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Volume and pages number were added in Dana, 1846. The references Forsskal, 1775 and Gardiner, 1898 are complete.

Short Communication

New ecological and phylogenetic insights in the boring barnacle *Bernʊtia* Utinomi 1950 (Acrothoracica: Lithoglyptidae) reveal higher diversity, new hosts, and range extension to the Western Indian Ocean

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Abstract AQ1

The acrot AQ2 horacican genus *Berndtia* Utinomi, 1950 includes small barnacles known to bore into the calcareous skeleton of living scleractinian corals of the genera *Psammocora* Dana, 1846 and *Leptastrea* Milne Edwards & Haime, 1849. The six known species of *Berndtia* are restricted to the tropical Western Pacific. We provide the first record of *Berndtia* from the hydrocoral *Millepora exaesa* Forsskål, 1775 from the central Red Sea, Saudi Arabia, and the scleractinian coral *Coscinaraea* cf. *monile* (Forsskål, 1775) from the Arabian Sea, Oman. These findings extend the known range and host use of the genus and raise questions about *Berndtia*'s host specificity. A molecular analysis of Saudi Arabian and Omani specimens suggests that they belong to two new lineages that may represent new species of *Berndtia*, each associated with multiple hosts. Further sampling around the Arabian Peninsula and the Western Indian Ocean and exploration of additional potential hosts would provide new insights into the species diversity of the genus.

Keywords

Saudi Arabia
Red sea
Oman
Fire corals
Symbiosis
Coral reefs

Communicated by B.W. Hoeksema

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1007/s12526-023-01379-4.

Introduction

The Acrothoracica (Arthropoda: Thecostraca: Cirripedia) are boring barnacles that penetrate into calcareous substrata and lack an external mineral shell (Chan et al. 2021). The majority of the 70 currently known species burrow into dead shells and other carbonates (Tomlinson 1987; Chan et al. 2013). However, species of *Berndtia* Utinomi 1950 bore in and are obligate symbionts of living scleractinian corals (Cnidaria: Anthozoa: Scleractinia). *Berndtia* species have so far been recorded from the host genera *Psammocora* Dana, 1846 and *Leptastrea* Milne Edwards & Haime, 1849 (Utinomi 1950; Tomlinson 1967, 1969; Chan et al. 2014, 2020), which belong to distinct, yet closely related, family level lineages within the scleractinian Robust clade (Kitahara et al. 2016; Quek et al. 2023). Contrary to most acrothoracicans that burrow into calcium carbonate matrixes of various origins without displaying specificity for the substrate (Botha et al. 2020), *Berndtia* appears to be highly host-specific (Chan et al. 2014). Currently, *Berndtia* contains six valid species, all from the tropical waters of the Western Pacific Ocean (Chan et al. 2014, 2020). Species distinction is based on several morphological characters and color patterns, as well as on host specificity (Chan et al. 2014). However, species boundaries inferred from molecular data within *Berndtia* have received limited attention. A number of molecular studies included sequences of *Berndtia* in the context of barnacle phylogenies (e.g., Chan et al. 2012, 2013; Lin et al. 2016) and barnacle character evolution (e.g. Yu et al. 2020; Dreyer et al. 2022), but have not examined phylogenetic relationships

within the genus. Chan et al. (2014) provided vouchered barcode sequences for COI and 16S genes for four species without presenting a phylogeny reconstruction.

The tropical and subtropical Western Indian Ocean is one of the most important marine biogeographical provinces in terms of endemic species (Briggs and Bowen 2012). Within this area, the Red Sea represents a major hotspot of endemism, as a result of its past and present geological configuration, as well as temporal and spatial environmental gradients (DiBattista et al. 2016a). The monsoonal-driven cold water upwelling in the eastern Arabian Sea acts as a major biogeographical barrier, separating the Red Sea and the Gulf of Aden from the rest of the Indian Ocean (Briggs and Bowen 2012; Veron et al. 2015). The increase of nutrients and consequent bloom of primary production driven by this peculiar circulation regime influences the ecosystem composition in the Arabian Sea coasts of Yemen and Oman (Narvekar et al. 2021). The great potential for biodiversity in these regions has been highlighted in a growing number of studies, with a focus on different invertebrate taxa (e.g. Claereboudt and Al Rashdi 2011; Maggioni et al. 2017a; Pearman et al. 2018; Carvalho et al. 2019; Anker 2022; DiBattista et al. 2022). Despite this increasing interest, however, our knowledge on marine invertebrate diversity and evolution remains poor especially on less common and visually obvious groups (Tsang et al. 2012; DiBattista et al. 2016b).

In this study, we present the first record of *Berndtia* from the Western Indian Ocean and report its association with two new host species. The first phylogenetic assessment of the genus based on the COI gene is also provided.

