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Diversity and distribution of coral gall crabs associated with Red Sea mesophotic corals

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Coral-dwelling gall crabs (Cryptochiridae) live in an obligate symbiosis with reef-building corals from shallow to deep waters. In particular, crabs of the genus *Opecarcinus* are known to occur across the tropical belt in association with the scleractinian family Agariciidae, down to a depth of 89 m. The Red Sea is a semi-enclosed basin that has long been recognized as a region of high marine biodiversity and endemism, with more than 230 decapod species recorded so far. There, nine *Opecarcinus* species are recorded from shallow and mesophotic corals. However, the occurrence of *Opecarcinus* below 30 m depth is documented only in the Saudi Arabian coast of the Northern Red Sea, and the rest of the Saudi Arabian Red Sea has remained unstudied. In this work, we assess the diversity and distribution of *Opecarcinus* from the mesophotic waters of the Saudi Arabian Red Sea. Through Remotely Operated Vehicles (ROV) and Submarines explorations, we collected 10 gall crab specimens associated with Agariciidae corals at mesophotic depths between 47 and 89 m. Two mitochondrial and one nuclear markers were used to obtain crab phylogenetic tree showing that three of the *Opecarcinus* species known from Red Sea shallow-water corals can also live at mesophotic depths. This is the first assessment of the depth distribution of the genus *Opecarcinus* in the Red Sea. It provides further evidence of the depth range adaptability of the *Opecarcinus*-Agariciidae association and highlights the need for a more in-depth investigation of the largely overlooked mesophotic coral-associated fauna.

KEYWORDS

mesophotic coral ecosystems (MCEs), crustacea, agariciidae, species diversity, phylogeny

Introduction

The gall crab family Cryptochiridae Paulson, 1875, is a widely distributed yet much-overlooked family on coral reefs (Simon-Blecher and Achituv, 1997; Hoeksema and van der Meij, 2013; Nogueira et al., 2014), living in obligate symbiosis with at least 66 tropical scleractinian coral genera from the Atlantic to the Indo-Pacific Ocean (Castro, 2015). Cryptochirids are primarily found in shallow-water reefs but can occur below 600 m depth (Kropp and Manning, 1987; Zibrowius and Gili, 1990; Manning, 1991). So far, only the Atlantic genus *Detocarcinus* Kropp and Manning, 1987, the circumtropical genus *Opecarcinus* Kropp and Manning, 1987, the Indo-Pacific genera *Zibrovia* Kropp & Manning, 1996, and *Luciades* Kropp and Manning, 1996 (probably a junior synonym of *Opecarcinus* – Xu et al., 2022) inhabit Mesophotic Coral Ecosystems (~30-150 m light-dependent tropical and subtropical reef communities – see Pyle and Copus, 2019 for an overview). In particular, the genera *Opecarcinus* and *Luciades* occur in the mesophotic in association with the agariciid genera *Agaricia* Lamarck, 1801(the former), exclusively occurring in the Atlantic, and the Indo-Pacific *Leptoseris* Milne Edwards and Haime, 1849 (both the two genera) (Kropp and Manning, 1996; Komatsu and Takeda, 2013; van der Meij et al., 2015; Xu et al., 2022; Vimercati et al., 2023). The ability of *Opecarcinus* to inhabit Agariciidae Gray, 1847 corals both in shallow and mesophotic reefs was linked to its depth range adaptability (van der Meij et al., 2015; van Tienderen and van der Meij, 2016) and to the fact that *Opecarcinus*' host-specificity can influence its depth range (Vimercati et al., 2023). However, further studies are still required to understand their mesophotic diversity and geographic distribution.

