Zootaxa 5506 (1): 001–034
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5506.1.1
http://zoobank.org/urn:lsid:zoobank.org:pub:AFDFAEE4-9B4A-4792-80E7-27DC9ECC23D8

The clownfish-hosting sea anemones (Anthozoa: Actiniaria): updated nomenclature, biogeography, and practical field guide.

BENJAMIN M. TITUS[1,2#,*], MORGAN F. BENNETT-SMITH[3,#], TOMMASO CHIODO[1,2] & ESTEFANÍA RODRÍGUEZ[4]

[1]*Department of Biological Sciences, University of Alabama, Tuscaloosa, AL, USA 35487*
https://orcid.org/0000-0003-1194-6005
[2]*Dauphin Island Sea Lab, 101 Bienville Blvd, Dauphin Island, AL, USA 36528*
[3]*Department of Biology, Boston University, 5 Cummington Mall, Boston, MA, USA, 02215*
https://orcid.org/0000-0002-7681-8939
[4]*Division of Invertebrate Zoology, American Museum of Natural History, New York, NY, USA*
https://orcid.org/0000-0002-5590-6606
[#]*Denotes equal contributions and shared first authorship*
**Corresponding author: bmtitus@ua.edu; https://orcid.org/0000-0002-0401-1570*

Abstract

Ten described species of sea anemones (Anthozoa: Hexacorallia: Actiniaria) serve as hosts to charismatic clownfishes (or anemonefishes) on coral reefs throughout the tropical Indo-West Pacific. Although not diverse in number, the clownfish-hosting sea anemones have large biogeographic ranges, exhibit extensive intraspecific phenotypic appearances, and have been surrounded by a great deal of historical and contemporary taxonomic and nomenclatural confusion. We believe these factors have created challenges for field scientists making real-time species-level identifications of host sea anemones. Subsequently, a surprising amount of peer-reviewed clownfish literature never accounts for the host sea anemone, omitting critical data for understanding the symbiosis ecologically and evolutionarily. Here, we leverage the revolution that has taken place in the realm of digital underwater photography over the past 30 years to provide an updated, practical field guide for the clownfish-hosting sea anemones. First however, we review and revise the nomenclature for each species to better reflect valid changes that were made in the historical literature but never broadly adopted. Next, we demonstrate that machine learning algorithms may be of limited use for automating sea anemone species IDs from digital photographs alone—highlighting the importance of organismal expertise for identifying these animals. Finally, we present high-resolution digital photographs that encompass much of the intraspecific phenotypic variation encountered underwater, discuss important characteristics useful for field IDs, and provide updated range maps for each species to better reflect the known biogeographic range of each host anemone. We hope the increased confidence in field identification provided by this guide will result in more papers incorporating the sea anemone host data into research frameworks and subsequent publications.

Key words: Cnidaria, Hexacorallia, Actinioidea, symbiosis, species identification

Introduction

Thirty years ago, Drs. Daphne Fautin and Gerald Allen published the seminal book titled "Field Guide to Anemone Fishes and their Host Sea Anemones" (Fautin & Allen 1992), providing a non-technical field guide accessible to the lay person as well as research scientists. At the time of their original publication, interest in the now iconic clownfish (or anemonefish)—sea anemone symbiosis had built to a sufficient degree to warrant devotion of an entire book to the subject of simply identifying these animals in the field—a nontrivial task. Decades and multiple major motion pictures later, the rationale for providing an updated field guide exists to an even greater degree than when Fautin and Allen published their original guide, which has received hundreds of citations and likely informed even greater numbers of scientific studies.

Over the past 30 years, the clownfish-sea anemone symbiosis has emerged as an important model system for

Accepted by M. Daly: 14 Jun. 2024; published: 5 Sept. 2024

exploring fundamental biological questions—underscored recently by the publication of a major textbook reviewing all aspects of clownfish evolution, ecology, and development (Laudet & Ravasi 2022). Field-based studies remain critical for understanding the ecology, distribution, host-use, behavior, evolution, and mutualism of the 28 described clownfishes and 10 nominal species of host sea anemones (e.g. Buston 2004; Huebner *et al.* 2012; Litsios *et al.* 2012; Branconi *et al.* 2020; Titus *et al.* 2020; Bennett-Smith *et al.* 2021, 2022). Their popularity within the ornamental aquarium trade has increased exponentially since the mutualism's cinematic popularization and has resulted in some species coming under increasing pressure from commercial over-harvesting (Jones *et al.* 2022). In addition, molecular systematics has transformed our understanding of the original taxonomic groupings of both clownfishes (e.g., Litsios *et al.* 2012; Marcionetti & Salamin 2023) and host sea anemones (Titus *et al.* 2019; Kashimoto *et al.* 2022; Yap *et al.* 2023).

Concurrently, the development of digital underwater photography and increased globalization has allowed SCUBA divers to visually capture a degree of the phenotypic and geographic variation that exists within and between clownfish and anemone species that was impossible when Fautin and Allen published their original field guide. The internet and community science databases (e.g. iNaturalist, OBIS, GBIF) now allow real-time georeferenced uploads of digital photographs. The emergence of machine learning algorithms and other artificial intelligence approaches have led to the development of programs that can produce highly accurate species identifications from photographs alone. More, and better, information and computational tools are available than ever before, but it has not been synthesized in a way to take advantage of the major advancements over the past few decades.

This scattered information is particularly problematic when it comes to identifying host sea anemones (Cnidaria: Anthozoa: Hexacorallia: Actiniaria). Sea anemones are challenging animals in that they are both morphologically simple, having only tissue-level organization, and phenotypically variable, in that their body size and shape can change rapidly (Shick 1991). They are essentially inflated underwater balloons with tentacles. Tentacle size, shape, color, and pattern can vary not only intraspecifically, but even intra-individually. In the field, these physical features are all a diver can use to make a species-level identification. How much intraspecific phenotypic variation exists within a putative species? When can tentacle shape be useful as a species identification? Color? Microhabitat? Other features? Fautin and Allen's original field guide was limited in the number of photographs per host anemone species, and while much of the subsequent text they provided for species IDs remains valid today, they could not visually capture the wide range of intraspecific phenotypic variation that exists in the field for any given anemone species. Here we build off Fautin and Allen (1992) and provide an updated field guide for the clownfish-hosting sea anemones that encompasses a far greater degree of the phenotypic variation at the species level. One of the major goals of the original field guide by Fautin and Allen was to establish a consistent way species names and identifications were applied by divers and scientists alike because the historical literature was hobbled by inconsistent nomenclatural usage for the host sea anemones. We believe they largely achieved this goal, as reflected by the way scientific names have been more consistently applied in the literature in the subsequent years. However, a surprising amount of peer-reviewed clownfish research simply never accounts for the host anemones or provides quantifiable data on host associations. We believe the vast amount of phenotypic variation that exists within host sea anemones creates uncertainty surrounding species identifications in the field, and ultimately, this uncertainty leads fish biologists and ecologists to omit the hosts from their broader projects.

Our goal for this updated field guide is thus to build upon the foundation set by Fautin and Allen (1992) and provide non-anemone biologists increased confidence in identifying the host anemones while conducting field research on the clownfish-sea anemone symbiosis. Further, the coral reef ecosystems where these animals reside are under unprecedented thermal stress from the massive bleaching events that are now occurring on annual cycles. The clownfish-hosting sea anemones, like stony corals, harbor photosymbionts from the family Symbiodineaceae and are similarly stressed and bleached by periods of elevated sea surface temperature (Hill & Scott 2012; Scott & Hoey 2017; Steinberg *et al.* 2020, 2022; Haguenauer *et al.* 2021). Yet these animals do not leave behind a stony skeleton that can provide a historical record of mortality and their clownfish symbionts disappear along with them. It is paramount that ecological data are collected more regularly than they have been historically. As we detail below, the taxonomy and nomenclature of these animals is challenging and in a state of major flux. The genomic, morphological, and systematic revision of the clownfish-hosting sea anemones is in progress, yet likely years from completion due to the complexities stemming from the difficulty of locating old type specimens, complicated morphology, and the presence of multiple cryptic species (Titus *et al.* 2019). We feel strongly that critical field data on these animals need to begin being collected immediately, even before a final taxonomic revision is completed. We hope the increased confidence in field identification provided by this guide will result in more papers incorporating the sea anemone host data into research frameworks and subsequent publications.