Materials and methods

A sample of *Coscinaraea* cf. *monile* (Forsskål, 1775; Catalog number: OM0437) ~~,~~ containing a single specimen of *Berndtia* sp. (OM0437A) was collected in January 2022 while scuba diving at a depth of 20 m off Mirbat, Dhofar, Southern Oman (16°57′50″N, 54°41′31″E). One month later, a fragment of a fire coral colony, *Millepora exaesa* Forsskål, 1775 (SA5239)~~,~~ was collected while scuba diving at a depth range of 5–10 m near Jeddah, Saudi Arabia (21°45′23″N, 21°45′23″E). Three specimens of *Berndtia* sp. (SA5239D-F) were found embedded in the calcareous skeleton of the hydrocoral. Two additional specimens of *Berndtia* sp. (SA5242A-B) were found on a fragment of the scleractinian *Psammocora profundacella* Gardiner, 1898 (a host previously reported for the genus, see Chan et al. 2014; Catalog number: SA5242)~~,~~, bordering the *M. exaesa* colony.

The Red Sea specimens were examined and photographed under a Leica M205 A stereomicroscope, equipped with a Leica DMC 5004 camera and then extracted from the coral skeleton, while the Omani specimen was photographed under the stereomicroscope only after preservation. All barnacles were preserved in 75% ethanol, while portions of host tissue were preserved in 96% ethanol. All the collected material was deposited at King Abdullah University of Science and Technology (KAUST).

Genomic DNA was extracted from a portion of the barnacle mantle sacs using Qiagen DNeasy® Blood and Tissue kit (Qiagen Inc., Hilden, Germany) following manufacturer's protocol. Primers LCO1490 and HCO2198 were used to amplify a portion of the mitochondrial cytochrome *c* subunit I gene (COI) (Folmer et al. 1994). A polymerase chain reaction (PCR) was performed for each sample, consisting of 1.2 µl of template DNA, 1.5 µl of each primer, 7.5 µl of *Taq* PCR Master Mix (Qiagen Inc., Hilden, Germany), and RNAse-free water to 15 µl final volume. The PCR protocol was the following: 95° for 15 min; 94° for 30 s, 51° for 1 min, 72° for 1min (40 cycles); and 72° for 5 min. PCR samples were purified with Illustra™ ExoStar™ 1-Step (GE Healthcare Life Sciences) at 37° for 30 min, followed by 85° for 15 min, and sent for direct sequencing in both forward and reverse directions using an ABI 3730xl DNA Analyzer (Applied Biosystems, Carlsbad, USA) at KAUST Bioscience Core Lab.

Forward and reverse chromatograms were visually inspected and assembled using Geneious R7 7.1.3. All available COI sequences of *Berndtia* spp. were downloaded from GenBank (Benson et al. 2012) and included in the analysis (Online Resource 1), together with three sequences of other acrothoracican barnacles, used as outgroups following Lin et al. (2016). Sequences alignment was performed using MAFFT V7.490 with the E-INS-I option (Katoh and Standley 2013). The alignment was manually checked for ambiguous gaps and edited using BioEdit v.7.2 (Hall 1999). The best substitution model was estimated under both Akaike and Bayesian information criteria using jModelTest2 v.2.1 (Darriba et al. 2012) and resulted in HKY + G. Phylogenetic inference was performed using Bayesian inference (BI) with MrBayes 3.2.6 (Ronquist et al. 2012): two independent runs for four Markov chains were conducted for 10 million generations, with trees sampled every 1000th generation, and burn-in set to 25%. Parameter estimates and convergence were checked using Tracer 1.6 (Rambaut et al. 2018). All phylogenetic analyses were performed on CIPRES server (Miller et al. 2010). Between- and within-group mean genetic distances were computed for all recovered molecular clades using MEGA X v10.2.4 (Kumar et al. 2018), as % uncorrected *p*-distances with 1000 bootstrap replicates. The obtained sequences were deposited in GenBank (see Online Resource 1).

~~Material examined~~ AQ3

~~*Berndtia* sp. 1~~

~~All specimens from Jeddah, Saudi Arabia, depth range 5–10 m, February 25th, 2022 (collector M.C): SA5239E on host coral *Millepora exaesa* (SA5239);~~ ~~SA5239F on host coral *Millepora exaesa* (SA5239); SA5242B on host coral *Psammocora profundacella* (SA5242).~~

Berndtia sp. 2

Specimens from Jeddah, Saudi Arabia, depth range 5–10 m, February 25th, 2022 (collector M.C): SA5239D on host coral *Millepora exaesa* (SA5239);SA5242A on host coral *Millepora exaesa* (SA5242).