The Red Sea is a young ocean basin (Ligi et al., 2012; Bonatti et al., 2015; Rasul et al., 2015; Augustin et al., 2021) characterized by high water temperature and salinity (Edwards, 1987; Roder et al., 2013). These environmental parameters in the Red Sea change gradually along latitude and depth (Sofianos and Johns, 2003; Raitsos et al., 2013; Rowlands et al., 2014, Rowlands et al., 2016; Chaidez et al., 2017; Berumen et al., 2019; Manasrah et al., 2019), making this body of water an optimal natural system to study the distribution of reef organisms (Berumen et al., 2019). As a result of its past and present geological configuration and its ecological conditions, the Red Sea has been recognized as a biodiversity hotspot with a high degree of endemism rate for shallow water organisms (Sheppard et al., 1992; Veron, 1995; Hughes et al., 2002; Obura, 2012; DiBattista et al., 2016a, DiBattista et al., 2016b; Berumen et al., 2019). However, our knowledge of the biota inhabiting Red Sea MCEs remains scarce due to logistical difficulties in reaching these environments (Hinderstein et al., 2010; Berumen et al., 2013, 2019). Studies on Red Sea MCEs are mainly limited to anthozoan corals of the Eilat coast of the Gulf of Aqaba (see, for example, Fricke and Hottinger, 1983; Fricke and Schuhmacher, 1983; Fricke and Knauer, 1986; Schlichter et al., 1986; Mass et al., 2007; Stambler et al., 2008; Alamaru et al., 2009; Einbinder et al., 2009; Nir et al., 2011), with some more recent explorations carried out along the Saudi Arabian Red Sea (see, for example, Ziegler et al., 2015; Chimienti et al., 2022; Terraneo et al., 2023; Vimercati et al., under revision; Vicario et al., submitted). To shed light on the biology and the ecology of MCEs, a focus on overlooked reef-associated invertebrates, such as cryptochirids, is crucial. In fact understanding how the diversity and ecology of coral-associated invertebrates change with increasing depth can be useful to establish the reef-associated invertebrates' roles within coral reef ecosystems, especially in regard to their impact on reef resilience, and can inform the steps needed for their conservation (Stella et al., 2011; van der Schoot and Hoeksema, 2024). In this context, Red Sea scleractinian corals are known to host nine cryptochirid species ascribed to the genus *Opecarcinus*, mostly occurring in shallow water (< 30 m) (Xu et al., 2022), with the notable exception of the depth generalist *Opecarcinus* identified by the preliminary code SET4 (Xu et al., 2022), recovered on one *Leptoseris* cf. *mycetoseroides* Wells, 1954, specimen at 89 m depth only in the North Red Sea (Vimercati et al., 2023). Hence, the diversity, distribution, and host association of coral-dwelling *Opecarcinus* along the mesophotic Red Sea latitudinal gradient remains unknown, mainly due to the lack of exploration and targeted sampling beyond SCUBA diving depths.

During different recent research cruises from 2020 to 2022, Remotely Operated Vehicle (ROV) and manned submersible vehicle sampling allowed us to collect 10 gall crab specimens from MCE corals in four distinct regions spanning the Saudi Arabian Red Sea coastline. This study assesses *Opecarcinus* mesophotic diversity and distribution along the Saudi Arabian Red Sea. We provide a phylogeny reconstruction for the genus *Opecarcinus* and report new geographic and depth records and coral host associations.

Materials and methods

Crab sampling

A total of 10 gall crab specimens belonging to the genus *Opecarcinus* were collected during the Red Sea Deep Blue Expedition in 2020 (n=2) and the Red Sea Decade Expedition in 2022 (n=8) on board the M/V OceanXplorer along the Saudi Arabian Red Sea MCEs (Table 1). Sampling of the host corals took place in four regions spanning the latitudinal range of the Saudi Arabian Red Sea from the North Red Sea (NEOM area) (two sites), Al Wajh (one site), Central Red Sea (one site), and South Red Sea (four sites) (Figures 1A, B). The *Opecarcinus* specimens were extracted from their dwellings using pliers and tweezers from coral colonies of the genus *Leptoseris* and *Pavona* Lamarck, 1801, sampled between 47 and 89 m in depth using an Argus Mariner XL ROV and a triton 3303/3 submersible with a Schilling T4 hydraulic manipulator. An example of an ongoing sampling is shown in Figures 1C–E. The ROV and the submersible dives were video-recorded, and frame grabs of the crab-inhabited coral colonies were extracted from the videos using the open-source software MPC-HC (Media Player Classic – Home Cinema) and Adobe Premier software PRO^{TM}, respectively, to obtain host and crab dwelling images *in situ*. Kongsberg HIPaP 501 USBL (Ultra-Short Baseline), Sonardyne Sprin INS (Inertial Navigation System), and Sonardyne Ranger Pro 2 USBL provided the underwater vehicles' geographic and depth position. The collected gall crabs

TABLE 1 List of the 10 *Opecarcinus* specimens collected in the Saudi Arabian Red Sea for this study, including the voucher code, species, host coral species, sampling depth, latitude, longitude, and locality.

