity (Bergsma and Martinez 2011), and survival of the partners (April 2020), while potentially influencing each other's evolution (deVienne *et al.*, 2013). However, despite the abundance and importance of symbiotic associations, many of the interactions occurring in the marine environment remain poorly known (Stella *et al.*, 2011). This is especially remarkable considering those occurring at mesophotic and aphotic depths (Turner *et al.*, 2017), where often obligate symbioses are necessary for the survival of both partners (Osman and Weinnig 2022). In fact, although coral associations with other invertebrates are fairly well explored in shallow-water hard corals (e.g., Bähr *et al.*, 2025, 2023; Macrina *et al.*, 2024a; Maggioni *et al.*, 2022a; Stella *et al.*, 2010; van der Schoot and Hoeksema 2024; Xu *et al.*, 2025), many symbiotic relationships involve octocoral hosts (Anker *et al.*, 2023; Lau *et al.*, 2020) at greater depths. Octocorals are major components of benthic environments, providing habitat and shelter to a variety of organisms across the water column (Schubert *et al.*, 2017), and forming dense communities known as marine animal forests (MAFs; Orejas *et al.*, 2022; Rossi *et al.*, 2017). Accordingly, various taxa have been reported in association with octocorals, establishing symbiotic relationships that can be very intricate (Fourreau *et al.*, 2024; Lourie and Randall 2003).

Mesophotic coral ecosystems (MCEs), particularly those dominated by MAFs, are increasingly recognised as biodiversity hotspots due to their structural complexity and the specialised taxa they support (Radice *et al.*, 2024; Rossi *et al.*, 2017). These ecosystems host organisms with unique adaptations to low light, high pressure, and nutrient-poor conditions (Denis *et al.*, 2024) and are listed as vulnerable marine ecosystems by the Food and Agriculture Organization of the United Nations (FAO), given their ecological value and susceptibility to impacts from

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fishing activities (FAO 2009). Nevertheless, our current understanding of the biodiversity and symbiotic relationships occurring in these ecosystems remains scarce (Radice et al., 2024), although their characterisation would be critical for both biodiversity assessments and effective conservation planning (Diaz et al., 2023; Nolan et al., 2025, 2024; Rossi et al., 2017).

Sea anemones can engage in symbioses with a variety of marine taxa, including the well-known association with anemonefish (Roux et al., 2020), but also, with hermit crabs (Ross and Zamponi 1982), gastropods (Mercier and Hamel 2008), black corals (Gress and Kaimuddin 2021), and octocorals (Ocaña et al., 2004). However, their associations with the latter are still understudied (e.g., Ocaña et al., 2004; Riemann-Zürneck and Griffiths 1999). Actinarian species such as *Amphianthus dohrnii* (Koch, 1878), *Calliactis palliata* (Müller, 1776), or *Stephanauge impedita* (Gravier 1918), attach to octocoral branches by maintaining their standard pedal disc structure and surrounding the colony with it (Carlgren 1934; Gravier 1918). In contrast, other species, such as those commonly known as ring sea anemones (RSA), appear to have modified their morphology into a pedal ring constituted of totally fused tissue surrounding the branches of octocoral colonies in a ring-like structure (Ocaña et al., 2004).

The first description of RSA belongs to Hiles (1899), who, while analysing octocoral colonies from the family Ellisellidae Gray, 1859, collected from Papua New Guinea by A. Willey, found and described the new sea anemone species *Peronanthus verrucellae* Hiles, 1899. Subsequently, Carlgren (1936) described *Stephanauge annularis* Carlgren, 1936, which was then recognised as another species of RSA (see Rodríguez et al., 2025) associated with sea pens of the genus *Balticina* Gray, 1870 (formerly *Halipterus* Kölliker, 1870). Thereafter, Ocaña et al. (2004) provided an overview of the known RSA and, based on morphology, assigned them to two groups: the first encompassing small RSA with a remarkable dimorphism between the upper part and the pedal ring (i.e., *P. verrucellae*, *Peronanthus* sp. 1 – sp. 3, and *S. annularis*), and the second

including bigger RSA with a thick mesoglea (i.e., *Peronanthus* sp. 4). Finally, a potential fifth species of *Peronanthus* (sp. 5) was documented by Ocaña et al. (2007) and assigned to the first of the two morphological groups.

To date, RSA are known to occur in associations with octocoral hosts of the genera *Keratoisis* Wright, 1869, *Ellisella* Gray, 1858, *Verrucella* Milne Edwards & Haime, 1857, *Anthothela* Verrill, 1879, and *Balticina*, from 30 m to aphotic depths in the Atlantic, Indian, and Pacific Oceans (Ocaña et al., 2004, 2007; WoRMS 2024; Figure 1). However, there are no records of RSA from the Red Sea, a basin where geological factors and environmental extremes are tightly linked to the diversity, evolution, and endemism of marine fauna as well as their symbiotic relationships (Berumen et al., 2019; DiBattista et al., 2016; McFadden et al., 2025).

In this study, we report the first record of RSA living on an octocoral colony from the Saudi Arabian Red Sea mesophotic zone. By combining morphological and molecular analyses, we provide an identification at the genus level and establish its phylogenetic position through DNA barcoding.

Materials and methods

Sampling

During the Red Sea Decade (RSDE) expedition onboard the M/V *OceanXplorer*, Remotely Operated Vehicle (ROV) and submersible dives occurred along the Saudi Arabian Exclusive Economic Zone of the Red Sea in mesophotic and aphotic waters from February to May 2022. Sampling for this study was carried out using a Triton 3300/3 submersible (Neptune), equipped with a Schilling T4 hydraulic manipulator. During a submarine survey on 2 March 2022, an octocoral colony was observed and collected at 97 m depth in the central Saudi Arabian Red Sea (20.73865 °N, 39.265010 °E) (Figure 1). Once at the surface, RSA were observed on the collected colony (octocoral colony voucher KAUST NTN0127BIO20). The