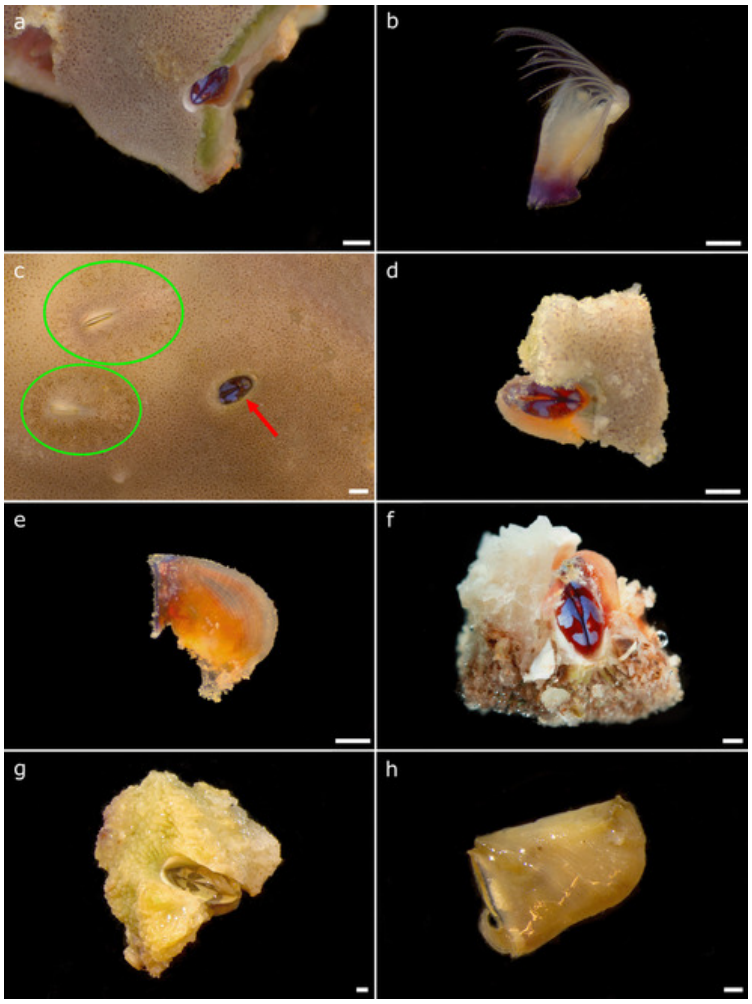
One specimen from Mirbat, Dhofar, Southern Oman, depth 20 m, January 21st, 2022 (collector M.C): OM0437A on host coral *Coscinaraea* cf. *monile* (SA0437).

Results and discussion

The material examined in this study extends the previously known distribution range of *Berndtia* from the Western Pacific to the Western Indian Ocean, including the Red Sea. In addition, two new host–coral species are recorded for *Berndtia* spp. for the first time. Most importantly, the finding of *Berndtia* boring into the skeleton of the hydrozoan *Millepora exaesa* (Fig. 1a–c) in the Red Sea represents a previously unknown association of an acrothoracican barnacle with the cnidarian class Hydrozoa. In addition, the scleractinian coral *Coscinaraea* cf. *monile* (Fig. 1e) is recorded for the first time as host of *Berndtia* sp. in southern Oman.

Fig. 1

Living and preserved individuals of **a**, **b** *Berndtia* sp.1 and **c–h** *Berndtia* sp.2; **a** Living barnacle embedded in the skeleton of *Millepora exaesa* from Jeddah, Saudi Arabia, showing color pattern of opercular bars; **b** Lateral view of freshly preserved specimen with mantle sac partly removed; **c** Living barnacle (red arrow) in the skeleton of the fire coral *Millepora exaesa*; green circles indicate two individuals of the fire coral-inhabiting barnacle *Wanella milleporae*; **d** Fragment of *Millepora exaesa* with living barnacle in its burrow; **e** Lateral view of the same individual with intact mantle sac; **f** Living barnacle and **g** preserved specimen in the skeleton of *Coscinaraea* cf. *monile* from Oman; **h** Lateral view of preserved specimen extracted from *Coscinaraea* cf. *monile*. Scale bars: 500 µm



Calcifying hydrocorals of the genus *Millepora* Linnaeus, 1758 are well known for the exceptionally powerful nematocysts of their polyps (Lewis 2006). Nevertheless, several invertebrates, including barnacles of the family Balanidae, establish symbiotic relationships with fire corals by settling onto their calcareous skeleton (Lewis 2006; Garcia et al. 2009). Different Indo-Pacific species of *Millepora*, including the three Red Sea endemics, i.e. *M. dichotoma, M. platyphylla*, and *M. exaesa* (see Arrigoni et al.

2018), have been observed to host the balanid *Wanella milleporae* (Fig. 1c; Darwin 1854; Mokady and Brickner 2001; Tsang et al. 2009). Acrothoracicans, however, have never been documented to associate with milleporids.

Host selection in coral-inhabiting barnacles has been proposed to depend on host-released chemical cues (Yap et al. 2023). Larvae of balanids associated with both scleractinians (Yap et al. 2023) and fire corals (Yap et al. 2022) have been observed initiating host exploration only in presence of their specific host coral, while actively avoiding non-specific substrata for settlement. Similarly, cyprids of *Berndtia* have been reported to actively swim towards their host immediately after exposure in laboratory condition (Dreyer et al. 2022). Our finding indicates that *Berndtia* possibly recognized *M. exaesa* as a suitable host, and actively settled on its skeleton. However, we could not exclude that settlement was triggered by the presence of the neighboring colony of the scleractinian coral *Psammocora profundacella*, a more typical host of *Berndtia* spp.