Code	*O. species*	Host coral	Depth	Latitude	Longitude	Locality
CHR0024_13B	SET4	*L.* cf. *mycetoseroides*	89	27.7073	35.1683	Duba
NTN0046_11B	SET4	*L.* sp. 1	70.57	27.73	35.2459	Duba
CHR0308_BIO16A	SET4	*L.* cf. *glabra*	67.63	25.407	36.7755	Al Wajh
CHR0267_BIO16A	SET7	*L. incrustans*	71.09	22.8367	38.7488	Rabigh
CHR0266_BIO8A	SET4	*L.* sp. 2	48.69	22.733099	38.790037	Rabigh
NTN0133_BIO21C	SET13	*P.* cf. *varians*	49	18.5105	40.6651	Al Qunfudhah
CHR0239_BIO16C	SET4	*L.* cf. *glabra*	60.3	18.8134	40.6393	Al Qunfudhah
CHR0242_BIO9C	SET4	*Leptoseris* cf. *scabra*	47.14	19.0988	40.3703	Al Qunfudhah
CHR0235_BIO18C	SET4	*L.* cf. *glabra*	66.22	17.8235	40.7108	Al Qunfudhah
CHR0239_BIO19C	SET7	*L. incrustans*	59.98	18.8134	40.6393	Al Qunfudhah

were preserved in 80% ethanol for future molecular analyses and examined and imaged under a Leica M205A stereomicroscope. The host coral and gall crab specimens are deposited at the King Abdullah University of Science and Technology (KAUST), Thuwal, Saudi Arabia.

DNA extraction, amplification, and sequence analyses

High-quality DNA was extracted from the fifth pereiopod muscle using Dneasy ® Blood and Tissue kit (Qiagen Inc., Hilden, Germany) following the manufacturer's protocol. DNA was amplified using the universal primers LCO1490/HCO2198 (Folmer et al., 1994) for the COI, the primers 16L2/16H10 (Schubart, 2009) for the 16S rRNA, and finally, the primers H3F/H3_R_SET (Colgan et al., 2000; van der Meij, 2015b) for the histone H3. The DNA amplification was performed in a 15 µL PCR volume of Multiplex Master Mix (Qiagen Inc., Hilden, Germany), 0.2 µL of each primer, and <0.1 ng of DNA. The PCR protocol for each primer followed the one of van der Meij (2015b). PCR samples were purified using Illustra™ Exostar™ 1-Step (GE Healthcare Life Sciences) following the manufacturer's protocol and directly sequenced in forward and reverse directions using an ABI 3730xl DNA analyzer (Applied Biosystems, Foster City, CA, USA) at KAUST Bioscience Core Lab.

Forward and reverse sequences were assembled and edited using Geneious Prime 2019 (Biomatters), and manually checked using BioEdit Sequence Alignment Editor v7.2 (Hall, 1999). The phylogenetic analysis was performed on a concatenated dataset of the three genes (COI, 16S, and H3). Two sequences of *Pseudohapalocarcinus ransoni* were added to the alignment due to its phylogenetic position within the genus *Opecarcinus* (see Xu et al., 2022). Moreover, 2 sequences of *Hapalocarcinus marsupialis sensu lato* Stimpson, 1859, were used as outgroup (Supplementary Table S1), following van der Meij and Nieman (2016). All sequences were concatenated using Geneious Prime 2019 (Biomatters) and aligned using MAFFT 7.520 (Katoh et al., 2013) under the E-INS0i strategy. General statistics concerning the obtained sequences were calculated with MEGA X (Kumar et al., 2018) and DnaSP6.11.1 (Librado and Rozas, 2009) PartitionFinder 2 (Lanfear et al., 2017) was used to calculate the sequence evolution best-fit substitution model for Bayesian Inference (BI) and Maximum Likelihood (ML) and to perform a partitioning scheme comparison. We used linked branch lengths, the greedy search algorithm for nucleotide sequence, and considered 7 partitions: 16S, the three codon positions of COI, and the three codon positions of H3. PartitionFinder 2 selected for RaxML the evolutionary model GTR+G for COI_pos1, COI_pos2, H3_pos1, H3_pos2, and H3_pos2, and the model GTR+I+G for COI_pos3 and 16S. For MrBayes, the evolutionary models GTR+G for COI_pos1, COI_pos2, and H3_pos2, F81+I for COI_pos3, GTR+I+G for 16S, F81+G for H3_pos1, and GTR for H3_pos3 were selected. The BI and ML analyses were run using MrBayes v3.2.7a (Ronquist et al., 2012) and RaxML v8.2.12 (Stamatakis, 2014), respectively, on the CIPRES server (Miller et al., 2011). In particular, the BI analyses were performed using four Markov chain Monte Carlo chains for 10 million generations, saving a tree every 1000th generation. Tracer 1.7.1 (Rambaut et al., 2018) was employed at the end of the runs to verify effective sampling size and unimodal posterior distribution stationarity. The first 25% of trees sampled were discarded as burn-in. The ML topology was derived using default parameters on the CIPRES server, with a multiparametric bootstrap analysis of 1000 replicates.