Nomenclature and the current taxonomy of the clownfish-hosting sea anemones

A great deal of historical and contemporary confusion exists surrounding the systematics of the clownfish-hosting sea anemones, which broadly serves as a reflection of the difficulties disentangling the systematics of the Order Actiniaria. Recent papers have highlighted and reviewed these difficulties (Titus *et al.* 2019; Bennett-Smith *et al.* 2021; Yap *et al.* 2023). What we do know is that all the clownfish-hosting species belong to the superfamily Actinioidea, which contains the bulk of tropical sea anemone diversity. Like the majority of the morphological features that distinguish various anemone groups, the traits that define the superfamily Actinioidea are primarily internal anatomical features and not readily diagnosable in the field (Rodríguez *et al.* 2014).

As reviewed by Titus *et al.* (2019), within Actinioidea, the clownfish-hosting sea anemones have been historically grouped into three families (Actiniidae, Stichodactylidae, and Thalassianthidae). Due to extensive confusion, misidentifications, and systematic disagreements, Dunn (1981) comprehensively revised the clownfish-hosting sea anemones. This resulted in the recognition of 10 host anemone species. Those in family Actiniidae included the bubble tip anemone *Entacmaea quadricolor* (Leuckart in Ruppell & Leuckart, 1828) and the former long-tentacle anemone *Macrodactyla doreensis* (Quoy & Gaimard, 1883). The sole host from Thalassianthidae was the adhesive anemone *Cryptodendrum adhaesivum* (Klunzinger, 1877). The remaining seven species were placed in family Stichodactylidae and included the genera *Stichodactyla* Brandt, 1835 and *Heteractis* Milne-Edwards & Haime, 1851. Those in the genus *Stichodactyla* are commonly referred to as the carpet anemones and include the giant carpet anemone (*S. gigantea* (Forsskål, 1775)), Haddon's carpet anemone (*S. haddoni* (Saville-Kent, 1893)) and Merten's carpet anemone (*S. mertensii* Brandt, 1835). Those in *Heteractis* included the beaded anemone (*H. aurora* (Quoy & Gaimard, 1883)), the leathery anemone (*H. crispa* (Hemprich & Ehrenberg in Ehrenberg, 1834)), the magnificent anemone (*H. magnifica* (Quoy & Gaimard, 1883)), and the malu anemone (*H. malu* (Haddon & Shackleton, 1893)).

Using molecular approaches, Titus *et al.* (2019) showed that the 10 recognized species belonged to three distantly related clades, but these did not align with Dunn's taxonomy (see Titus *et al.* 2019). The clades recovered by Titus *et al.* (2019) were coined *Entacmaea*, Stichodactylina, and Heteractina. The *Entacmaea* clade encompassed only *E. quadricolor*. The Stichodactylina included members of the genus *Stichodactyla*, the entire family Thalassianthidae, as well as the magnificent anemone *H. magnifica*. The Heteractina included the remaining host species *H. aurora*, *H. crispa*, *H. malu*, and former *M. doreensis*. These results revealed widespread para- and poly-phyly at the family and genus level and highlighted the need for further systematic revisions and nomenclatural changes to better reflect the true taxonomy of these species.

Titus *et al.* (2019) refrained from proposing nomenclatural and taxonomic changes due to a lack of phylogenetic resolution using a suite of five traditional molecular markers for sea anemones (12S rDNA, 16S rDNA, CO3, 18S rDNA, 28S rDNA, see Rodríguez *et al.* 2014), and recognized that nomenclatural changes should ideally be accompanied by peer reviewed morphological revisions as well. Recently, an Indo-Pacific field guide (Rowlett 2020) proposed radical changes to the nomenclature and taxonomy of the clownfish-hosting sea anemones. These changes were made without peer review or examination of any reference, type, or comparative material, and lacked new family, genus, and species level diagnoses accompanying the sweeping changes. In addition, other authors after Dunn (1981) but prior to Fautin and Allen (1992), Titus *et al.* (2019), Rowlett (2020), and Yap *et al.* (2023) have published formal morphological and nomenclatural revisions of the clownfish-hosting sea anemones that have been largely overlooked and unadopted for the past 30 years. The most extensive of these changes come from England (1987, 1988), but also from the monograph of sea anemone nomenclature by Fautin (2016). Here, we recognize these works as recent and valid taxonomic and nomenclatural changes for these animals. While we would ideally maintain the nomenclatural stability established by Dunn (1981), ongoing revisionary work for the clownfish-hosting sea anemones must necessarily consider the morphological work and nomenclatural changes made by both England (1987, 1988) and Fautin (2016) as the most recent valid work conducted on this group.

Below we detail the current nomenclature and taxonomy of the clownfish-hosting sea anemones, which now includes newly adopted changes established by England (1987, 1988), Fautin (2016) and Yap *et al.* (2023), together with conclusions based on the molecular results from Titus *et al.* (2019); we consider and reject Rowlett's (2020) changes because he based his conclusions only on images, and as discussed, these can be misleading for actiniarians if taken without anatomical and molecular examinations. All changes are now listed as the accepted nomenclature and taxonomy in the World List of Actiniaria (Rodríguez *et al.* 2024), the portal for Actiniaria within the World Register of Marine Species (WoRMS).

Family Actiniidae Rafinesque, 1815

In the revisionary work by England (1987), the clownfish-hosting species *Entacmaea quadricolor* was moved from family Actiniidae to the Stichodactylidae based on the presence of a type of cnidae (microbasic amastigophores) in the column, tentacles, or both regions in members of Stichodactylidae but not in those of Actiniidae. However, despite England's (1987) claims, this type of cnidae is also present in the column and/or tentacles of other species within Actiniidae (e.g. *Isoaulactinia*, *Phialoba*, see Barragán *et al.* 2019) and thus this feature does not differentiate these families. This fact, together with recent molecular results that do not support a close relationship between *E. quadricolor* and members of Stichodactylidae (Titus *et al.* 2019; Yap *et al.* 2021, 2023), we consider *E. quadricolor* within family Actiniidae until a comprehensive revision of the group is available.

The other fish-hosting taxon included within Actiniidae was the former *Macrodactyla doorensis*, which Fautin (2016) returned to the genus *Condylactis* Duchassaing de Fombressin & Michelotti, 1864 because the generic name *Macrodactyla* Haddon, 1898 had been claimed to be a junior homonym of a coleopteran genus and thus unavailable for use in sea anemones (Fautin 2016, Neave 1940). However, Yap *et al.* (2023) clarified that the name *Macrodactyla* is not a junior homonym of a coleopteran genus and it can be retained as a genus name for sea anemones. In addition, Yap *et al.* (2023) showed that former *M. doreensis* is not closely related to the type species of *Macrodactyla* but nested within other species of *Heteractis* and created a new combination name for this species, *Heteractis doreensis* (Quoy & Gaimard, 1883), based on molecular data.

Included Taxa

Entacmaea quadricolor (Leuckart in Ruppell & Leuckart, 1828)

Family Heteractidae Andres, 1883

England (1988) formally reinstated and modified the diagnosis of the family Heteractidae to include new data about members of the genus *Heteractis* and its type species, *H. aurora* (Quoy & Gaimard, 1883), which become monotypic. He left the remaining members formerly belonging to the genus *Heteractis* in the family Stichodactylidae, moving them to the resurrected genus *Radianthus* Kwietnewski, 1896 (*R. crispa, R. magnifica, R. malu*) (England, 1988). *Heteractis* and *Radianthus* are differentiated by the presence of macrobasic amastigophore nematocysts (= *p*-mastigophores A with looped tubule according to cnidae terminology in Gusmão *et al.* 2018) in *H. aurora* that are absent in species of *Radianthus.* Because the former *Macrodactyla doreensis* (*Heteractis doreensis* after Yap *et al.* 2023) does not have macrobasic *p*-amastigophores (ER unpubl. data), this species is referred to the genus *Radianthus* (as *R. doreensis*) until phylogenetic relationships of former members of *Heteractis* are clarified.