Similarly to coral-inhabiting barnacles of the family Pyrgomatidae (Cirripedia: Thoracica: Balanomorpha), cypris larvae of *Berndtia* possess spear-shaped antennules, a morphology suggested to be essential for coral tissue penetration during settlement phases (Brickner and Høeg 2010; Yu et al. 2020; Dreyer et al. 2022). The presence of *Berndtia* burrowed into the skeleton of *M. exaesa* suggest that this barnacle is capable of penetrating into hydrocoral epithelium and embed in the calcareous matrix it deposits (Fig. 1a). Host tissue and calcium carbonate penetration might be mediated by chemical secretions, similarly to what has been suggested for other coral- (Dreyer et al. 2022) and sponge-inhabiting barnacles (Yu et al. 2020). This host invasion mechanism is in contrast with the settlement mode of other barnacles commonly associated with fire corals, e.g., *Wanella milleporae* and *Megabalanus ajax* (Thoracica: Balanomorpha: Balanidae), which instead reside epibiotically on their host (Dreyer et al. 2022; Yap et al. 2022). The antennules of these latter barnacles larvae are bell-shaped and do not allow penetration in the coral tissue (Dreyer et al. 2022). Cypris larvae of *Wanella milleporae* have been observed to deactivate *Millepora* polyps and avoid nematocysts triggering during exploration of the fire coral host, possibly through a chemically mediated suppress mechanism (Yap et al. 2022). It is possible that *Berndtia* possesses defenses similar to those proposed for *Wanella* larvae, allowing interaction and settlement on *M. exaesa*, while avoiding polyp predation. Further studies are needed to elucidate settlement preferences of *Berndtia* in the presence of both fire corals and scleractinians, and to unveil the modalities with which this barnacle genus interacts with, and invades, *Millepora* hydrocorals.

The symbiosis between *Berndtia* and *Coscinaraea* cf. *monile* is less unexpected, as the family Coscinaraeidae, to which this host species belong, shares a lineage with Psammocoridae, Leptastreidae, and Fungiidae (Benzoni et al. 2012), all but the last of which are documented hosts of *Berndtia* species and are the only corals previously known to host this genus (Chan et al. 2014). More extensive sampling of coral barnacles targeting, in addition to coral taxa closely related to the known hosts, other fire coral and scleractinian coral species could extend the host-range record of *Berndtia*.

The first phylogeny reconstruction of the genus *Berndtia*, including sequences from the Western Indian Ocean material and previously deposited sequences is presented here (Fig. 2). Our phylogenetic hypothesis supports the distinction of *B. denticulata* Chan et al., 2014, *B. haradai* Chan et al., 2014, *B. purpurea* Utinomi, 1950 and *B. utinomii* Chan et al., 2014, and recovers the new analyzed material in two well supported lineages, hereafter referred to as *Berndtia* sp. 1 and *Berndtia* sp. 2 (Posterior Probability, PP = 1.00 for both clades, Fig. 2). All three specimens of *Berndtia* sp. 1 were collected in the Red Sea, whereas *Berndtia* sp. 2 contains the two remaining sequences from the Red Sea and one from Oman. It is remarkable that, in both lineages, specimens were found inhabiting multiple hosts. This is in contrast to previous observations for this genus, where all species have been reported to form species-specific associations (Chan et al. 2014). However, other symbionts of scleractinian corals show variable levels of host-specificity even in closely related species, such as in the coral-associated *Zanclea* hydrozoans. This group comprises clades associated with a single genus, as well as generalist clades associated with numerous coral genera (Maggioni et al. 2022). Interspecific genetic distances among the four confirmed Western Pacific species and the two molecular clades from the Western Indian Ocean range between 12.7 and 21.0% (Table 1), an order of magnitude higher than the intraspecific distances (≤ 1.1 ± 0.4%). Phylogenetic studies on thoracican (Chan et al. 2007) and acrothoracican barnacles (Lin et al. 2016) show similar levels of inter- and intraspecific distances when comparing congeneric species, supporting the hypothesis that *Berndtia* sp. 1 and *Berndtia* sp. 2. are distinct species. Color and pigmentation patterns (i.e., shape and disposition of black and blue stripes) of the opercular bars of. *Berndtia* sp. 1 and *Berndtia* sp. 2 do not appear to show consistent differences between these two lineages, with all six specimens analyzed essentially resembling *B. purpurea* in having symmetrical blue strips in the anterior, posterior, and middle part of the opercular bar, separated by black strips (Fig. 1a, c–d, f; compared with Chan et al. 2014: Fig. 3d–f). Further anal **AQ4** yses on more samples employing a broader set of molecular markers and a thorough examination of morphological characters need to be performed before taking any formal taxonomic actions on these taxa.