Results

Phylogenetic analyses

In total, 23 sequences were obtained for COI (9), 16S (10), and H3 (4) markers (Supplementary Table S1). A total of 129 additional sequences for COI (55), 16S (41), and H3 (34) were retrieved from GenBank, based on previous molecular studies (van der Meij and

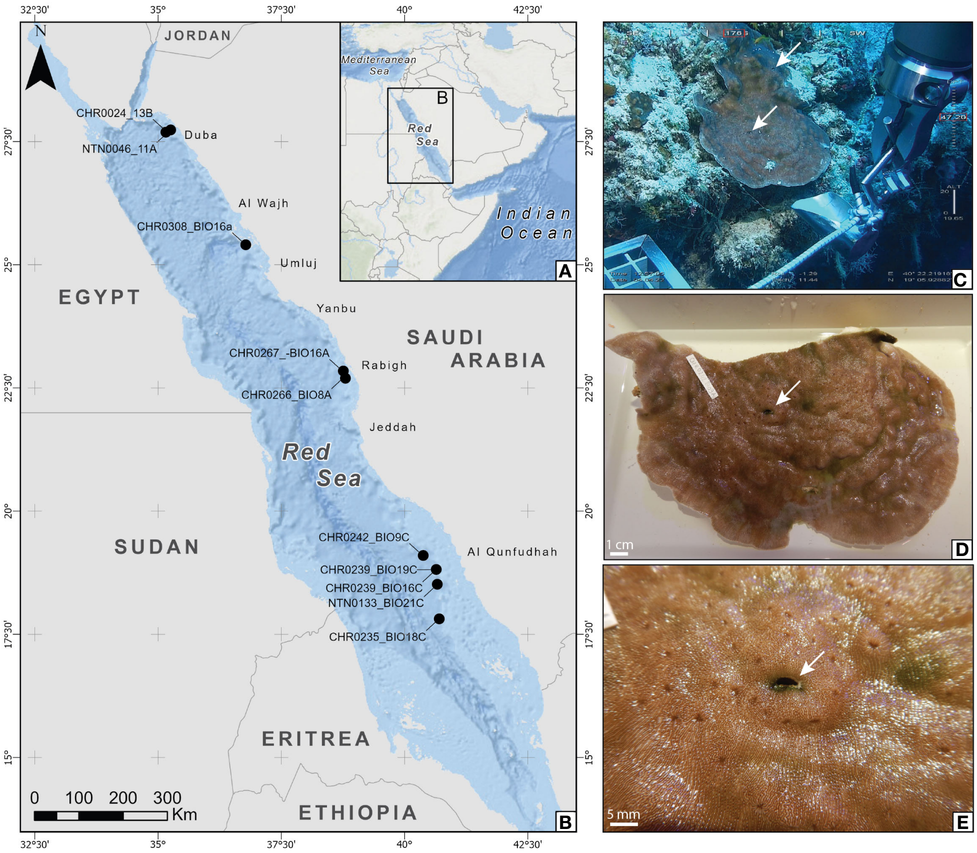

FIGURE 1
(A, B) Map of the Red Sea **(A)** showing the sampling area for this study **(B)** where the sampling site for each specimen is shown. CHR codes refer to ROV dives, and NTN code refers to submarine dives. **(C–E)** Sampling of CHR0242_BIO9C in association with *Leptoseris* cf. *scabra* at 47.14 m depth. **(C)** Sampling of the coral colony. **(D, E)** Gall crab (*Opecarcinus* SET4) dwelling in *L.* cf. *scabra*. The arrows indicate the dwellings. Map created using ArcGIS® software by Esri. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used herein under license. Copyright © Esri. All rights reserved. For more information about Esri® software, please visit www.esri.com.

Nieman, 2016; van Tienderen and van der Meij, 2016; Xu et al., 2022; Vimercati et al., 2023), and added to the alignment as reference sequences (Supplementary Table S1). Of these sequences, 31 were chosen from the Saudi Arabian Red Sea to cover the currently known *Opecarcinus* diversity from the basin (van der Meij and Nieman, 2016; Xu et al., 2022; Vimercati et al., 2023) (Supplementary Table S1). The final three loci concatenated alignment consisted of 1625 bp (625 bp for the COI, 646 bp for the 16S, and 354 bp for the H3), including 1210 conservative sites and 405 variable sites, of which 368 were parsimony-informative, and 36 were singletons. Moreover, DNAsp6 retrieved 281 mutations, not considering the 48 ambiguous bases that occurred in the GenBank sequences.