Included Taxa

Heteractis aurora (Quoy & Gaimard, 1883)

Differentiated from other members formerly in the genus *Heteractis* by the presence of macrobasic amastigophores in several regions of the body. Although molecular data do not differentiate *H. aurora* from members formerly in the genus (Titus *et al.* 2019; Yap *et al.* 2023), we follow England (1988) until further revision is available.

Family Stichodactylidae Andres, 1883

Dunn (1981) circumscribed Andres' (1883) family Stichodactylidae to include only members of genera *Stichodactyla* and *Heteractis*. Following the reinstatement of family Heteractidae, England (1988) resurrected the genus *Radianthus* for the remaining members of the genus *Heteractis* that do not have macrobasic amastigophores in several regions of the body. However, recent molecular work recovered members of Thalassianthidae and *R. magnifica* nesting within *Stichodactyla* (e.g. Titus *et al.* 2019) rendering Stichodactylidae in its current circumscription paraphyletic. Rearrangement of the familial and generic circumscriptions and membership of Stichodactylidae and Thalassianthidae are anticipated, following a comprehensive revision of the group.

Included Taxa

Radianthus crispa (Hemprich & Ehrenberg, 1834)
Formerly *Heteractis crispa*; England (1988) moved this species into the genus *Radianthus*.
Radianthus doreensis (Quoy & Gaimard, 1883)
Formerly *Macrodactyla doreensis*; Yap *et al.* (2023) moved this species into genus *Heteractis* but did not acknowledge England's (1988) changes.
Radianthus magnifica (Quoy & Gaimard, 1883)
Formerly *Heteractis magnifica;* England (1988) moved this species into the genus *Radianthus*.
Radianthus malu (Haddon & Shackleton, 1893)
Formerly *Heteractis malu;* England (1988) moved this species into the genus *Radianthus*.
Stichodactyla haddoni (Saville-Kent, 1893)
No changes (see note below) *
Stichodactyla gigantea (Forskal, 1775)
No changes (see note below) *
Stichodactyla mertensii Brandt, 1835
No changes

Notes on *Stichodactyla haddoni* & *Stichodactyla gigantea*

Among the most complicated nomenclatural problems to arise among the clownfish-hosting sea anemones is the one that involves the species that have long been recognized by Dunn (1981) and the broader community as *S. haddoni* (Saville-Kent, 1893) and *S. gigantea* (Forsskål, 1775). Recently, Bennett-Smith *et al.* (2021) demonstrated that what Dunn (1981) recognized as *S. gigantea* does not occur in the Red Sea, nor in the broader Indian Ocean West of the Bay of Bengal. Their conclusion was that the species currently recognized as *S. gigantea* has never occurred in the Red Sea, and thus, Dunn (1981) had misattributed Forsskål's 1775 description of *Priapus giganteus* to the wrong clownfish-hosting sea anemone species. Bennett-Smith *et al.* (2021) document two clownfish-hosting species from the Red Sea in the genus *Stichodactyla*: *S. haddoni* and *S. mertensii*. Unfortunately, as Dunn (1981) and Bennett-Smith *et al.* (2021) both noted, Forsskål's description is not diagnostic and the type specimen has not been found. Dunn (1981) ultimately elevated Forsskål as the authority of the species she recognizes as *S. gigantea* based on Forsskål's comment on the extreme adhesiveness of the tentacles. Both *S. haddoni* and *S. mertensii* have adhesive tentacles where they co-occur in the Red Sea and combined with the lack of diagnostic description from Forsskål, the name *S. gigantea* could equally be applied to either species.

Further complicating matters is Dunn's nomenclature for these three taxa in the genus *Stichodactyla* have been consistently applied in the scientific community for over 30 years, and *S. haddoni* is an especially popular animal in the ornamental aquarium trade. Swapping and synonymizing species names for two animals that have long been recognized as clownfish-hosting sea anemones does not foster nomenclatural stability and will likely serve to further the long-standing confusion surrounding the taxonomy and identification of these anemones in the literature and among aquarium trade hobbyists. As such, we have petitioned the ICZN to retain Dunn's (1981) usage for *S. haddoni* (Saville-Kent, 1893) and *S. gigantea* (Forsskål, 1775) (Rodríguez *et al.* in press: case 3885). This will maintain nomenclatural stability at the species level while minimizing the number of species-level name changes among these close relatives until a thorough revision of morphological and genomic data is completed.

Family Thalassianthidae Milne Edwards, 1857

Included Taxa

Cryptodendrum adhaesivum Klunzinger, 1877
No changes

Field guide for the clownfish-hosting sea anemones

Can species identification be automated?
The ability to accurately and consistently identify species forms the basis for all systematic research and is the first and most critical step in the experimental design of ecological and evolutionary research. Automating this process in a way that makes identifying species fast and accurate for non-specialists is a major recent goal of biodiversity research (reviewed by Wäldchen & Mäder 2018). Machine learning algorithms have emerged as one of the most promising approaches. To automate the species identification process, machine learning approaches leverage the vast amount of open-source digital photographs on various online databases to train computer algorithms to identify species (reviewed by Wäldchen & Mäder 2018).

In an effort to create an automated open-source tool, we attempted to develop a deep neural network algorithm to identify sea anemones that host clownfishes using a training set of several thousand images. To do this, we used an open-source platform for machine learning called TensorFlow (TensorFlow: Large-scale machine learning on heterogeneous systems 2016. Software available from tensorflow.org) and compiled an image bank of over 3000 manually verified host sea anemone images from photographs taken by the authors of this study as well as from publicly available databases like iNaturalist (Table 1). After assembly, our image bank was split into a training dataset to train the algorithm (80% of all images from each species), and a test dataset to determine its accuracy (20% of all images from each species).

TABLE 1. Results from a machine learning neural network analysis to automate species identification for the clownfish-hosting sea anemones. Sample size reflects the total number of digital photographs aggregated for this analysis. Precision represents the percent accuracy of the neural network in identifying a given species correctly.

Species	Sample Size	Precision	Recall	Fl-score	Support
Cryptodendrum adhaesivum	90	0.36	0.13	0.20	30
Entacmaea quadricolor	992	0.55	0.60	0.57	310
Heteractis aurora	150	0.21	0.19	0.20	42
Radianthus crispa	290	0.26	0.24	0.25	74
Radianthus doreensis	129	0.27	0.23	0.25	44
Radianthus magnifica	1053	0.55	0.65	0.60	302
Radianthus malu	34	0.00	0.00	0.00	10
Stichodactyla gigantea	135	0.38	0.29	0.32	42
Stichodactyla haddoni	204	0.47	0.37	0.41	68
Stichodactyla mertensii	317	0.28	0.20	0.23	82
Accuracy				0.48	1004
Macro avg.		0.33	0.29	0.30	1004
Weighted avg.		0.46	0.48	0.46	1004

Our neural network was largely unsuccessful in correctly identifying host anemones (Table 1). The species identified with the greatest precision (55% correctly identified) were *E. quadricolor* and *R. magnifica*, which both had the largest samples sizes in our training dataset. These results point to multiple issues with automated machine learning approaches for species identification for the clownfish-hosting sea anemones: 1) the complex and highly variable morphology of these species makes it difficult for machine learning algorithms to key in on morphological characters that are consistently photographed within a species. 2) Greater samples sizes are needed. Increased sample sizes did lead to greater accuracy for two species, but our dataset represents the majority of the publicly available images that can be aggregated and downloaded en masse from online biodiversity databases such as iNaturalist. Taken together, our automated approach underscores the importance of organismal expertise for identifying these animals in the field and pressing need for a practical field guide for this group.