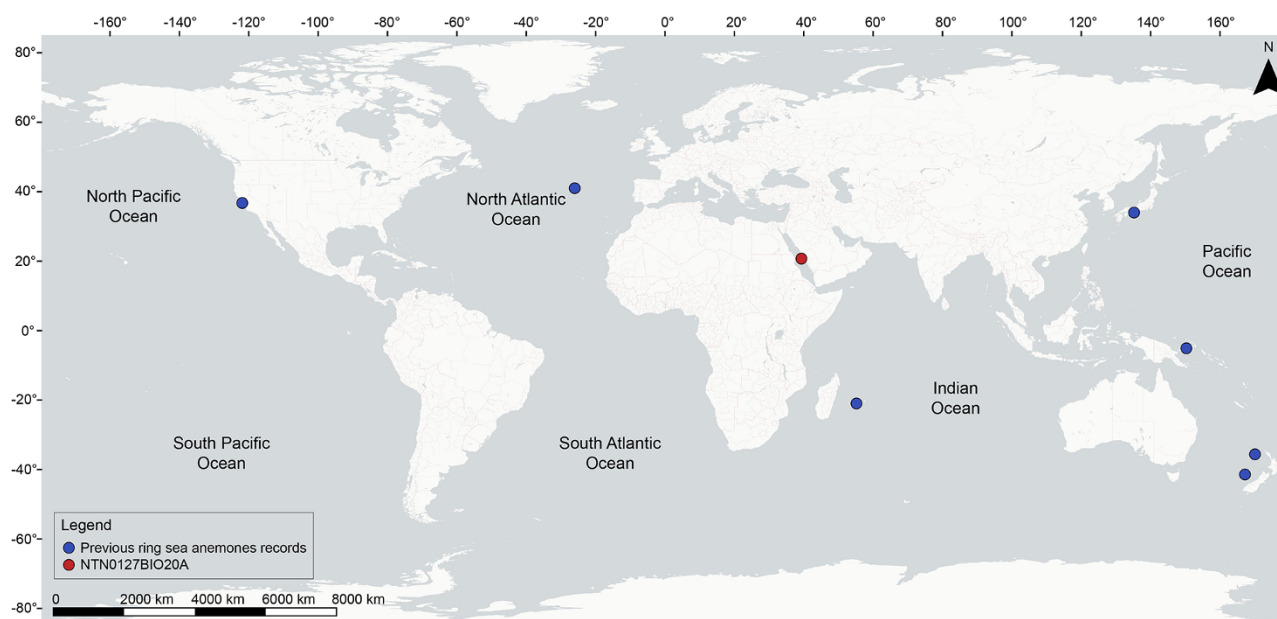


Figure 1. Map showing the sampling locality of the octocoral colony and symbiotic RSA in the central Saudi Arabian Red Sea (red dot). Blue dots indicate other locations where RSA are known from previous studies. A summary with coordinates of the previously known records is reported in Supplementary Table S1. The map was created with QGIS v3.32.2 (QGIS Development Team 2025).

octocoral specimen and associated anemones were processed aboard the research vessel and the apical part of one colony branch, including RSA, was subsampled and fixed in 99% ethanol immediately after collection for subsequent molecular analyses. The rest of the octocoral colony was air-dried out of direct sunlight for 24 hours and stored for subsequent morphological examination.

Morphological analyses and identification

At the King Abdullah University of Science and Technology (KAUST, Thuwal, Saudi Arabia), the octocoral dry colony and ethanol-preserved branches, as well as the anemones, were photographed using a Nikon D7500 camera with a Nikkor 18–55 mm lens. Detailed microscopical images of the anemones, of the octocoral polyps, and of the disposition and morphology of the octocoral's skeletal elements were taken using a Leica M205A stereomicroscope equipped with a Leica DMC 5004 camera (Leica Microsystems, Wetzlar, Germany). Octocoral sclerites were characterised using a Quattro S Environmental Scanning Electron Microscope (Thermo Fisher Scientific, Wilmington, USA) at KAUST Imaging Core Laboratories (Thuwal, Saudi Arabia), following the workflow for sclerite preparation outlined in Macrina *et al.* (2024b).

Both the actinians and the octocoral colony were identified based on morphological characters used in traditional taxonomy and reported in original descriptions and subsequent revisions (e.g., Milne-Edwards and Haime 1857; Hiles 1899; Bayer and Grasshoff 1994; Ocaña *et al.*, 2004). The octocoral dry colony and the ethanol-preserved samples, including the symbiotic anemones, are stored at KAUST.

DNA extraction, amplification, and sequencing

Total DNA was extracted from one of the symbiotic anemones (sea anemone voucher KAUST NTN0127BIO20A) using a DNeasy® Blood and Tissue Kit (Qiagen Inc., Hilden, Germany), following the manufacturer's protocol. Polymerase chain reaction (PCR) was used to amplify a portion of the small subunit of ribosomal RNA (rRNA) 12S using the primer couple ANTMT12SF (5' – AGCCACACTTTTCACTGAAACAAGG – 3') and ANTMT12SR (5' – GTTCCCYWYCYCTYACYATGTTACGAC – 3') (Chen and Yu 2000). The amplification was performed in a 15 µL volume obtained with 7.5 µL 2X Multiplex PCR Master Mix (Qiagen Inc., Hilden, Germany), 1.5 µL of each primer (2 µM), 3.3 µL of H₂O, and 1.2 µL of raw DNA. The thermal profile used for the amplification of the 12S rRNA region consisted of 95 °C for 15 min, followed by 4 cycles of 95 °C for 30 sec, 50 °C for 1 min, and 72 °C for 2 min, followed by 30 cycles of 95 °C for 30 sec, 55 °C for 1 min, and 72 °C for 2 min (Chen *et al.*, 2002). Success of the amplification was tested using a QIAxcel Advanced System (Qiagen Inc., Hilden, Germany). The amplified product was then purified using Illustra™ ExoProStar™ (Global Life Sciences Solutions Operations UK Ltd, Buckinghamshire, UK), following the manufacturer's protocol, and directly sequenced in both forward and reverse directions using an ABI 3730xl DNA analyser (Applied Biosystems, Massachusetts, USA) at KAUST BioSciences Core Laboratories (Thuwal, Saudi Arabia). Raw DNA is stored at KAUST. A barcode sequence for the octocoral host is available in Macrina *et al.* (2025) (GenBank Accession Number: PV707296).

Phylogenetic analyses

Chromatograms of the forward and reverse sequences were manually checked, edited and assembled using Geneious® v10.1.3 (Biomatters Ltd, Auckland, New Zealand). To infer the phylogenetic position of the newly produced sequence, it was aligned with 69 previously deposited sequences available on GenBank database (<https://www.ncbi.nlm.nih.gov/genbank/>) and representing specimens belonging to the order Actiniaria (Supplementary Table S2) using MAFFT v7.490 (Kato and Standley 2013) through the E-INS-i settings. The alignment was manually inspected and edited using the software AliView v1.28 (Larsson 2014). The newly produced sequence was deposited in GenBank database (Accession number: PQ481953). The alignments' statistics were checked using MEGA v11 (Tamura *et al.*, 2021). Prior to running phylogenetic analyses, evolutionary models were checked through jModelTest2 (Darriba *et al.*, 2012) on CIPRES (Miller *et al.*, 2010), under the Akaike Information Criterion (AIC), which selected the model GTR+G. Phylogenetic trees were then inferred using both Maximum Likelihood (ML) with RAxML-HPC2 on XSEDE v8 (Stamatakis 2014) and Bayesian Inference (BI) through MrBayes on XSEDE v3.2.7a (Ronquist *et al.*, 2012) on the CIPRES portal. ML analyses were run using the default parameters and 1,000 bootstrap 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%. Phylogenetic trees were visualized using FigTree v1.4.4 (<http://tree.bio.ed.ac.uk/software/figtree/>) and rooted to *Relicanthus daphneae* (Daly, 2006) based on a previously published Actiniaria phylogeny (Rodríguez *et al.*, 2014; Supplementary Table S2).

Results

Morphological results

The octocoral host (KAUST NTN0127BIO20) consisted of a densely branched colony, with short and thick branches presenting anastomoses (Figure 2A). Polyps were monomorphic, contractile, but not retractile, and arranged around the branches (Figure 2A–2I). Surface sclerites were orange, while subsurface sclerites were colourless. Sclerites consisted of symmetrical spindles and double-headed clubs (Figure 3). Based on these morphological characters, the octocoral colony was assigned to the family Ellisellidae and to an unidentified species in the genus *Verrucella*.