The phylogenetic tree reconstruction inferred from Bayesian Inference (BI) (Figure 2) included six of the nine previously described *Opecarcinus* species (Shaw and Hopkins, 1977; Kropp, 1989; van der Meij, 2014b) and 19 species reported by Xu et al. (2022), up to 15 of which are formally undescribed *Opecarcinus* species identified by preliminary codes, which are awaiting formal description (Xu et al., 2022; Vimercati et al., 2023; Xu et al., in prep). *Pseudohapalocarcinus ransoni* Fize & Serène, 1956, nested together with *Opecarcinus*, in agreement with previous reconstructions (van der Meij and Klaus, 2015; van der Meij and Nieman, 2016; Xu et al., 2022) (Figure 2). Moreover, coherently with Xu et al. (2022), material from the Red Sea was retrieved in 10 distinct clades, namely nine *Opecarcinus* and one of *P. ransoni* (Figure 2). The 10 mesophotic Red Sea specimens sampled in this study were recovered in 3 distinct and well-supported molecular lineages (Figure 2). In particular, seven gall crab specimens (one already published in Vimercati et al., 2023, and six from this study) (Supplementary Table S1) were retrieved with *Opecarcinus* SET4 (Xu et al., 2022) (Figure 2). Moreover, two mesophotic Red Sea specimens clustered together with the available sequences of *Opecarcinus* SET7 (Xu et al., 2022) (Figure 2). Finally, one specimen was recovered with *Opecarcinus* SET13 (Xu et al., 2022) (Figure 2).

New locality, depth, and host records

For the first time, *Opecarcinus* SET4 was collected from Al Wajh and the Central Red Sea and *Opecarcinus* SET7 from the Central Red Sea (Table 1). *Opecarcinus* SET13 was sampled in the South Red Sea, where it has been previously reported inhabiting euphotic scleractinians (Xu et al., 2022) (Table 1).

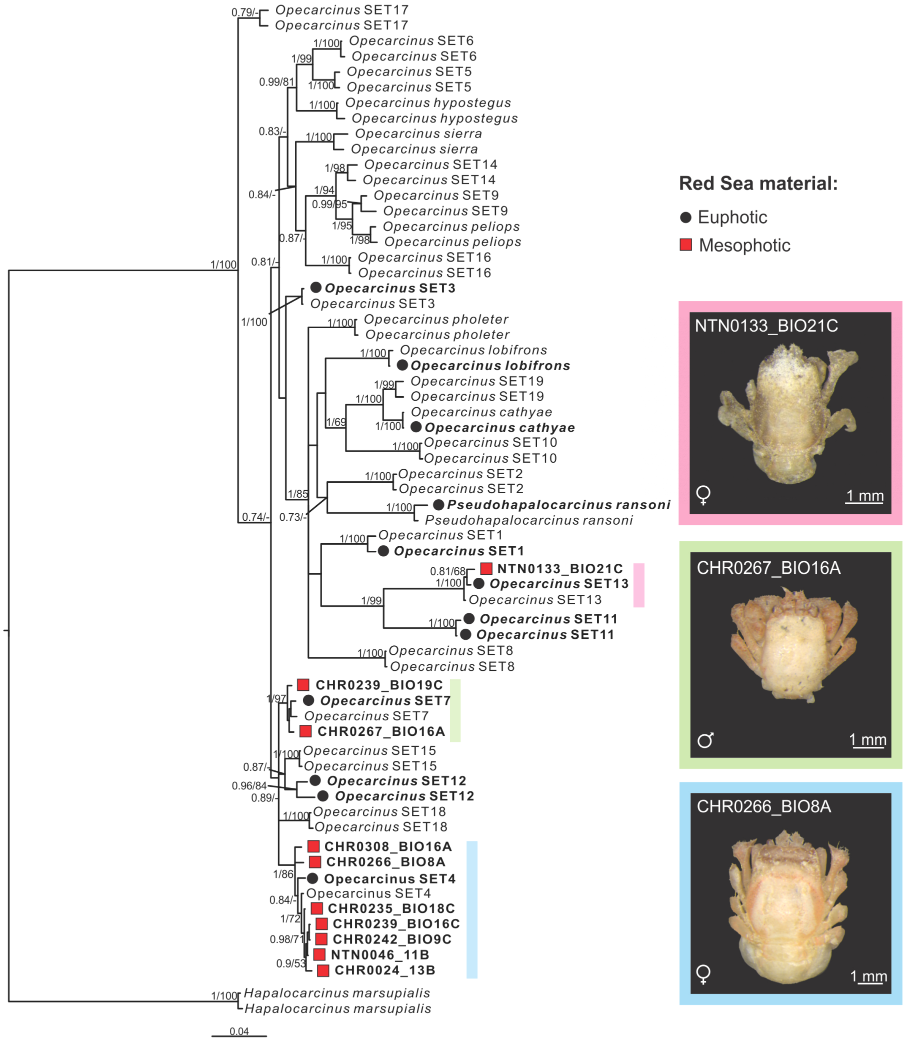

FIGURE 2
Mesophotic *Opecarcinus* phylogenetic reconstruction inferred from Bayesian Inference (BI) analysis of the combined mitochondrial (COI,16S) and nuclear (H3) datasets. Node values are posterior Bayesian Probability and Maximum Likelihood (ML) bootstrap values. Posterior Bayesian probabilities below 0.7 and ML bootstrap values below 50% are indicated by a dash (-). Red Sea samples are in bold. Black dots represent the currently known *Opecarcinus* species from the Red Sea (van der Meij and Nieman, 2016; Xu et al., 2022), while red squares highlight the mesophotic specimens collected for this study from the basin. Species without dots are representative of other Indo-Pacific localities. *Hapalocarcinus marsupialis* was used as an outgroup. Insert photographs by SV.