How to use this guide

The purpose of this guide is to provide increased confidence to the biologist and ecologist in accurately identifying the clownfish-hosting sea anemones *in the field*, and thus, encourage the increased incorporation of sea anemone host data into research frameworks and subsequent publications on the clownfish-sea anemone mutualism. Our guide is meant to be practical, and to present, to the best of our ability, high-quality short external descriptions, illustrations, and digital photographs that encompass the majority of the phenotypic variation present in each nominal species. We provide a glossary of terms to guide the use of our dichotomous key and the understanding of the group as well as a table with combinations of traits for each species (Table 2).

We also provide updated range maps for each species that properly reflects the known biogeographic distribution of each of the 10 clownfish-hosting species. Range maps were generated using Rv4.2.2 (R Core Team 2022) and a derived dataset downloaded from the Global Biodiversity Information Facility (GBIF; 30 March 2023; derived dataset https://doi.org/10.15468/dd.u2yyzx). Our GBIF dataset includes aggregated occurrence data from 45 different sources, including >2,000 research grade observations from iNaturalist alone. 60 m bathymetry data was included in each range map to reflect shallow water habitat availability throughout the range of each species. Bathymetry data were obtained from Bio-ORACLE v2.0 (Assis *et al.* 2017).

Finally, we purposefully do *not* provide information on clownfish-sea anemone host associations. Symbiosis with clownfishes, although important, is not a diagnostic character. Host anemone species can, and are, found solitarily—especially at high latitudes. It is also well documented that a great deal of variation exists in how many anemone species each of the 28 described clownfish species have been documented in association with. Counterintuitively, we feel that our understanding of clownfish-host associations will be better served if host anemone species identifications are made independent of the clownfish species that may be present. Clownfish host associations are not fixed, and we want to avoid giving the impression that the identity of the fish can be used to help identify the host anemone. Many clownfish species remain poorly studied. New combinations of clownfishes and host anemones have since been reported on occasion (reviewed by Hoepner *et al.* 2022) and more are undoubtedly awaiting discovery and may help transform our understanding of the entire symbiosis once information about the host is taken into account.

Glossary

Column: Body-wall. Directly underneath the tentacle-bearing oral disc. The column might bear a variety of structures or specialized outgrowths such as verrucae, vesicles, tubercles or tenaculi, among others. For many species, the column is obscured by the oral disc, extends into crevices in the reef substrate, or is completely burrowed in sediment. The top (distal) portion of the column is typically visible by gently folding back one part of the oral disc (Figure 1).

TABLE 2. Combination of external features for each species of clownfish hosting sea anemones.

Species	Types of tentacles	Tentacle length/ shape	Tentacle tips	Oral disc	Column	Verrucae (presence/shape)	Pedal disc	Growth pattern	Habitat
Cryptodendrum adhaesivum	2 types: inner branched/outer bulbous; row of nematospheres in margin; densely packed	Short (<2 cm) / slender and branched (inner) bulbous (outer), very sticky	Branched (inner) / bulbous (outer)	Flat and round or wavy when wedged into crevices	Short, never exposed, with verrucae in longitudinal rows distally	Verrucae conspicuous, variable in color, non-adhesive	Attached to hard substrate and crevices	Solitary	Wide depth range, in crevices and holes of rocky reefs
Entacmaea quadricolor	1 type, densely packed	Long / smooth with bulbous swellings near tip or digitiform	Blunt ended	Covered by tentacles	Smooth, without verrucae	No verrucae	Burrowed deeply in reef crevices	Large solitary / small clonal in aggregations	Hard reef substrate
Heteractis aurora	1 type, sparse	Long / swelled at intervals (i.e. beaded)	Taper gradually towards tip	Visible	With verrucae, red or orange	Verrucae different color than column, with debris adhered	Flat on sand or rubble	Solitary	Sandy or rubble substrate
Radianthus crispa	1 type, numerous, densely packed	Long / tapering, might curl slightly	Taper gradually towards tip	Usually visible	Thick, with conspicuous verrucae in longitudinal rows	Verrucae raised and conspicuous, same color as column, with debris adhered	Burrowed deeply in sand	Solitary	Sand pockets near hard reef/ hard substrate in fore reefs
Radianthus doreensis	1 type, sparse	Long / smooth, digitiform, often curling or forming spirals	Taper gradually towards tip	Usually visible	With verrucae in longitudinal rows distally	Verrucae conspicuous, lighter in color than column, non-adhesive	Flat on sand or rubble	Solitary	Sand pockets in reefs or sand flats near reefs
Radianthus magnifica	1 type, densely packed	Long/ digitiform, elongate, bluntly rounded	Blunt ended, often small dot in center of tip	Covered by tentacles	Exposed with verrucae in longitudinal rows only distally	Verrucae inconspicuous, same color as column, non-adhesive	Attached to hard substrate, exposed	Solitary / clonal in extensive aggregations	Hard stable substrate in fore reefs / calm patch reefs or on extremely shallow reef flats

...continued on the next page

TABLE 2. (Continued)

Species	Types of tentacles	Tentacle length/ shape	Tentacle tips	Oral disc	Column	Verrucae (presence/shape)	Pedal disc	Growth pattern	Habitat
Radianthus malu	1 type, sparse	Short / bulbous, stubby and irregularly shaped	Blunt ended tip, often small colored dot in center of tip	Visible, often stripped with radial pattern	With verrucae in longitudinal rows distally	Verrucae, same color as column, with debris adhered strongly	Buried in sand or sediment	Solitary	Sand pockets in or near reefs or calm sandy habitats
Stichodactyla gigantea	1 type, densely packed	Short / thin, taper to blunt point; very sticky, easily tear off	Taper to a blunt tip	Deeply folded, covered by tentacles	Short, with verrucae in longitudinal rows only distally	Verrucae, different color than column, non-adhesive	Buried in sand pockets or reef crevices	Solitary	Calm shallow water habitats, rocky and sandy
Stichodactyla haddoni	1 type but exocoelic tentacles at margin 2-3 times enlarged, densely packed	Short / rounded and globular	Globular	Flared, covered by tentacles, stripped pattern	Smooth, without conspicuous verrucae	Verrucae inconspicuous, same color as column, non-adhesive	Buried deeply in sand	Solitary	Calm sand flats and seagrass beds away from fore reef
Stichodactyla mertensii	1 type, inner tentacles around mouth longer than marginal ones, not too densely packed	Inner longer than outer / digitiform	Blunt ended	Visible, sometimes stripped pattern	With verrucae in longitudinal rows along entire column	Verrucae conspicuous, brighter than column and contrasting, non-adhesive	Attached to crevices on hard reef substrate	Solitary	Fore reefs, in hard reef substrates

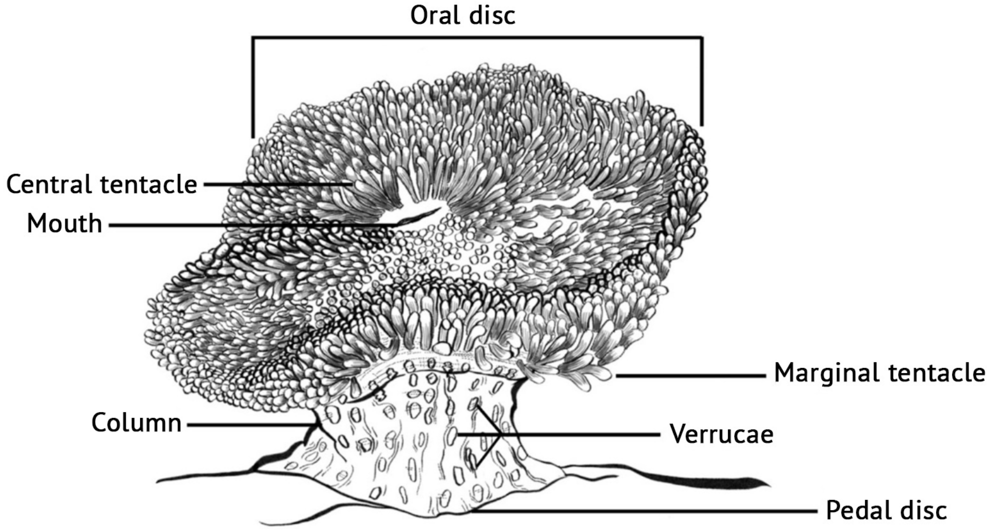

FIGURE 1. Labeled illustration of Merten's carpet anemone *Stichodactyla mertensii*.