Upon examination, the *Verrucella* sp. branches appeared to be covered in white RSA (Figure 2B) which surrounded the host branches through a pedal ring (Ocaña *et al.*, 2004) constituted by the pedal disk tissue and part of the column (Figure 2A, 2B, 2H, 2I), which had to be broken to be detached from the octocoral colony. Most of the anemones' tissue was arranged in their upper part, grouping the oral disc, tentacles, pharynx, and mesenteries, while their pedal rings surrounded the branches of the octocoral colony and appeared as a thin tissue junction with sparse external scars (Figure 2H, 2I). Based on these morphological characters, the RSA were assigned to the genus *Peronanthus* given their correspondence with the features of the first of the two morphological groups reported by Ocaña *et al.* (2004), and shared characters with *Peronanthus* sp. 3 (Ocaña *et al.*, 2004).

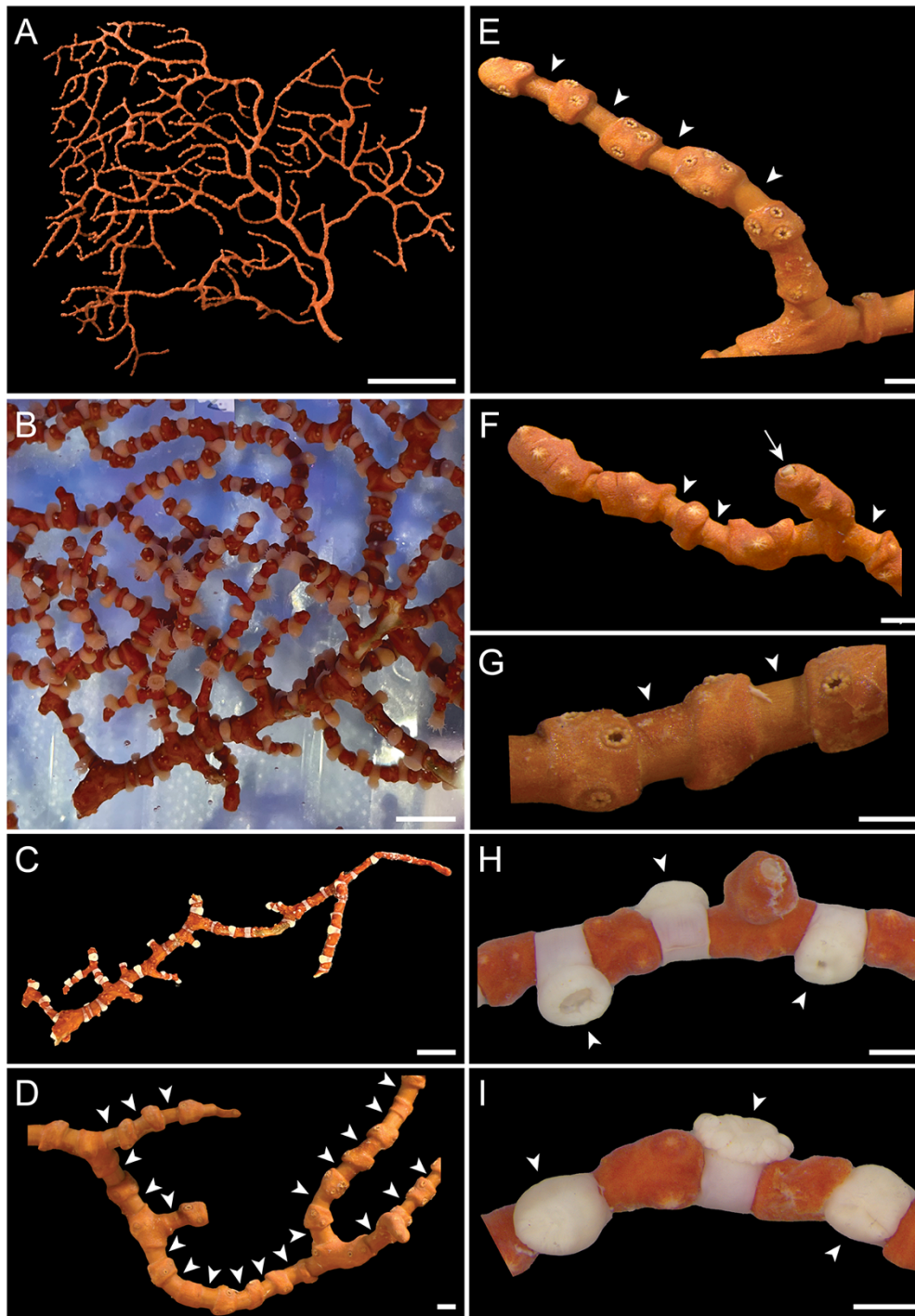


Figure 2. Details of the analysed octocoral colony (voucher KAUST NTN0127BIO20) and associated RSA: (A) Full dry colony; (B) Portion of the freshly collected octocoral colony with associated RSA; (C) Branch of the ethanol-preserved colony; (D–E) Microscopic pictures of the octocoral skeleton showing the polyps and the marks from the RSA on its branches (indicated by arrowheads); (F) Microscopic picture of a branch of the colony showing the marks left by the RSA on the host (indicated by arrowheads) and the axis of the octocoral left exposed by the epibiont (indicated by the arrow); (G) Microscopic picture of a portion of a colony branch showing the marks left by the RSA on the host coenenchyme (indicated by arrowheads); (H–I) Ethanol-preserved octocoral polyps and associated RSA (indicated by arrowheads). Scale bars: A, 5 cm; B, C, 1 cm; D–I, 1 mm.

Molecular results

The newly generated 12S rRNA sequence (RSA voucher KAUST NTN0127BIO20A) was analysed along with 69 previously published Actiniaria sequences (Supplementary Table S2), in a final alignment of 974 bp. The alignment included 373 conserved sites,

539 variable sites, 391 parsimony-informative sites, and 142 singletons. The tree topologies resulting from the BI and ML analyses were concordant and confirmed that the sequenced specimen belongs to the superorder Enthemonae, superfamily Metridioidea Carlgren, 1893, family Amphianthidae Hertwig, 1882, and genus *Peronanthus* (Figure 4).