The current Red Sea depth distribution range of Agariciidae-associated *Opecarcinus* is 89 m for *Opecarcinus* SET4 (Vimercati et al., 2023). In this work, we further extended the known depth distribution of *Opecarcinus* SET7 to 71 m depth and *Opecarcinus* SET13 to 49 m depth (Table 1).

Moreover, our study provides the first evidence of new host records for *Opecarcinus* in the Red Sea. In particular, *Opecarcinus* SET4 was sampled from dwellings in the coralla of different *Leptoseris* species, namely *L.* cf. *mycetoseroides* (Vimercati et al., 2023), *Leptoseris* cf. *scabra* Vaughan, 1907, *Leptoseris* sp. 1 (previously identified as *Leptoseris* cf. *fragilis* Milne Edwards & Haime, 1849, *sensu* Terraneo et al., 2017), *Leptoseris* sp. 2 (previously identified as *Leptoseris* sp. *sensu* Terraneo et al., 2017), and *Leptoseris* cf. *glabra* Dinesen, 1980 (Table 1). *Opecarcinus* SET7 was observed in association with *Leptoseris incrustans* (Quelch, 1986) (Table 1). Finally, *Opecarcinus* SET13 was retrieved on a mesophotic colony identified as *Pavona* cf. *varians* Verrill, 1864 (Table 1).

Discussion

During different recent research cruises from 2020 to 2022, we surveyed the Saudi Arabian mesophotic and deep reefs ranging from depths of 45 to 600 m, collecting 10 cryptochirid specimens at depths between 47 and 89 m (Figures 1A, B). Our phylogeny reconstruction analyses of the combined mitochondrial (COI, 16S) and nuclear (H3) datasets retrieved the collected material in 3 distinct and well-supported molecular clades, already published as *O.* SET4, *O.* SET7, *O.* SET13 by Xu et al. (2022). The records of mesophotic coral-dwelling gall crabs examined in this work significantly extend the previously known depth distribution range of *Opecarcinus* in the Red Sea. Moreover, the three species were found in association with previously unreported Agariciidae hosts, thus also allowing us here to extend the known host range for this gall crab genus.

Mesophotic Opecarcinus diversity and host coral abundance

Currently, the genus *Opecarcinus* includes at least 25 species, 9 of which are described (van der Meij, 2014b; DecaNet eds., 2023), up to 15 of which are currently devoid of a formal taxonomic description and identified by preliminary codes (Xu et al., 2022). Although it occurs in the tropical belt spanning the Atlantic and the Indo-Pacific regions (e.g., Scott, 1985, Scott, 1987; Kropp and Manning, 1987; Kropp, 1989; van der Meij, 2014b; Chan et al., 2020), most of the studies on its depth distribution focus on the Caribbean (van der Meij et al., 2015; van Tienderen and van der Meij, 2016) (Figure 3), with only 10 mesophotic records in the Indo-Pacific (two of them belonging to the genus *Luciades*) (Shen, 1936; Kropp and Manning, 1996; Komatsu and Takeda, 2013; Xu et al., 2022; Vimercati et al., 2023) (Figure 3). In particular, the single Atlantic *Opecarcinus* species follows the depth distribution of its host corals (van Tienderen and van der Meij, 2016). This cryptochirid species has a higher prevalence at greater depths (van Tienderen and van der Meij, 2016), where the coral genus *Agaricia* forms dense high-cover assemblages (Bongaerts et al., 2013, Bongaerts et al., 2015; Hoeksema et al., 2017). Hence, the Red Sea *Opecarcinus* mesophotic diversity reported in this study is unsurprising if we consider the associated host corals and their depth distribution and abundance in MCEs. In fact, *Leptoseris* is one of the most abundant scleractinian genera in MCEs (Fricke et al., 1987; Hinderstein et al., 2010; Rooney et al., 2010; Kahng et al., 2014, Kahng et al., 2017; Loya et al., 2019). The strict association between gall crabs and scleractinian corals and the cryptochirid host specificity at host species, genera, or families (*e.g.*, van der Meij, 2015a, 2015b; van der Meij et al., 2015; Bähr et al., 2021; Xu et al., 2022; van der Schoot and Hoeksema, 2024) led to hypothesize that the number of host corals could predict the number of cryptochirids (van der Meij, 2015a; van der Schoot and Hoeksema, 2024). Moreover, Kohn and Leviten (1976) showed that habitat availability affects the abundance and diversity of coral-associated invertebrates. In this context, the high occurrence of the genus *Leptoseris* in the Red Sea MCEs could explain the mesophotic gall crab diversity found in this work.