Fig. 2

Bayesian inference phylogenetic tree based on the COI gene for the genus *Berndtia*, including publicly available sequences of *B. denticulata*, *B. haradai*, *B. purpurea*, and *B. utinomii*, as well as sequences from the present study, *Berndtia* sp. 1 (orange, dotted line) and *Berndtia* sp. 2 (light blue, dashed line). Statistical support for each node is given as posterior probability. Host species are reported in square brackets; general sampling areas is indicated for the newly examined material. Number of sequences for each clade is

indicated in brackets next to each clade's name

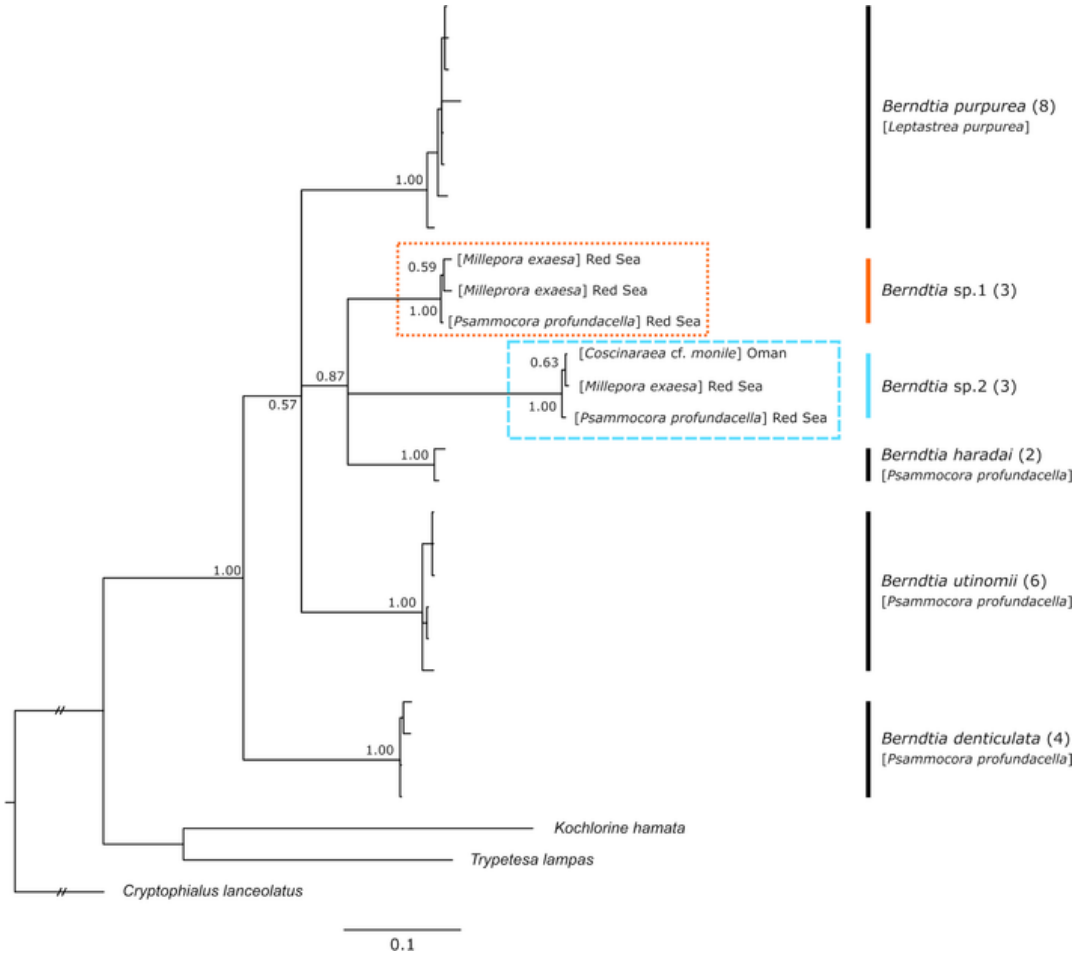


Table 1

Intra- and interspecific pairwise genetic distances (± standard deviation) among and between molecular clades of *Berndtia* retrieved in the present study **AQ5**

	B. denticulata	*B. haradai*	*B. purpurea*	*B. utinomii*	*Berndtia* sp.1	*Berndtia* sp.2
B. denticulata	**0.7 (± 0.3)**					
B. haradai	19.8 (± 2.1)	**1.1 (± 0.4)**				
B. purpurea	19.0 (± 2.1)	16.4 (± 2.0)	**1.1 (± 0.3)**			
B. utinomii	21.0 (± 2.2)	16.6 (± 1.9)	17.6 (± 2.1)	**1.0 (± 0.3)**		
Berndtia sp.1	18.1 (± 2.0)	12.7 (± 1.7)	15.6 (± 1.9)	15.4 (± 1.8)	**0.8 (± 0.3)**	
Berndtia sp.2	20.4 (± 2.2)	18.1 (± 2.1)	20.5 (± 2.2)	18.9 (± 2.1)	19.1 (± 2.2)	**0.4 (± 0.2)**