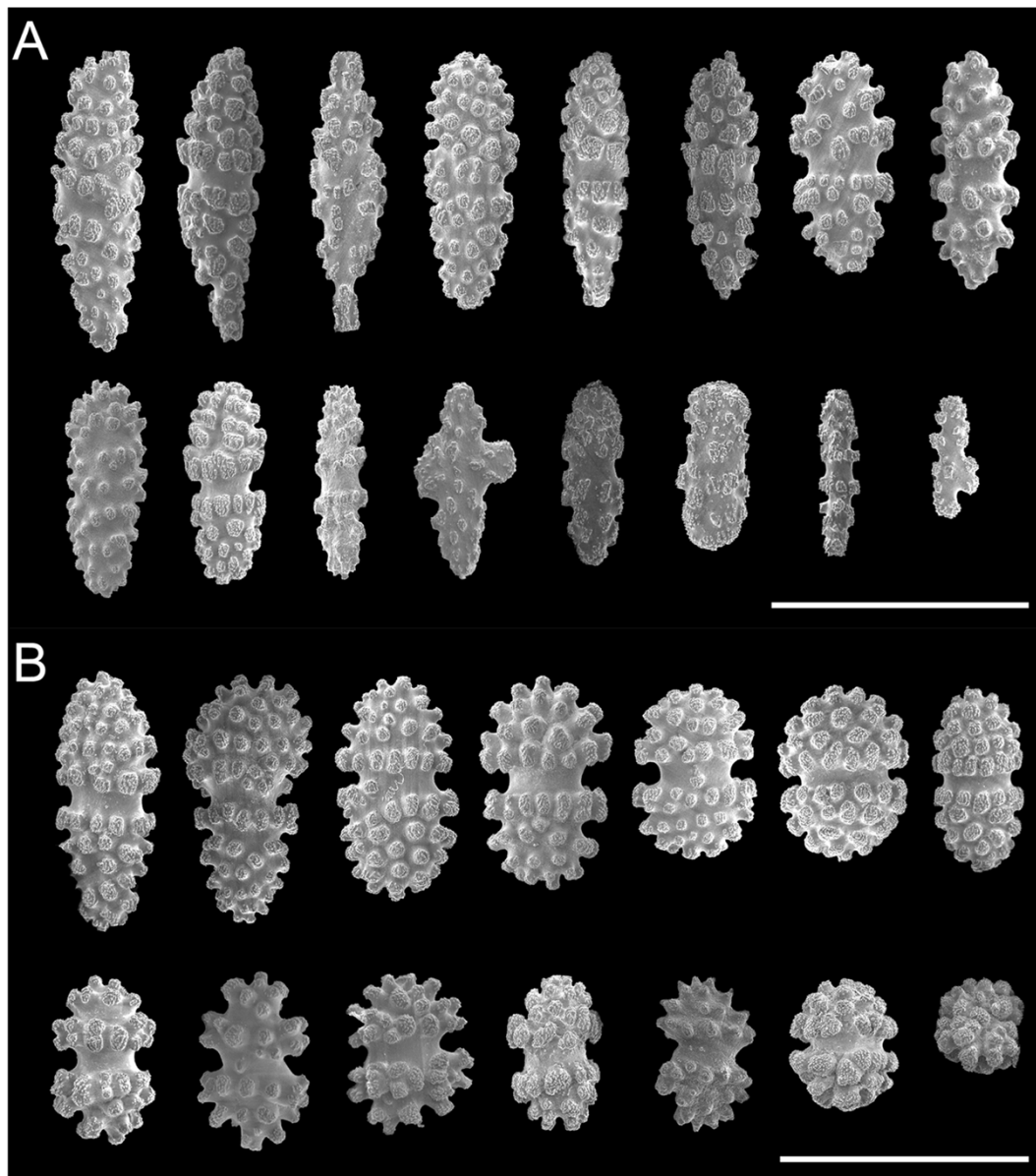


Figure 3. Sclerites of the *Verrucella* sp. colony characterised through scanning electron microscopy (SEM): (A) Symmetrical spindles; (B) Double-headed sclerites. Scale bars: 100 µm.

Discussion

Morphological and molecular analyses confirmed that the actiniarian specimens associated with the octocoral colony sampled at 97 m in the central Saudi Arabian Red Sea belonged to the genus *Peronanthus*. Identification at the genus level was confirmed by our integrative analyses, and the RSA reported here correspond to the first morphological group established by Ocaña *et al.* (2004). However, species level assignment could not be confirmed at this stage due to the specimens being fixed in ethanol, which made their study difficult for histological and taxonomic purposes, and the geographical distance from the original collection locations of previously reported *Peronanthus* specimens (Supplementary Table S1; Hiles 1899; Ocaña *et al.*, 2004, 2007). Further and more detailed taxonomic studies aiming at clarifying the actual diversity of these organisms may overcome these limitations by preserving specimens for histological examination

and internal anatomy (Fautin 2009), and by comparing freshly collected RSA with the type material of *P. verrucellae* and related taxa (Carlgren 1936; Hiles 1899; Ocaña *et al.*, 2004, 2007). Moreover, sequencing additional loci (e.g., Yap *et al.*, 2020) or employing next-generation sequencing techniques may offer insights into the evolutionary relationships of these organisms in the context of the order Actiniaria's systematics (Fautin 2016; Fautin *et al.*, 2007; Rodríguez *et al.*, 2014) and help refine the phylogenetic placement of the specimen reported here beyond what was possible to achieve by sequencing the 12S rRNA marker alone. Such an integrated approach would be critical for resolving species-level relationships within the genus *Peronanthus* as well as to clarify whether any of the organisms reported to date represent undescribed species. Nevertheless, the RSA record reported here represents the first one known from the Red Sea, marking a significant expansion of the known distribution of the genus *Peronanthus*, beyond its



Figure 4. Bayesian Inference phylogenetic reconstruction of Actiniaria inferred from the sequencing of the small subunit 12S rRNA region, showing the phylogenetic position of one of the newly sampled Red Sea RSA (voucher KAUST NTN0127BIO20A in red). Node circles correspond to Bayesian posterior probability (≥ 0.8) and node values correspond to ML bootstrap values (≥ 80). The tree was rooted to *Relicanthus daphneae*.

previously observed range in the North Atlantic, Western Indian, and Pacific Oceans (Hiles 1899; Ocaña *et al.*, 2004; Rodríguez *et al.*, 2025).

The finding of RSA associated with a *Verrucella* sp. colony at mesophotic depths is particularly relevant as octocorals of the family Ellisellidae can provide habitat and three-dimensional structure in MAF ecosystems (Chimienti *et al.*, 2021; Moccia *et al.*, 2020). Hence, it underscores the importance of characterising the biodiversity of these communities at both the host and symbiont levels, particularly in MCEs, where obligate associations may be key to species survival (Kahng *et al.*, 2014). Symbiotic interactions

involving actiniarians and octocorals are rare but biologically intriguing, especially those comprising *Peronanthus*, whose morphological adaptation suggests a high degree of host specificity and functional integration, potentially reflecting a long coevolutionary history. Unlike many shallow-water anemones that retain a free-living capacity or use loosely attached pedal discs (e.g., *Calliactis* spp. with hermit crabs), RSA are obligately epibiotic and appear to be structurally dependent on their hosts (Ocaña *et al.*, 2004). The evolution of the ring-like pedal morphology may have arisen as a species-specific adaptation to the host colonies (see, e.g., van der Schoot and Hoeksema 2024 for other examples) or as a strategy to

exploit specific ecological niches (such as the gorgonian branches) and avoid habitat competition (Ocaña *et al.*, 2004). In fact, this modification mirrors similar adaptations seen in other symbionts of octocorals and black corals at depth, such as ovulid gastropods and zoantharians, which often exhibit host-specific tissue modifications to maintain long-term attachment and access to host resources (Ocaña and Brito 2004; Reijnen *et al.*, 2010). Accordingly, the ring morphology could represent a parallel evolutionary strategy to ensure stability in exposed habitats, by maximising the contact with the host tissues and ensuring epibiotic attachment. Furthermore, the structural integration seen in *Peronanthus* may drive selective pressures on both partners' morphology and physiology (Appril 2020; Dimijian 2000). Comparative research on other mesophotic coral symbioses, such as the sponge-octocoral associations in the Caribbean, revealed that such interactions are often shaped by a combination of environmental constraints and evolutionary patterns (Lourie and Randall 2003). As such, the highly specialised *Peronanthus*-octocoral association may serve as a valuable model for exploring host-symbiont coevolution in MAFs.