Distal: Oral part of the animal, closer to the mouth.

Endocoelic tentacles: Tentacles arising in the space between a pair of mesenteries.

Exocoelic tentacles: Tentacles arising in the space adjacent to a pair of mesenteries. In *Stichodactyla haddoni* these tentacles are often longer than the endocoelic tentacles and serve as an important diagnostic character for the species.

Macrobasic *p*-mastigophores (= *p*-mastigophores A with looped tubule): Type of nematocyst with a thin-walled capsule and a V-shaped notch at the end of unfired shaft. The shaft loops at the base. The fired capsule has a very long, armed thread.

Mesenteries: Membranous, internal, radial tissue walls dividing the gastrovascular (or internal) cavity. They grow from the interior of the column towards the actinopharynx. Mesenteries can be **perfect/complete** (when they are attached to the actinopharynx) or **imperfect/incomplete** (when the mesenteries do not attach to the actinopharynx).

Mouth: Sole opening to the body cavity in the center of the oral disc, usually slit-like (Figure 1).

Nematocyst: Microscopic, intracellular stinging capsule with eversible tubule armed with spines that is characteristic of all members of Cnidaria.

Oral disc: Transverse distal sheet of tissue perforated in the center by the mouth and bearing around its edge a fringe of hollow tentacles. The only part of the body where tentacles are located (Figure 1).

Pedal disc: The aboral end or base of the sea anemone, opposite the oral disc, consisting of a thin sheet of tissue that the animal uses to adhere to hard substrate, such as reef rock, rubble, shell, or other foreign bodies (Figure 1). Among the clownfish-hosting sea anemones, the pedal disc is typically only exposed and visible in the magnificent anemone, *Radianthus magnifica.*

Proximal: Aboral part of the animal, closer to the pedal disc.

Tentacles: Hollow projections arising from the oral disc and surrounding the mouth. Variable in length and width, even within an individual. Used for prey capture and defense. Can arise from both exocoelic and endocoelic spaces.

Verrucae: Adhesive specialization of the column used to adhere to surrounding substrate and often holding debris such as sand, sediment, or pieces of mollusk shell. Verrucae can extend the entire length of the column, just the upper (distal) portion of the column directly under the oral disc or be absent entirely. Can be strikingly pigmented and conspicuous or the same color as the surrounding tissue of the column. Can appear scattered or arranged in longitudinal rows. Among the most important diagnostic characters for field identification (Figure 1).

Dichotomous Key for Field Identification

1 - Two tentacle types: outer tentacles bulbous, forming a thick, distinct band around the entire circumference of the anemone resembling a pizza crust. Inner tentacles branched ***Cryptodendrum adhaesivum* (Table 2)**

- All tentacles of same type but might be of different shapes and lengths **2**

2(1) - Verrucae (wart-like blotches) present and conspicuous on column underneath oral disc **3**

\- Verrucae inconspicuous or absent on column underneath oral disc **4**

3(2) - Tentacles heavily beaded, diagnostic for this species. Tentacles in some individuals are variable in shape, with some tentacles smoother or less beaded. Some individuals can have beaded outer tentacles and smoother inner tentacles . . . . ***Heteractis aurora* (Table 2)**

\- Tentacles not beaded. **6**

4(2) - Tentacles are short (<2 cm), rounded, and densely packed. Enlarged exocoelic tentacles protrude from the fringe of the oral disc and are diagnostic. Column and pedal disc buried deeply in sandy substrate and not visible. Oral disc lies flat on sandy substrate . . . . ***Stichodactyla haddoni* (Table 2)**

\- Tentacles elongate (>2 cm), rounded, and densely packed. Exocoelic tentacles indistinguishable from endocoelic tentacles. Column not buried in sandy substrate. Oral disc does not lie flat on sandy substrate **5**

5(4) Verrucae absent. Column smooth, with thin body wall. Tentacles may have characteristic "bubble-tips" or be elongate and digitiform. Pedal disc attached to hard substrate, typically deep in crevices in the reef. When disturbed, animal retracts rapidly and completely into reef rockwork. . . . . ***Entacmaea quadricolor* (Table 2)**

\- Verrucae on distal (upper) portion of column but not prominent. Verrucae non-adhesive, same color or darker as column, forming longitudinal rows. Body wall thick. Column and pedal disc fully visible. The only host anemone with visible pedal disc. Anemone perched prominently on hard substrate. Cannot retract completely into reef. Instead retracts into a large "ball" leaving only a small tuft of tentacles visible. Typically, the most conspicuous species in fore reef habitats; large body size, up to 1 m in oral disc diameter . . . . ***Radianthus magnifica* (Table 2)**

6(3) - Verrucae adhesive, the same color as the surrounding column **7**

\- Verrucae non-adhesive, significantly lighter, or different in color, than the surrounding column. **8**

7(6) - Tentacles long (>2 cm) and thinly tapered . . . . ***Radianthus crispa* (Table 2)**

\- Tentacles short (<2 cm), stubby, of unequal shape and length when animal is not disturbed . . . . . ***Radianthus malu* (Table 2)**

8(6) - Pedal disc and column burrowed deeply in sandy substrate. Verrucae are light in color and contrast sharply against a darker gray/brown column. Tentacles are long and often form corkscrew spirals . . . . ***Radianthus doreensis* (Table 2)**

\- Pedal disc attached directly to hard reef substrate. Verrucae not white. Tentacles do not form corkscrew spirals **9**

9(8) - Tentacles around the mouth often longer than peripheral tentacles. Tentacles rounded, adhesive but will not easily rip off or detach. Verrucae pigmented and contrast highly with tan or gray column; verrucae extend to pedal disc. Oral disc diameter can exceed 1 m. Found attached to, and often draped directly over, hard reef substrate in fore reef environments. Typically found in water depths exceeding 5 m . . . . ***Stichodactyla mertensii* (Table 2)**

\- All tentacles the same size. Tentacles taper towards the tips taking on a slightly pointed appearance. Tentacles extremely sticky to the touch and easily rip off. Verrucae are typically a lighter color than surrounding column and do not extend to pedal disc. Oral disc deeply folded. Typically found in shallow water (≤ 2 m). . . . . ***Stichodactyla gigantea* (Table 2)**

Family Actiniidae

Entacmaea quadricolor (Leuckart in Ruppell & Leuckart, 1828) (Figure 2; Figure S1)

The bubble-tip sea anemone *Entacmaea quadricolor* is among the most iconic and phenotypically variable clownfish-hosting sea anemone species in terms of color, pattern, tentacle morphology, and growth patterns (Figure 2; Figure S1). This species gets its common name from the characteristic bulbous swellings that commonly form at, or near, the tentacle tips. When bulbs are present, this species is easy to identify underwater. However, tentacle shape is highly