Distances are in percentage values and were calculated as uncorrected *p* distances. Intraspecific distances are given along the diagonal in bold

The monsoon-driven upwelling along the southern Oman coasts creates a biogeographical barrier between the Gulf of Aden (and the Red Sea) and the rest of the Arabian Sea that limits larval dispersal and influences the distribution of sessile organisms, such as barnacles (Tsang et al. 2012). Animals with lecithotrophic larval stages, such as species of *Berndtia* (Dreyer et al. 2022), could consequently experience isolation, potentially resulting in allopatric speciation (Tsang et al. 2012). For example, the fire coral-inhabiting barnacle *Wanella milleporae* from the Red Sea and Taiwan form two separate, highly divergent phylogenetic lineages (Tsang et al. 2009). Similarly, the coral-associated hydrozoan *Zanclea gallii* shows a clear distinction between Red Sea, Indian Ocean, and Pacific Ocean populations (Maggioni et al. 2017b). It is possible that geographic isolation explains the high divergence observed for *Berndtia* species in the Western Pacific and around the Arabic Peninsula (Fig. 2 and Table 1). Extensive sampling across the whole Indo-Pacific is needed to define the biogeography and distribution of this coral-associated barnacle genus.

Publisher's Note

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval No animal testing was performed during this study. This study was conducted in compliance with all relevant policies and procedures of King Abdullah University of Science and Technology (KAUST).

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgements, if applicable. The study is compliant with CBD and Nagoya protocols.

Data availability The sequences generated during the current study are available in the GenBank repository, accession numbers OQ940852-OQ940857.

Author contribution M.C. acquired the data. M.C. and S.V. performed the analyses. A.A. contributed to barnacle identification. F.B. provided host identification. M.C., F.B., D.M., S.V., and T.I.T. conceived the manuscript. M.C. wrote the original draft of the manuscript. S.V. and G.P. provided valuable comments to the manuscript. F.B., D.M., A.A., and T.I.T supervised the work and reviewed and edited the manuscript. F.B. and G.P. provided funding for the study. All authors read and agreed to the published version of the manuscript.

Supplementary Information

Below is the link to the electronic supplementary material.

Supplementary file1 (DOCX 22 KB)

References AQ6

Anker A (2022) Three new species of the shrimp genus Salmoneus Holthuis, 1955 from the Red Sea, with a new record of S. pou pini Anker, 2010 (Malacostraca: Decapoda: Alpheidae). Zootaxa 5138:261–282. https://doi.org/10.11646/zootaxa.5138.3.3

Arrigoni R, Maggioni D, Montano S et al (2018) An integrated morpho-molecular approach to delineate species boundaries of *Mi llepora* from the Red Sea. Coral Reefs 37:967–984. https://doi.org/10.1007/s00338-018-01739-8

Benson DA, Cavanaugh M, Clark K et al (2012) GenBank. Nucleic Acids Res 41:D36–D42. https://doi.org/10.1093/nar/gks1195

Benzoni F, Arrigoni R, Stefani F, Stolarski J (2012) Systematics of the coral genus *Craterastrea* (Cnidaria, Anthozoa, Scleractinia) and description of a new family through combined morphological and molecular analyses. Syst Biodivers 10:417–433. https://doi.org/10.1080/14772000.2012.744369

Botha TPA, Griffiths CL, Maneveldt GW (2020) Coralline red algae—a new host taxon for burrowing barnacles (Cirripedia, Acro thoracica). Mar Biodivers 50:6. https://doi.org/10.1007/s12526-019-01038-7

Brickner I, Høeg JT (2010) Antennular specialization in cyprids of coral-associated barnacles. J Exp Mar Biol Ecol 392:115–124. https://doi.org/10.1016/j.jembe.2010.04.015

Briggs JC, Bowen BW (2012) A realignment of marine biogeographic provinces with particular reference to fish distributions: ma rine biogeographic provinces. J Biogeogr 39:12–30. https://doi.org/10.1111/j.1365-2699.2011.02613.x

Carvalho S, Aylagas E, Villalobos R et al (2019) Beyond the visual: using metabarcoding to characterize the hidden reef cryptobi ome. Proc R Soc B Biol Sci 286:20182697. https://doi.org/10.1098/rspb.2018.2697

Chan BKK, Tsang LM, Chu KH (2007) Morphological and genetic differentiation of the acorn barnacle *Tetraclita squamosa* (Cru stacea, Cirripedia) in East Asia and description of a new species of *Tetraclita*. Zool Scr 36:79–91. https://doi.org/10.1111/j.1463-6409.2007.00260.x

Chan BKK, Kolbasov GA, Cheang C-C (2012) Cryptic diversity of the acrothoracican barnacle *Armatoglyptes taiwanus* in the In do-Pacific waters, with description of a new species from the Mozambique Channel collected from the MAINBAZA cruise. Zoos ystema 34:5–20. https://doi.org/10.5252/z2012n1a1