Although the nature of the symbiosis between octocorals and RSA has not been fully clarified to date, the latter are known to engage in complex interactions with their hosts, including mutualistic and commensal relationships (Ocaña *et al.*, 2004). Nevertheless, Morton (1989) advanced the hypothesis that the genus *Peronanthus* may be an octocoral parasite, harming the host colonies, and this may be the case of the association reported in this study. In fact, RSA were clearly causing damage to the collected octocoral host, by reducing the thickness of its coenenchyme (Figure 2D–2G) and removing polyps to reach the colony's axis (Figure 2H–2I), in a relationship that could be linked to a metabolic dependence of the parasite on the host (Ocaña *et al.*, 2007). However, such interactions may also vary depending on environmental conditions and the health of the corals, with potential for mutualistic or commensal associations under different circumstances (Goulet and Goulet 2021).

In the Red Sea, a basin known for its extreme environmental conditions (Berumen *et al.*, 2019), clarifying the mechanisms behind the symbioses of *Peronanthus* sea anemones and Ellisellidae octocorals could offer insights into their relationship and roles in MCEs and MAFs (Cuecuecha-Pérez and Ávila-García 2025). At these depths in the warm waters of the Red Sea, organisms like *Peronanthus* may have evolved specialized adaptations to secure a stable substrate for survival, as shown for instance in hydrothermal environments (Zhou *et al.*, 2023). With ongoing explorations at depth, this finding contributes to the growing body of evidence highlighting the mesophotic zone of the Red Sea (Loya *et al.*, 2019) as a reservoir of undocumented biodiversity (e.g., Anker *et al.*, 2023; Benayahu *et al.*, 2018a, 2018b; Chimienti *et al.*, 2022; Macrina *et al.*, 2025; Maggioni *et al.*, 2022b; Nolan *et al.*, 2025; Terraneo *et al.*, 2023; Vicario *et al.*, 2024; Vimercati *et al.*, 2023), underscoring the ecological complexity and biogeographic uniqueness of these underexplored ecosystems. Given the higher diversity found in the mesophotic zone of the Red Sea compared to the euphotic and aphotic counterparts for organisms such as octocorals (Macrina *et al.*, 2025) and black corals (Vicario *et al.*, 2024), this record warrants further examination of the patterns of evolution and coevolution among octocorals and symbiotic taxa in the basin, especially considering the Ellisellidae and associated symbionts at depth.

Conclusions

Records of invertebrate associations such as the one reported in this study can be useful to elucidate the occurrence and establishment of symbioses among benthic taxa in MAFs, providing insights into the nature of these interactions and mechanisms of host selection. This new record of *Peronanthus* sp. in the Saudi Arabian Red Sea mesophotic zone not only extends the known range of this genus but also emphasizes the significance of mesophotic habitats in supporting complex ecological relationships. It is therefore crucial to continue the investigation of the diverse and often intricate symbioses existing in these environments, as they may provide valuable clues to the evolutionary dynamics and ecological processes shaping the biodiversity, resilience, and long-term dynamics of mesophotic ecosystems.

Supplementary material. The supplementary material for this article can be found at [10.1017/S0025315425100787](https://doi.org/10.1017/S0025315425100787).

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Author contributions. L.M. and F.B. conceptualised the study. L.M. performed molecular work and formal analyses, designed the figures, and wrote the manuscript with suggestions from F.B. and T.I.T. T.I.T. collected the sample. L.M. and C.S.M. identified specimens. F.B., T.I.T., C.S.M., and G.C. provided supervision. F.B. acquired funds for sample processing and analyses at KAUST. F.B., V.P., M.Q., and C.M.D. administered the expedition and led data collection. All authors have read and agreed to the final version of the manuscript.

Data availability statement. The data that support the findings of this study are openly available in the NCBI GenBank database (<https://www.ncbi.nlm.nih.gov/genbank/>) under accession number PQ481953.

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Competing of interest. The authors declare no conflicts of interest.

References

Anker A, Vimercati S, Barreca F, Marchese F, Chimienti G, Terraneo TI, Rodrigue M, Eweida AA, Qurban M, Duarte C, Pieribone V and