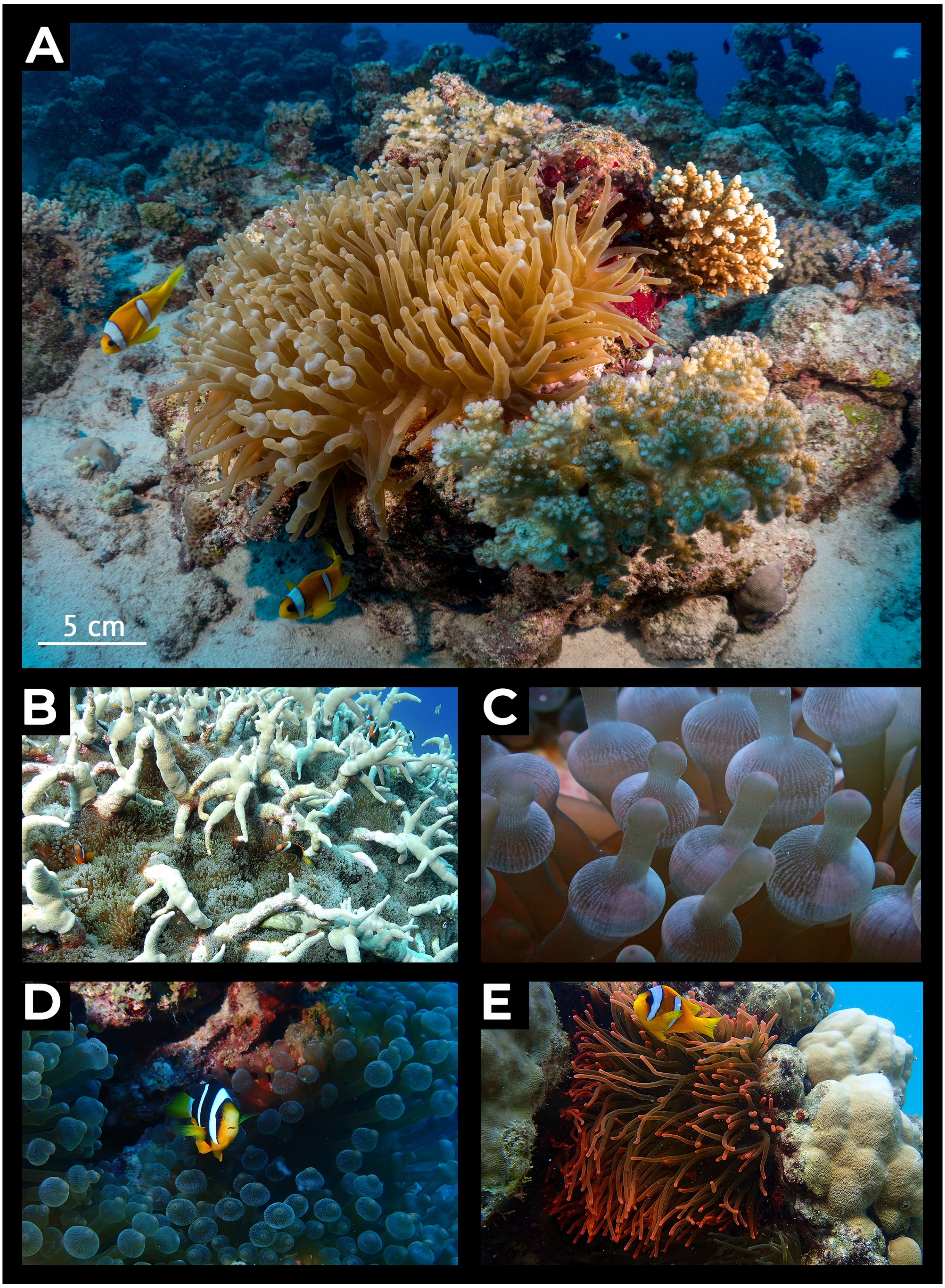

FIGURE 2. Representative images of the bubble-tip sea anemone *Entacmaea quadricolor* encompassing a broad range of geographic and phenotypic variation. A) Wide angle photograph of large solitary individual highlighting typical microhabitat requirements for the species. Note the tentacles are both bulbous and digitiform within this individual (Saudi Arabia, Red Sea). B) Dense aggregation of hundreds of small clonal sea anemones growing among a shallow branching stony coral serving as hosts to a colony of *Amphiprion melanopus* (Kwajalein Atoll, Marshall Islands). C) Macro photograph of characteristic bubble tips. Note the striated pattern of the tentacle (Fares-Maathodaa, Maldives). D) Individual anemone with all tentacles exhibiting characteristic bulbous tentacle morphology (Fares-Maathodaa, Maldives). E) Red solitary individual with long digitiform tentacles hosting (Saudi Arabia, Red Sea). Photographs by Morgan Bennett-Smith, Benjamin M. Titus, and Scott Johnson.

variable both intra-specifically and even intra-individually. It is not uncommon to encounter individuals whose tentacles are simultaneously bulbed and digitiform (smooth, not-bulbed, uniformly shaped; Figure 2A), completely bulbous (Figure 2B, C, D), or completely digitiform and long (up to 100 mm; Figure 2E). Tentacle tips, as a rule, are blunt ended. Tentacle color is typically brown/tan or green (Figure 2A-D) but can also be bright red or orange (Figure 2E). Tentacle tips are frequently purple/magenta. Tentacle patterns are variable. Some tentacles take on a dull matte appearance (Figure 2A; Figure S1D), but can also be striated (Figure 2C), translucent (Figure S1A, C), speckled (Figure S1A, C), or some combination thereof. In many individuals the equator of the bulb is a mottled white pattern (Figure 2; Figure S1). Tentacles are densely packed, typically obscuring the oral disc and mouth. Verrucae are absent on the column *E. quadricolor* (Figure S1C). Column color is usually bright red or magenta. The column and pedal disc are not typically visible and burrowed deep in a crevice or hole in the reef. The body wall is thin and tentacles tear easily.

Entacmaea quadricolor exhibits two primary growth patterns and can be found as either large (up to 400 mm in oral disc diameter) solitary individuals (Figure 2A) or clonal aggregations of smaller individuals. Depending on habitat and geography, clonal aggregations can be comprised of small clusters of medium-sized individuals (typically 2-6 anemones per cluster), or dense aggregations of small individuals that can form extensive fields of anemones (dozens to hundreds of individuals; Figure 2B). This latter growth form is typically found in the Coral Triangle to Central Pacific Ocean in shallow habitats where anemones grow on tops of reefs or among the branches of shallow stony corals (Figure 2A). Both shallow aggregations and large solitary individuals can be found on the same reefs and typically segregate by depth, with the large solitary individuals occurring in deeper water. Regardless of growth form, *E. quadricolor* requires hard stable substrate and is never found with its pedal disc and column burrowed in the sand. This species generally requires calm habitats with low wave exposure. When disturbed, *E. quadricolor* can disappear fully from view by withdrawing into the reef structure.

The geographic range of this species is broad, ranging from the very Northern Red Sea, throughout the Indian Ocean, Coral Triangle, and into the Central Pacific reaching the Marshall Islands but not East to French Polynesia (Figure 3). High-latitude populations of this species are also common, nearly reaching temperate habitats in the Japanese Archipelago to the North, as well as marginal reef habitats in Australia (Solitary Islands) and South Africa. This is among the most common host anemones encountered throughout its range and almost always is found in association with clownfishes. However, in marginal reef habitats in high latitudes it is not uncommon for this species to be found without fish symbionts, particularly the small clonal populations.