Chan BKK, Cheang CC, Chen I-H, Kolbasov GA (2013) Acrothoracican barnacles (Lithoglyptida) in Taiwan, including the taxon omic status of *Balanodytes taiwanus* Utinomi, 1950 and cryptic diversity of *Auritoglyptes bicornis* (Aurivillius, 1892). Zootaxa 3 694:221. https://doi.org/10.11646/zootaxa.3694.3.3

Chan BKK, Kolbasov GA, Hirose M et al (2014) Biodiversity and biogeography of the coral boring barnacles of the genus *Berndt ia* (Cirripedia: Acrothoracica) in the West Pacific, with description of three new species. J Nat Hist 48:1503–1541. https://doi.org/10.1080/00222933.2014.896488

Chan BKK, Wong KJH, Cheng Y-R (2020) Biogeography and host usage of coral-associated crustaceans: barnacles, copepods, an d gall crabs as model organisms. Nat Hist Crustac Evol Biogeogr Crustac 8:183–215. https://doi.org/10.1093/oso/9780190637842.003.0008

Chan BKK, Dreyer N, Gale AS et al (2021) The evolutionary diversity of barnacles, with an updated classification of fossil and li ving forms. Zool J Linn Soc 193:789–846. https://doi.org/10.1093/zoolinnean/zlaa160

Claereboudt M, Al Rashdi K (2011) Shallow-water sea cucumber inventory in the Sultanate of Oman. SPC Beche-De-Mer Inf Bul l 31:25–29

Dana JD (1846) Zoophytes. United States exploratory expedition 1836–1842. Lea and Blanchard, Philadelphia 7: 1-740.

Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. Nat Meth ods 9:772–772. https://doi.org/10.1038/nmeth.2109

Darwin C (1854) A monograph on the sub-class Cirripedia, with figures of all the species. The Balanidae, (or sessile cirripedes); t he Verrucidae, etc. etc. etc. Ray society, London

DiBattista JD, Howard Choat J, Gaither MR et al (2016a) On the origin of endemic species in the Red Sea. J Biogeogr 43:13–30. https://doi.org/10.1111/jbi.12631

DiBattista JD, Roberts MB, Bouwmeester J et al (2016b) A review of contemporary patterns of endemism for shallow water reef f auna in the Red Sea. J Biogeogr 43:423–439. https://doi.org/10.1111/jbi.12649

DiBattista JD, Berumen ML, Priest MA et al (2022) Environmental DNA reveals a multi-taxa biogeographic break across the Ara bian Sea and Sea of Oman. Environ DNA 4:206–221. https://doi.org/10.1002/edn3.252

Dreyer N, Tsai P, Olesen J et al (2022) Independent and adaptive evolution of phenotypic novelties driven by coral symbiosis in b arnacle larvae. Evolution 76:139–157. https://doi.org/10.1111/evo.14380

Folmer O, Black M, Hoeh W et al (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from di verse metazoan invertebrates. Mol Mar Biol Biotechnol 3:294–299

Forsskål P (1775) Descriptiones animalium, avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali observ avit. Heineck et Faber, Hauniæ, ex officina Mölleri, pp 131–139

Garcia TM, Matthews-Cascon H, Franklin-Junior W (2009) *Millepora alcicornis* (Cnidaria: Hydrozoa) as substrate for benthic fa una. Braz J Oceanogr 57:153–155. https://doi.org/10.1590/S1679-87592009000200009

Gardiner JS (1898) On the Fungid corals collected by the author in the South Pacific. In: Proceedings of the Zoological Society o f London. Blackwell Publishing Ltd., pp 525–539

Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucle ic Acids Symp Ser 41:95–98

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usabil ity. Mol Biol Evol 30:772–780. https://doi.org/10.1093/molbev/mst010

Kitahara MV, Fukami H, Benzoni F, Huang D (2016) The new systematics of Scleractinia: integrating molecular and morphologic al evidence. In: Goffredo S, Dubinsky Z (eds) The Cnidaria, past, present and future. Springer, Berlin, pp 41–59

Kumar S, Stecher G, Li M et al (2018) MEGA X: Molecular evolutionary genetics analysis across computing platforms. Mol Biol Evol 35:1547–1549. https://doi.org/10.1093/molbev/msy096

Lewis JB (2006) Biology and ecology of the hydrocoral *Millepora* on coral reefs. Adv Mar Biol 50:1–55. https://doi.org/10.1016/S0065-2881(05)50001-4

Lin H-C, Kobasov GA, Chan BKK (2016) Phylogenetic relationships of Darwin's "Mr. Arthrobalanus": the burrowing barnacles (Cirripedia: Acrothoracica). Mol Phylogenet Evol 100:292–302. https://doi.org/10.1016/j.ympev.2016.03.016