- Benzoni F** (2023) Mesophotic and bathyal palaemonid shrimp diversity of the Red Sea, with the establishment of two new genera and two new species. *Diversity* **15**, 1028. <https://doi.org/10.3390/d15101028>
- Appril A** (2020) The role of symbioses in the adaptation and stress responses of marine organisms. *Annual Review of Marine Science* **12**, 291–314. <https://doi.org/10.1146/annurev-marine-010419-010641>
- Bähr S, Dunn N, van der Meij SET, Chowdhury J and Benzoni F** (2025) Temporal dynamics and disturbance responses in coral-dwelling decapods provide a novel perspective on their ecological role in coral reef systems. *Ecology and Evolution* **15**, e71474. <https://doi.org/10.1002/ece3.71474>
- Bähr S, van der Meij SET, Terraneo TI, Xu T and Benzoni F** (2023) Interspecific coral competition does not affect the symbiosis of gall crabs (Decapoda: Cryptochiridae) and their scleractinian hosts. *Ecology and Evolution* **13**, e10051. <https://doi.org/10.1002/ece3.10051>
- Bayer FM and Grasshoff M** (1994) The genus group taxa of the family Ellisellidae, with clarification of the genera established by J.E. Gray. *Senckenbergiana Biologica* **74**, 21–45.
- Benayahu Y, McFadden CS and Shoham E** (2018a) Search for mesophotic octocorals (Cnidaria, Anthozoa) and their phylogeny: I. A new sclerite-free genus from Eilat, northern Red Sea. *ZooKeys* **680**, 1–11. <https://doi.org/10.3897/zookeys.680.12727>
- Benayahu Y, McFadden CS, Shoham E and van Ofwegen LP** (2018b) Search for mesophotic octocorals (Cnidaria, Anthozoa) and their phylogeny: II. A new zooxanthellate species from Eilat, northern Red Sea. *ZooKeys* **676**, 1–12. <https://doi.org/10.3897/zookeys.676.12751>
- Bergsma GS and Martinez CM** (2011) Mutualist-induced morphological changes enhance growth and survival of corals. *Marine Biology* **158**, 2267–2277. <https://doi.org/10.1007/s00227-011-1731-6>
- Berumen ML, Voolstra CR, Daffonchio D, Agusti S, Aranda M, Irigoien X, Jones BH, Morán XAG and Duarte CM** (2019) The Red Sea: Environmental gradients shape a natural laboratory in a nascent ocean. In Voolstra CR and Berumen ML (eds), *Coral Reefs of the Red Sea*. Springer: Cham, Vol. 11, 1–10. https://doi.org/10.1007/978-3-030-05802-9_1
- Brown SD, Terraneo TI, Moore JM, Paulay G, White KN, Berumen ML and Benzoni F** (2025) The diversity and phylogenetic relationships of a *Chaetopterus* symbiont community in Djibouti, with redescription of *Chaetopterus djiboutiensis* Gravier, 1906 Stat. Nov. (Annelida: Chaetopteridae). *Diversity* **17**, 366. <https://doi.org/10.3390/d17050366>
- Carligen O** (1934) Ceriantharia, Zoantharia and Actiniaria from the 'Michael Sars' North Atlantic Deep-sea Expedition 1910. *Report on the Scientific Results of the 'Michael Sars' North Atlantic Deep-Sea Expedition 1910* **5**, 1–27.
- Carligen O** (1936) Some west American sea anemones. *Journal of the Washington Academy of Sciences* **26**, 16–23.
- Chen CA, Wallace CC and Wolstenholme J** (2002) Analysis of the mitochondrial 12S rRNA gene supports a two-clade hypothesis of the evolutionary history of scleractinian corals. *Molecular Phylogenetics and Evolution* **23**, 137–149. [https://doi.org/10.1016/S1055-7903\(02\)00008-8](https://doi.org/10.1016/S1055-7903(02)00008-8)
- Chen CA and Yu J-K** (2000) Universal primers for amplification of mitochondrial small subunit ribosomal RNA-encoding gene in scleractinian corals. *Marine Biotechnology* **2**, 146–153. <https://doi.org/10.1007/s101269900018>
- Chimienti G, Aguilar R, Maiorca M and Mastrototaro F** (2021) A newly discovered forest of the whip coral *Viminella flagellum* (Anthozoa, Alcyonacea) in the Mediterranean Sea: A non-invasive method to assess its population structure. *Biology* **11**, 39. <https://doi.org/10.3390/biology11010039>
- Chimienti G, Terraneo TI, Vicario S, Marchese F, Purkis SJ, Eweida AA, Rodrigue M and Benzoni F** (2022) A new species of *Bathypathes* (Cnidaria, Anthozoa, Antipatharia, Schizopathidae) from the Red Sea and its phylogenetic position. *Zookeys* **1116**, 1–22. <https://doi.org/10.3897/zookeys.1116.79846>
- Cuecuecha-Pérez LF and Ávila-García AE** (2025) Symbiotic relationships in octocorals: The role of gorgonians. *CIENCIA Ergo-sum* **31**, e286. <https://doi.org/10.30878/ces.v32n0a27>
- Darriba D, Taboada G, Doallo R and Posada D** (2012) jModelTest 2: More models, new heuristics and parallel computing. *Nature Methods* **9**, 772. <https://doi.org/10.1038/nmeth.2109>
- Denis V, Ferrier-Pagès C, Schubert N, Coppari M, Baker DM, Camp EF, Gori A, Grottoli AG, Houlbrèque F, Maier SR, Mancinelli G, Martinez S, Özdilek ŞY, Radice VZ, Ribes M, Richter C, Viladrich N and Rossi S** (2024) Heterotrophy in marine animal forests in an era of climate change. *Biological Reviews* **99**, 965–978. <https://doi.org/10.1111/brv.13053>
- deVienne DM, Refrégier G, López-Villavicencio M, Tellier A, Hood ME and Giraud T** (2013) Cospeciation vs host-shift speciation: Methods for testing, evidence from natural associations and relation to coevolution. *New Phytologist* **198**, 347–385. <https://doi.org/10.1111/nph.12150>
- Diaz C, Howell KL, Robinson E, Hosegood P, Bolton A, Ganderton P, Arber P, Attrill M and Foster NL** (2023) Light and temperature drive the distribution of mesophotic benthic communities in the Central Indian Ocean. *Diversity and Distributions* **29**, 1578–1593. <https://doi.org/10.1111/ddi.13777>
- DiBattista JD, Roberts MB, Bouwmeester J, Bowen BW, Coker DJ, Lozano-Cortes DE, Choat JH, Gaither MR, Hobbs JPA, Khalil MT, Kochzius M, Myres RE, Paulay G, Robitzsch VSN, Saenz-Agudelo P, Salas E, Sinclair-Taylor TH, Toonen RJ, Westneat MW, Williams ST and Berumen ML** (2016) A review of contemporary patterns of endemism for shallow water reef fauna in the Red Sea. *Journal of Biogeography* **43**, 423–439. <https://doi.org/10.1111/jbi.12649>
- Dimijian GG** (2000) Evolving together: The biology of symbiosis, part 1. *Baylor University Medical Center Proceedings* **13**, 217–226.
- FAO** (2009) *International Guidelines for the Management of Deep-Sea Fisheries in the High Seas*. Rome: FAO 73 pp.
- Fautin DG** (2009) Structural diversity, systematics, and evolution of cnidae. *Toxicon* **54**, 1054–1064. <https://doi.org/10.1016/j.toxicon.2009.02.024>
- Fautin DG** (2016) Catalog to families, genera, and species of orders Actiniaria and Corallimorpharia (Cnidaria: Anthozoa). *Zootaxa* **4145**, 1–449. <https://doi.org/10.11646/zootaxa.4145.1.1>
- Fautin DG, Zelenchuk T and Raveendran D** (2007) Genera of orders Actiniaria and Corallimorpharia (Cnidaria, Anthozoa, Hexacorallia), and their type species. *Zootaxa* **1668**, 183–244. <https://doi.org/10.11646/zootaxa.1668.1.12>
- Fourreau CJL, Macrina L, Lalas JAA, Takahata A, Koido T and Reimer JD** (2024) The Trojan seahorse: Citizen science pictures of a seahorse harbour insights into the distribution and behaviour of a long-overlooked polychaete worm. *Proceedings of the Royal Society B* **291**, 20241780. <https://doi.org/10.1098/rspb.2024.1780>
- Gittenberger A and Gittenberger E** (2011) Cryptic, adaptive radiation of endoparasitic snails: Sibling species of *Leptoconchus* (Gastropoda: Coralliophiliidae) in corals. *Organisms Diversity & Evolution* **11**, 21–41. <https://doi.org/10.1007/s13127-011-0039-1>
- Goulet TL and Goulet D** (2021) Climate change leads to a reduction in symbiotic derived cnidarian biodiversity on coral reefs. *Frontiers in Ecology and Evolution* **9**, 636279. <https://doi.org/10.3389/fevo.2021.636279>
- Gravier C** (1918) Note préliminaire sur les Hexactinaires recueillis au cours des croisières de la Princesse-Alice et de l'Hirondelle de Monaco 346, 1–24. Gray JE (1860) Description of some new genera of lithophytes or stony zoophytes. *Proceedings of the Zoological Society of London*, 479–486.
- Gress E and Kaimuddin M** (2021) Observations of sea anemones (Hexacorallia: Actiniaria) overgrowing black corals (Hexacorallia: Antipatharia). *Marine Biodiversity* **51**, 45. <https://doi.org/10.1007/s12526-021-01184-x>
- Hiles I** (1899) The gorgonacea collected by Dr. Willey. Zoological results based on material from New Britain, New Guinea, Loyalty Islands and elsewhere, collected during the years 1895, 1896 and 1897, by Arthur Willey, part. 2, 195–206.
- Hoeksema BW** (2017) The hidden biodiversity of tropical coral reefs. *Biodiversity* **18**, 8–12. <https://doi.org/10.1080/14888386.2017.1307787>
- Kahng SE, Copus JM and Wagner D** (2014) Recent advances in the ecology of mesophotic coral ecosystems (MCEs). *Current Opinion in Environmental Sustainability* **7**, 72–81. <https://doi.org/10.1016/j.cosust.2013.11.019>
- Katoh K and Standley DM** (2013) MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution* **30**, 772–780. <https://doi.org/10.1093/molbev/mst010>