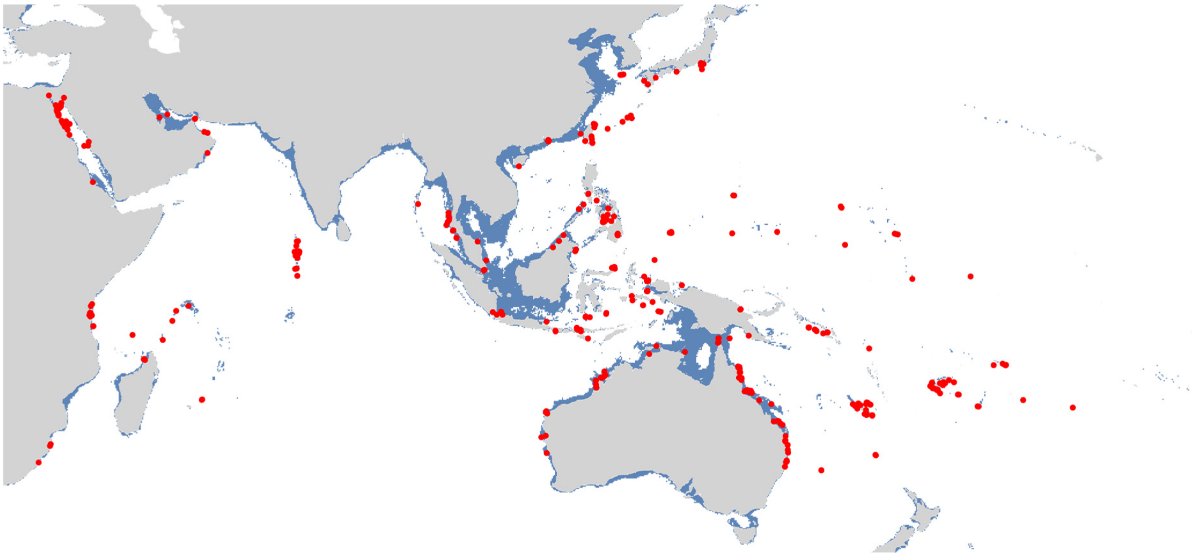

FIGURE 3. Confirmed geographic range of *Entacmaea quadricolor* in the Indo-West Pacific. Red dots represent species observations from the Global Biodiversity Information Facility (GBIF). Blue shaded area represents shallow water habitat (60 m bathymetry).

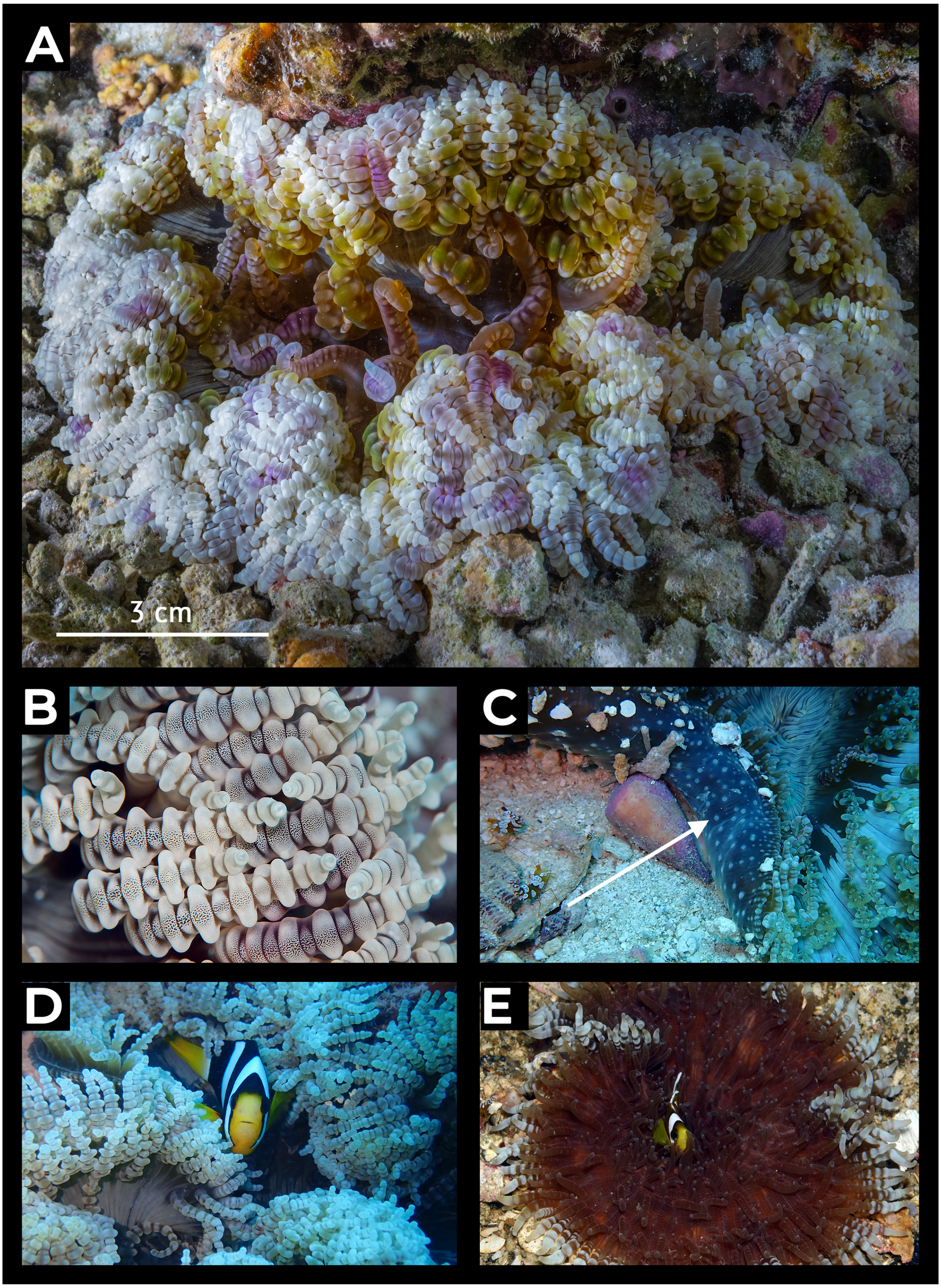

FIGURE 4. Representative images of the beaded sea anemone *Heteractis aurora* encompassing a broad range of geographic and phenotypic variation. A) Multi-colored, whole individual in typical rubble microhabitat with characteristic beaded tentacle morphology (Maldives) B) Macro photograph of stereotypical beaded tentacle morphology (Kwajalein Atoll, Marshall Islands). C) Partially retracted/folded oral disc revealing highly contrasting white verrucae on gray column (arrow). Also note zebra-striped oral disc pattern (Fares-Maathodaa, Maldives). D) White phenotype hosting *Amphiprion clarki* (Fares-Maathodaa, Maldives). E) Individual with partially beaded tentacles. White peripheral tentacles with lightly beaded morphology with inner brown tentacles without beads and horizontal stripes (Anilao, Philippines). Photographs by Morgan Bennett-Smith, Benjamin M. Titus, and Scott Johnson.

Family Heteractidae

Heteractis aurora (Quoy & Gaimard, 1883) (Figure 4; Figure S2)

Heteractis aurora, commonly referred to as the "beaded anemone", is a highly distinctive clownfish-hosting species and sole member of the family Heteractidae (Figure 4, Figure S2). Tentacles (50-60 mm in length) often have characteristic swellings at regular intervals along the tentacle and take on a resulting "beaded" appearance that make this species impossible to misidentify in the field when present (Figure 4A, B, D). The base body and tentacle color of this species is often variable whites/browns/beiges but can take on purplish or greenish hues as well (Figure 4, Figure S2). This is a small to medium sized host anemone, with a broadly flared oral disc (up to 300 mm in diameter) that lays flat or undulating over sandy or rubbly substrate (Figure 4, Figure S2). Tentacles sparse, leaving oral disc and mouth highly visible. Oral disc can take on a "zebra" stripe pattern similar to that of *Radianthus doreensis*. Verrucae on the column of this species are lighter in color than the surrounding column and extend from the oral disc downward to mid-column (Figure 4C). Verrucae often hold debris such as sand, shell, or other loose rubble (Figure 4C). The lower column, typically obscured by sediment is often red or orange.

Although the beaded tentacle morphology is diagnostic and not shared by any other host anemone species, some individuals have partially or lightly beaded tentacles, making field identifications difficult in some cases. In some individuals, only the marginal (outer) tentacles are beaded while inner tentacles (those closer to the month) may only be striped with horizontal lines (Figure 4E). In other cases, the "beads" may only occur on one side of the tentacle, or may take on a more swollen bulging appearance rather than well-defined beads (Figure 4E, Figure S2E). These partially beaded individuals are particularly common in the Red Sea and other parts of the Indian Ocean, with the exception of the Maldives which harbor individuals with well-defined beads. Individuals with partially or lightly beaded tentacles can easily be misidentified as *Radianthus crispa* or *Radianthus doreensis* due to similar microhabitats. *Radianthus crispa* typically has longer tentacles than *H. aurora* and harbors verrucae that are similarly colored to the surrounding column, while *R. doreensis* also has longer tentacles but these form spiral patterns.