New coral-gall crab associations in the Saudi Arabian Red Sea mesophotic zone

Unlike the Atlantic generalist gall crab species *Troglocarcinus corallicola* Verrill, 1908, most cryptochirids show host-specificity, inhabiting a single coral species or several closely related ones (Castro, 2015). In the Red Sea, Xu et al. (2022) reported *Opecarcinus* in association with 3 Agariciidae genera, namely *Gardineroseris* Scheer and Pillai, 1974, *Pavona*, and *Leptoseris*. Coral identification was mostly at the genus level, possibly due to the objective challenges posed by the unresolved taxonomic scenario of the family Agariciidae (Luck et al., 2013; Terraneo et al., 2017; Benzoni, 2022). In this study, most of the coral specimens collected didn't match the morphology of any previously described nominal species. Consequently, we here report on new coral-gall crab associations from the Red Sea mesophotic zone, with the coral hosts identified at the species level for the first time (Table 1). Moreover, the genus *Pavona* has previously been reported down to 52 m in the Red Sea (Fricke and Schuhmacher, 1983; Scheer and Pillai, 1983), but our study marks the first record of a gall crab-*Pavona* association at a depth below 30 m.

MCEs Opecarcinus diversity in the Saudi Arabian Red Sea: new insights and implications for conservation

To date, in the Red Sea, specialists have recorded the occurrence of more than 40 cryptochirid species in association with scleractinian hosts (van der Meij, 2015a; van der Meij et al., 2018; Bähr et al., 2021; Xu et al., 2022), with the Red Sea identified as a center of biodiversity for gall crabs, second only to the Coral Triangle (van der Meij, 2015a; Bravo et al., 2021). For this work, 10 cryptochirid specimens were collected at depths between 47 and 89 m (Figures 1A, B), thus reporting unknown cryptochirid biodiversity at these depths (Figure 3). Moreover, half of them were retrieved from the South Red Sea (Table 1) (Figures 1A, B). A previous study on Red Sea shallow waters reported a higher cryptochirid abundance in the South compared to the central part of the basin, suggesting that the South's high productivity could facilitate the settlement of coral-dwelling crabs (van der Meij, 2015a). However, in our study, the difference in distribution could be related to a very limited number of specimens collected compared to other studies focusing on shallow water (see van der Meij, 2015a; Xu et al., 2022). In this context, it is important to highlight that assessing the mesophotic coral associates' diversity and distribution poses significant challenges due to the logistical difficulties and costs associated with mesophotic explorations (Hinderstein et al., 2010; Berumen et al., 2013, 2019). However, different studies focused on the importance of increasing our knowledge of coral-associated invertebrates (see Stella et al., 2011, for an overview; Hoeksema, 2017; Montano, 2020, Bravo et al., 2021; Montano, 2022), in light of current global and local threats coral reefs are facing (Hughes et al., 2003, Hughes et al., 2017; Hoegh-Guldberg et al., 2007; Burke et al., 2011; Cinner et al., 2016). Given the limited knowledge of reef-affiliated invertebrates, it is, thus, crucial to continue to investigate MCEs' biodiversity to enhance our understanding of these low-light environments and to implement more effective conservation measures.

Conclusions

In conclusion, this study represents the first assessment of the diversity and distribution of the genus *Opecarcinus* in mesophotic corals along the Saudi Arabian Red Sea. We collected 10 specimens along the basin, with half of them sampled in the South Red Sea. We