- Larsson A (2014) AliView: A fast and lightweight alignment viewer and editor for large data sets. *Bioinformatics* **30**, 3276–3278. <https://doi.org/10.1093/bioinformatics/btu531>
- Lau WY, Polisen A, Kushida Y, Quere G and Reimer JD (2020) The classification, diversity and ecology of shallow water octocorals. *Encyclopaedia of the World's Biomes* **4**, 597–611. <https://doi.org/10.1016/B978-0-12-409548-9.12109-8>
- Lourie SA and Randall JE (2003) A new pygmy seahorse, *Hippocampus denise* (Teleostei: Syngnathidae), from the Indo-Pacific. *Zoological Studies* **42**, 284–291.
- Loya Y, Puglise KA and Bridge TCL (2019) Mesophotic Coral Ecosystems Mesophotic coral ecosystems. In Loya Y, Puglise KA and Bridge TCL (eds.) Cham: Springer, 12 ix–x <https://doi.org/10.1007/978-3-319-92735-0>
- Macrina L, Nolan MKB, Terraneo TI, Oury N, Augustin N, van der Zwan FM and Benzoni F (2024b) The deepest record of the octocoral *Acanthogorgia* from the Red Sea. *Frontiers in Marine Science* **10**, 1305420. <https://doi.org/10.3389/fmars.2023.1305420>
- Macrina L, Terraneo TI, Arrigoni R, Maggioni D, Tietbohl MD, Anker A, Lasley RM Jr, Pappas M, Berumen ML and Benzoni F (2024a) Molecular diversity and patterns of co-occurrence of decapod crustaceans associated with branching corals in the central Red Sea. *Marine Biodiversity* **54**, 65. <https://doi.org/10.1007/s12526-024-01457-1>
- Macrina L, Terraneo TI, McFadden CS, Chimienti G, Marchese F, Vimercati S, Vicario S, Reimer JD, Purkis SJ, Eweida AA, Pieribone V, Qurban M, Duarte CM, Rodrigue M, van der Zwan FM, Augustin N, Westphal H and Benzoni F (2025) The hidden diversity of Saudi Arabian Red Sea octocorals revealed through a morpho-molecular assessment across bathymetric and latitudinal gradients. *Scientific Reports* **15**, 33651. <https://doi.org/10.1038/s41598-025-17136-5>
- Maggioni D, Arrigoni R, Seveso D, Galli P, Berumen ML, Denis V, Hoeksema BW, Huang D, Manca F, Pica D, Puce S, Reimer JD and Montano S (2022a) Evolution and biogeography of the Zanclea-Scleractinia symbiosis. *Coral Reefs* **41**, 779–795. <https://doi.org/10.1007/s00338-020-02010-9>
- Maggioni D, Terraneo TI, Chimienti G, Marchese F, Pica D, Cairns SD, Eweida AA, Rodrigue M, Purkis SJ and Benzoni F (2022b) The first deep-sea stylasterid (Hydrozoa, Stylasteridae) of the Red Sea. *Diversity* **14**, 241. <https://doi.org/10.3390/d14040241>
- McFadden CS, Erickson KL, Lane A, Nassongole B, Aguilar S, Dunakey SK, Durkin KM, Lallas JAA, Kushida Y, Macrina L, Minor NP, Morales-Paredes M, Nelson J, Peddada A, Poole S, Porto R, Purow-Ruderman R, Snyder KE, Wismar T, Samimi-Namin K, Baria-Rodriguez MV, Benzoni F, Huang D, Reimer JD, Paulay G, Quattrini AM, Ekins M and Benayahu Y (2025) Biodiversity and biogeography of zooxanthellate soft corals across the Indo-Pacific. *Scientific Reports* **15**, 15461. <https://doi.org/10.1038/s41598-025-98790-7>
- Mercier A and Hamel J-F (2008) Nature and role of newly described symbiotic associations between a sea anemone and gastropods at bathyal depths in the NW Atlantic. *Journal of Experimental Marine Biology and Ecology* **358**, 57–69. <https://doi.org/10.1016/j.jembe.2008.01.011>
- Miller MA, Pfeiffer W and Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)*, New Orleans, LA, 1–8. <https://doi.org/10.1109/GCE.2010.5676129>
- Milne-Edwards A and Haime J (1857). *Histoire naturelle des Coralliaires ou polypes proprement dits. Tome troisième: Suite de la section des Madréporaires apores*. Roret Paris, 560.
- Moccia D, Cau A, Bramanti L, Carugati L, Canese S, Follesa MC and Cannas R (2020) Spatial distribution and habitat characterization of marine animal forest assemblages along nine submarine canyons of Eastern Sardinia (central Mediterranean Sea). *Deep Sea Research Part I: Oceanographic Research Papers* **167**, 103422. <https://doi.org/10.1016/j.dsr.2020.103422>
- Montano S (2022) Diversity of coral-associated fauna: An urgent call for research. *Diversity* **14**, 765. <https://doi.org/10.3390/d14090765>
- Morton B (1989) Partnerships in the sea: Hong Kong's marine symbioses. Hong Kong: Hong Kong University Press and E. J. Brill 124 pp.
- Nolan MKB, Falkenberg P, Marchese F, Ezeta Watts MA, Dunn N, Macrina L, Nunes-Peinemann V, Chimienti G, Vimercati S, Terraneo TI, Qurban M, Pieribone V, Duarte CM and Benzoni F (2025) Modelling the habitat distribution of the endemic azooxanthellate coral *Madracis interjecta* from the mesophotic to the deep Red Sea. *Ecology and Evolution* **15**, e71456. <https://doi.org/10.1002/ece3.71456>
- Nolan MKB, Marchese F, Purkis SJ, Ouhssain M, Kheireddine M, Terraneo TI, Chimienti G, Rodrigue M, Eweida AA, Jones B and Benzoni F (2024) Habitat suitability models reveal extensive distribution of deep warm-water coral frameworks in the Red Sea. *Communications Earth & Environment* **5**, 709. <https://doi.org/10.1038/s43247-024-01830-9>
- Ocaña O and Brito A (2004) A review of Gerardiidae (Anthozoa: Zoantharia) from the Macaronesian Islands and the Mediterranean Sea with the description of a new species. *Revista de la Academia Canaria de Ciencias* **3-4**, 159–189.
- Ocaña O, den Hartog JC and van Ofwegen LP (2004) Ring sea anemones, an overview (Cnidaria, Anthozoa, Actiniaria). *Graellsia* **60**, 143–154.
- Ocaña O, Henriques A and Porteiro F (2007) An occurrence of ring sea anemones (Anthozoa, Actiniaria) in the Azores Region. *Graellsia* **63**, 359–362.
- Orejas C, Carreiro-Silva M, Mohn C, Reimer JD, Samaai T, Allcock LA and Rossi S (2022) Marine Animal Forests of the world: Definition and characteristics. *Research Ideas and Outcomes* **8**, e96274. <https://doi.org/10.3897/rio.8.e96274>
- Osman EO and Weinnig AM (2022) Microbiomes and obligate symbiosis of deep-sea animals. *Annual Review of Animal Biosciences* **10**, 151–176. <https://doi.org/10.1146/annurev-animal-081621-112021>
- QGIS Development Team (2025) QGIS Geographic Information System. <http://qgis.osgeo.org>. Accessed May 12, 2025.
- Radice VZ, Hernández-Agreda A, Pérez-Rosales G, Booker R, Bellworthy J, Broadribb M, Carpenter GE, Diaz C, Eckert RJ, Foster NL, Gijssbers JC, Gress E, Laverick JH, Micaroni V, Pierotti M, Rouzé H, Stevenson A, Sturm AB and Bongaerts P (2024) Recent trends and biases in mesophotic ecosystem research. *Biology Letters* **20**, 20240465. <https://doi.org/10.1098/rsbl.2024.0465>
- Reijnen BT, Hoeksema BW and Gittenberger E (2010) Host specificity and phylogenetic relationships among Atlantic Ovulidae (Mollusca: Gastropoda). *Contributions to Zoology* **79**, 69–78. <https://doi.org/10.1163/18759866-07902002>
- Riemann-Zürneck K and Griffiths CL (1999) *Korsaranthus natalensis* (Carlgrén, 1938) nov. comb. (Cnidaria: Actiniaria) a mobile sea anemone attacking octocorals. *South African Journal of Zoology* **34**, 190–196. <https://doi.org/10.1080/02541858.1999.11448508>
- Rodríguez E, Barbeitos MS, Brugler MR, Crowley LM, Grajales A, Gusmão L, Häussermann V, Reft A and Daly M (2014) Hidden among sea anemones: The first comprehensive phylogenetic reconstruction of the order Actiniaria (Cnidaria, Anthozoa, Hexacorallia) reveals a novel group of hexacorals. *PLoS ONE* **9**, e96998. <https://doi.org/10.1371/journal.pone.0096998>
- Rodríguez E, Fautin D and Daly M (2025) World List of Actiniaria. accessed at <https://www.marinespecies.org/actiniaria> on 2025-09-18.
- Rodríguez-Troncoso AP, Rodríguez-Zaragoza FA, Mayfield AB and Cupul-Magaña AL (2019) Temporal variation in invertebrate recruitment on an Eastern Pacific coral reef. *Journal of Sea Research* **145**, 8–15. <https://doi.org/10.1016/j.seares.2018.12.007>
- Ronquist F, Teslenko M, van der Mark P, Ayres D, Darling A, Höhna S, Larget B, Liu L, Suchard M and Huelsenbeck J (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61**, 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Ross D and Zamponi M (1982) A symbiosis between *Paracalliactis mediterranea* n. sp. (Anthozoa-Actiniaria) and *Pagurus variabilis* A. Milne-Edwards and Bouvier. *Vie Et Milieu* **32**, 175–181.
- Rossi S, Bramanti L, Gori A and Orejas C (2017) Animal Forests of the World: An Overview. In Rossi S, Bramanti L, Gori A and Orejas C (eds.), *Marine Animal Forests*. Cham: Springer, 1–28. https://doi.org/10.1007/978-3-319-21012-4_1