Maggioni D, Galli P, Berumen ML et al (2017) Astrocoryne cabela, gen nov. et sp. Nov. (Hydrozoa : Sphaerocorynidae), a new sp onge-associated hydrozoan. Invertebr Syst 31:734. https://doi.org/10.1071/IS16091

Maggioni D, Montano S, Arrigoni R et al (2017b) Genetic diversity of the *Acropora*-associated hydrozoans: new insight from the Red Sea. Mar Biodivers 47:1045–1055. https://doi.org/10.1007/s12526-017-0632-4

Maggioni D, Arrigoni R, Seveso D et al (2022) Evolution and biogeography of the *Zanclea*-Scleractinia symbiosis. Coral Reefs 4 1:779–795. https://doi.org/10.1007/s00338-020-02010-9

Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES science gateway for inference of large phylogenetic trees. In: 20 10 Gateway Computing Environments Workshop (GCE). IEEE, New Orleans, LA, USA, pp 1–8

Milne Edwards H, Haime J (1849) Recherches sur les polypiers. Mémoire 4. Monographie des Astréides. Ann Des Sci Nat, Zool, Ser 3:95–197

Mokady O, Brickner I (2001) Host-associated speciation in a coral-inhabiting barnacle. Mol Biol Evol 18:975–981. https://doi.org/10.1093/oxfordjournals.molbev.a003898

Narvekar J, Chowdhury RR, Gaonkar D et al (2021) Observational evidence of stratification control of upwelling and pelagic fish ery in the eastern Arabian Sea. Sci Rep 11:1–13. https://doi.org/10.1038/s41598-021-86594-4

Pearman JK, Leray M, Villalobos R et al (2018) Cross-shelf investigation of coral reef cryptic benthic organisms reveals diversity patterns of the hidden majority. Sci Rep 8:8090. https://doi.org/10.1038/s41598-018-26332-5

Quek ZBR, Jain SS, Richards ZT et al (2023) A hybrid-capture approach to reconstruct the phylogeny of Scleractinia (Cnidaria: Hexacorallia). Mol Phylogenet Evol 186:107867. https://doi.org/10.1016/j.ympev.2023.107867

Rambaut A, Drummond AJ, Xie D et al (2018) Posterior summarization in Bayesian phylogenetics using tracer 1.7. Syst Biol 67: 901–904. https://doi.org/10.1093/sysbio/syy032

Ronquist F, Teslenko M, van der Mark P et al (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice ac ross a large model space. Syst Biol 61:539–542. https://doi.org/10.1093/sysbio/sys029

Tomlinson JT (1967) *Berndtia nodosa* sp. nov. (Cirripedia, Acrothoracica), a new burrowing barnacle from Singapore. Bull Nat Mus Singap 33:101–105

Tomlinson JT (1969) The burrowing barnacles (Cirripedia: order Acrothoracica). Bull U S Natl Mus 296:1–162

Tomlinson JT (1987) The burrowing barnacles (Acrothoracica). In: Barnacle biology (Crustacean Issue 5), 1st edn. A. A. Balkem a, Rotterdam, pp 63–71

Tsang LM, Chan BKK, Shih F-L et al (2009) Host-associated speciation in the coral barnacle *Wanella milleporae* (Cirripedia: Pyr gomatidae) inhabiting the *Millepora* coral. Mol Ecol 18:1463–1475. https://doi.org/10.1111/j.1365-294X.2009.04090.x

Tsang LM, Achituv Y, Chu KH, Chan BKK (2012) Zoogeography of intertidal communities in the West Indian Ocean as determin ed by ocean circulation systems: patterns from the *Tetraclita* barnacles. PLoS ONE 7:e45120. https://doi.org/10.1371/journal.pon e.0045120

Utinomi H (1950) A new remarkable coral-boring Acrothoracican cirriped. Mem Coll Sci Univ Kyoto, Ser B 19:87–94

Veron J, Stafford-Smith M, DeVantier L, Turak E (2015) Overview of distribution patterns of zooxanthellate Scleractinia. Front Mar Sci 1:81. https://doi.org/10.3389/fmars.2014.00081

Yap F-C, Høeg JT, Chan BKK (2022) Living on fire: deactivating fire coral polyps for larval settlement and symbiosis in the fire coral-associated barnacle Wanella milleporae (Thoracicalcarea: Wanellinae). Ecol Evol 12:e9057. https://doi.org/10.1002/ece3.90 57

Yap F-C, Chen H-N, Chan BKK (2023) Host specificity and adaptive evolution in settlement behaviour of coral-associated barna cle larvae (Cirripedia: Pyrgomatidae). Sci Rep 13:9668. https://doi.org/10.1038/s41598-023-33738-3

Yu M-C, Dreyer N, Kolbasov GA et al (2020) Sponge symbiosis is facilitated by adaptive evolution of larval sensory and attachm ent structures in barnacles. Proc R Soc B Biol Sci 287:20200300. https://doi.org/10.1098/rspb.2020.0300