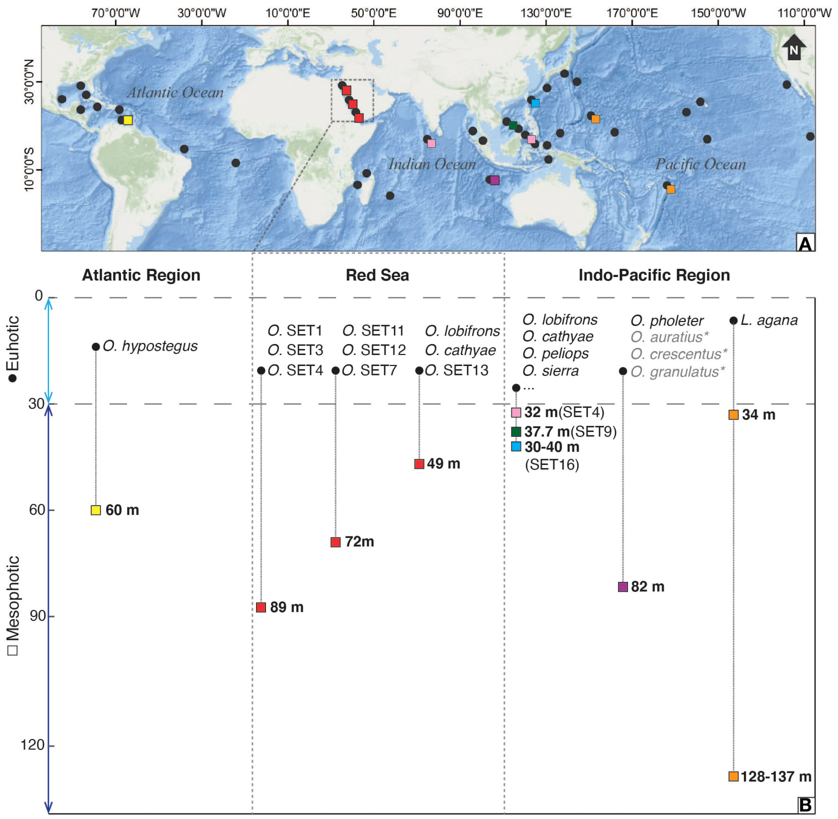

FIGURE 3
(A) Map of the Atlantic and Indo-Pacific Oceans (Red Sea included) showing the *Opecarcinus* and *Luciades* distribution in shallow waters (black dots) and the mesophotic deepest records in Curaçao (yellow square), in the Red Sea (red square), in Christmas Island (purple square), in Maldives and Lembeh (pink squares), in Spratly Islands (green square), in Taiwan (light blue square), and in Guam and Tonga (orange squares) based on literature distribution records (Kropp and Manning, 1987; Kropp, 1989; Kropp and Manning, 1996; Komatsu and Takeda, 2013; van der Meij et al., 2018; van Moorsel and van der Meij, 2018; Chan et al., 2020; Xu et al., 2022; Vimercati et al., 2023) and this study. **(B)** List of *Opecarcinus* and *Luciades* species with their photic (0-30 m) and mesophotic (~30-150 m) depth distribution in 3 main regions: the Atlantic Region, the Red Sea, and the Indo-Pacific Region. The formally undescribed *Opecarcinus* species identified by preliminary codes occurring in the Indo-Pacific (namely *O.* SET1-10, *O.* SET12-19) (Xu et al., 2022), are reported in **(A)** but not listed in **(B)**, where they are indicated by three dots (…). Species in grey refer to the 3 *Opecarcinus* accepted species not analyzed molecularly in this study: *Opecarcinus auratius* Kropp, 1989, *Opecarcinus crescentus* (Edmondson, 1925), and *Opecarcinus granulatus* (Schen, 1936). Map created using ArcGIS® software by Esri. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used herein under license. Copyright © Esri. All rights reserved. For more information about Esri® software, please visit www.esri.com.

found 3 depth generalist species currently under taxonomic description, reconfirming that the genus *Opecarcinus* host specificity influences the depth range (Vimercati et al., 2023). Further investigation of mesophotic reefs is necessary to understand the role of depth on reef-affiliated invertebrates and to unravel the mesophotic diversity and depth zonation of cryptic reef-associated taxa, such as the gall crabs. Moreover, it is crucial to deepen our understanding of cryptochirids concerning their bathymetrical ranges and phylogenetic relationships of their host taxa to comprehend the evolutionary history of these mesophotic associations (García-Hernández et al., 2020) and to understand the role they play in coral reef ecosystems (Stella et al., 2011), in light of the current climate change scenario and consequent reef degradation.

Data availability statement

The sequence data supporting this study's findings is openly available in GenBank of NCBI at https://www.ncbi.nlm.nih.gov/genbank, under accession numbers listed in Table S1.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

SV: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. TT: Conceptualization, Supervision, Validation, Writing – review & editing. FM: Writing – review & editing. AA: Data curation, Funding acquisition, Project administration, Resources, Writing – review & editing. MR: Data curation, Resources, Writing – review & editing. VP: Data curation, Funding acquisition, Project administration, Resources, Writing – review & editing. MQ: Funding acquisition, Project administration, Resources, Writing – review & editing. CD: Funding acquisition, Project administration, Resources, Writing – review & editing. FB: Conceptualization, Data curation, Funding acquisition, Resources, Supervision, Validation, Project administration, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2024.1305396/full#supplementary-material

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