- Roux N, Salis P, Lee S-H, Besseau L and Laudet V (2020) Anemonefish, a model for Eco-Evo-Devo. *EvoDevo*, 11. <https://doi.org/10.1186/s13227-020-00166-7>
- Rouzé H, Leray M, Magalon H, Penin L, Gélín P, Knowlton N and Fauvelot C (2017) Molecular characterization reveals the complexity of previously overlooked coral-exosymbiont interactions and the implications for coral-guild ecology. *Scientific Reports*, 7. <https://doi.org/10.1038/srep44923>
- Schubert N, Brown D and Rossi S (2017) Symbiotic versus nonsymbiotic octocorals: Physiological and ecological implications. In Rossi S, Bramanti L, Gori A and Orejas C (eds), *Marine Animal Forests*. Cham: Springer, 1–32. https://doi.org/10.1007/978-3-319-21012-4_54
- Stamatakis A (2014) RAxML Version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30, 1312–1313. <https://doi.org/10.1093/bioinformatics/btu033>
- Stella JS, Jones GP and Pratchett MS (2010) variation in the structure of epifaunal invertebrate assemblages among coral hosts. *Coral Reefs* 29, 957–973. <https://doi.org/10.1007/s00338-010-0648-8>
- Stella JS, Pratchett MS, Hutchings PA and Jones GP (2011) Coral-associated invertebrates: Diversity, ecological importance and vulnerability to disturbance. *Oceanography and Marine Biology* 49, 43–104. <https://doi.org/10.1201/B11009-4>
- Tamura K, Stecher G and Kumar S (2021) MEGA11: Molecular evolutionary genetics analysis version 11. *Molecular Biology and Evolution* 38, 3022–3027. <https://doi.org/10.1093/molbev/msab120>
- Terraneo TI, Ouhssain M, Bocanegra Castano C, Aranda M, Hume BCC, Marchese F, Vimercati S, Chimienti G, Eweida AA, Voolstra CR, Jones BH, Purkis SJ, Rodrigue M and Benzoni F (2023) From the shallow to the mesophotic: A characterization of Symbiodiniaceae diversity in the Red Sea NEOM region. *Frontiers in Marine Science*, 10. <https://doi.org/10.3389/fmars.2023.1077805>
- Turner JA, Babcock RC, Hovey R and Kendrick GA (2017) Deep thinking: A systematic review of mesophotic coral ecosystems. *ICES Journal of Marine Science* 74, 2309–2320. <https://doi.org/10.1093/icesjms/fsx085>
- van der Schoot RJ and Hoeksema BW (2024) Host specificity of coral-associated fauna and its relevance for coral reef biodiversity. *International Journal for Parasitology* 54, 65–88. <https://doi.org/10.1016/j.ijpara.2023.09.002>
- Vicario S, Terraneo TI, Chimienti G, Maggioni D, Marchese F, Purkis SJ, Eweida AA, Rodrigue M and Benzoni F (2024) Molecular diversity of black corals from the Saudi Arabian Red Sea: A first assessment. *Invertebrate Systematics* 38, IS23041. <https://doi.org/10.1071/IS23041>
- Vimercati S, van der Meij SET, Terraneo TI, Chimienti G, Marchese F, Eweida AA, Purkis SJ, Rodrigue M and Benzoni F (2023) A Red Sea depth record of the coral-dwelling crab *Opecarcinus* (Decapoda: Cryptochiridae) in the mesophotic zone. *Diversity* 15, 723. <https://doi.org/10.3390/d15060723>
- WoRMS (2024) World Register of Marine Species. Available from <https://www.marinespecies.org> at VLIZ (accessed 18 12 2024).
- Xu T, Bravo H, Scholten YJH, Borgstein NM and van der Meij SET (2025) Depth influences coral-dwelling faunal symbiont communities in the Caribbean, independently of colony size. *Coral Reefs*. <https://doi.org/10.1007/s00338-025-02662-5>
- Yap NWL, Quek ZBR, Tan R, Nugroho A, Lee JN, Berumen ML, Tan KS and Huang D (2020) Carlgren's hesitation allayed: Redescription and systematics of *Heteranthus verruculatus* Klunzinger, 1877 (Cnidaria, Actiniaria), with a redefinition of Heteranthidae Carlgren, 1900. *Contributions to Zoology* 90, 155–182. <https://doi.org/10.1163/18759866-BJA10015>
- Zhou Y, Liu H, Feng C, Lu Z, Liu J, Huang Y, Tang H, Xu Z, Pu Y and Zhang H (2023) Genetic adaptations of sea anemone to hydrothermal environment. *Science Advances* 9, eadh0474. <https://doi.org/10.1126/sciadv.adh0474>