The geographic range of *H. aurora* is extensive, from the Northern Red Sea throughout the Indian Ocean, and into the Central Pacific to the Marshall Islands and Fiji (Figure 5). This species is a sand/rubble dwelling anemone that occupies sand pockets in coral reef habitats, or occupies sand flats adjacent to reefs. It is only known to reproduce sexually and does not form large aggregations.

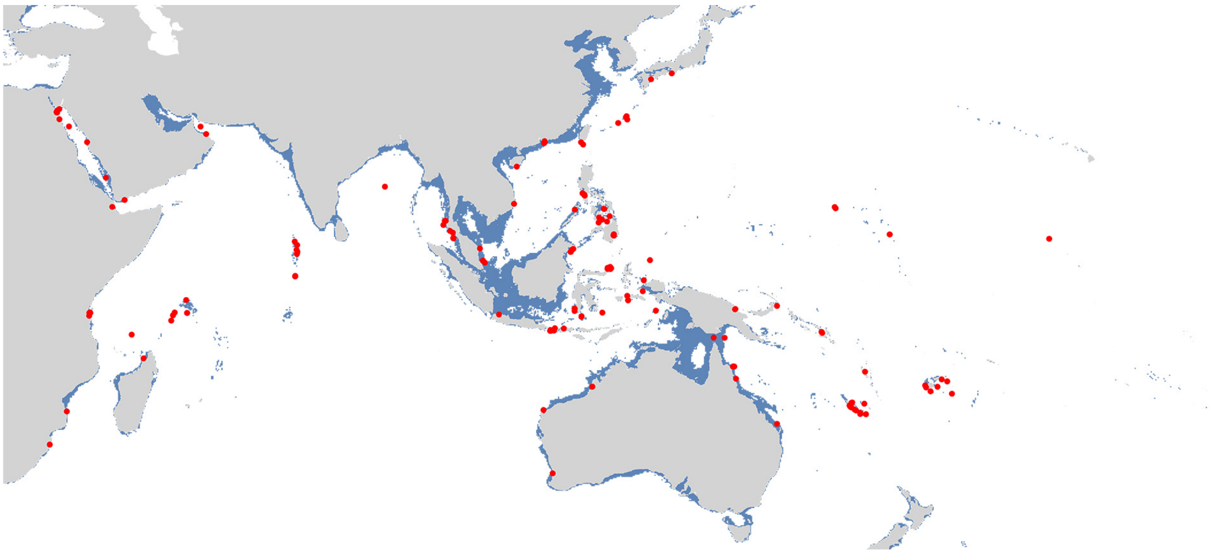

FIGURE 5. Confirmed geographic range of *Heteractis aurora* in the Indo-West Pacific. Red dots represent species observations from the Global Biodiversity Information Facility (GBIF). Blue shaded area represents shallow water habitat (60 m bathymetry).

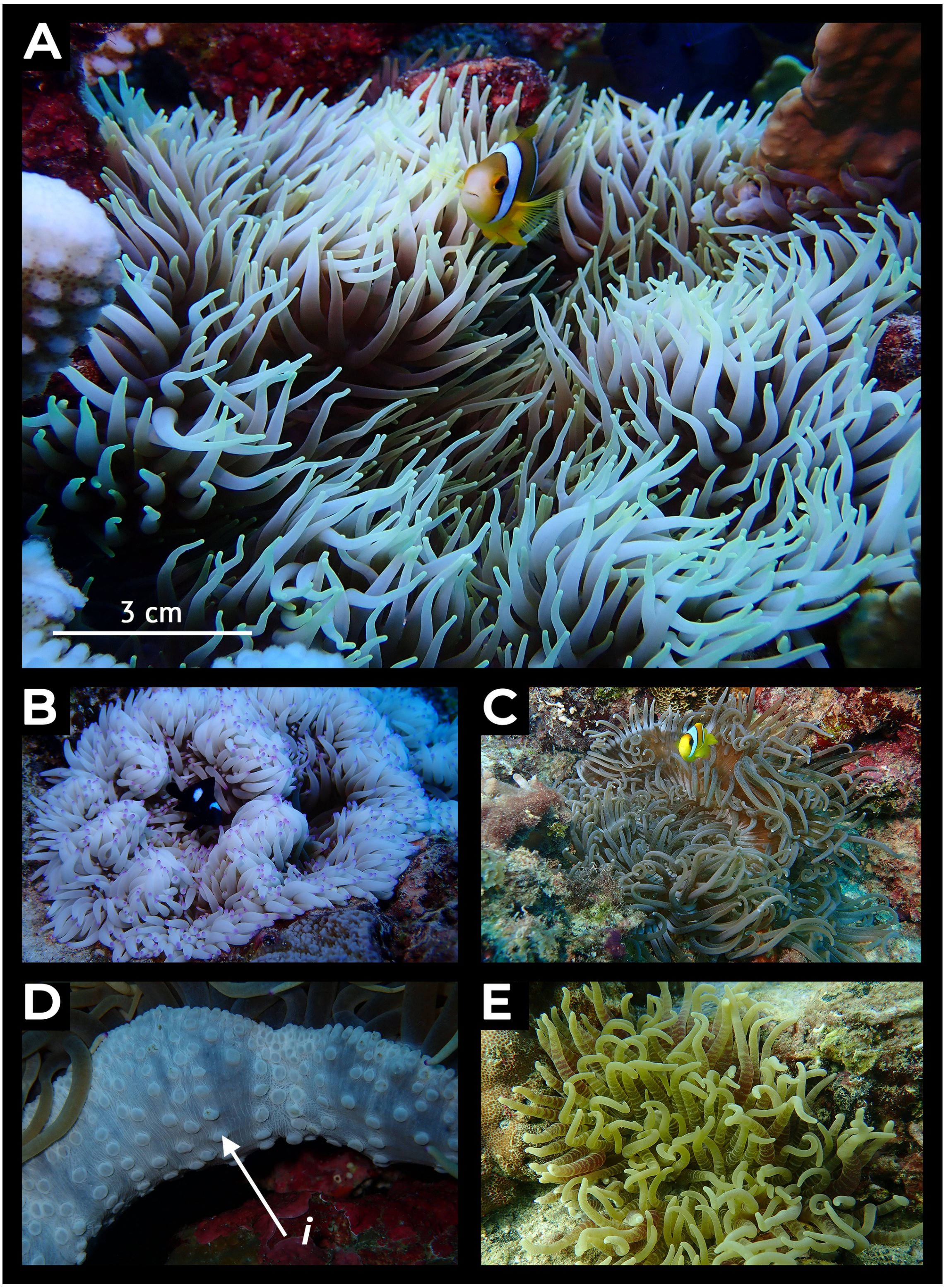

FIGURE 6. Representative images of the leathery sea anemone *Radianthus crispa* encompassing a broad range of geographic and phenotypic variation. A) Yellow individual hosting juvenile *Amphiprion chrysopterus* on a typical fore reef environment in the Pacific Ocean. Note the densely packed tentacles with tapered tips coming to a point (Moorea, French Polynesia). B) White individual with pink tentacle tips (Moorea, French Polynesia). C) Tan/Brown individual with less densely packed tentacles that curl slightly (Saudi Arabia, Red Sea). D) Macro photograph underneath oral disc. *i* = well-defined raised verrucae that are similarly colored to the surrounding column (Okinawa, Japan). E) Small individual in stereotypical sandy microhabitat with slightly curled tentacled tips and horizontally striated tentacle pattern (Gulf of Oman, United Arab Emirates). Photographs by Benjamin M. Titus and James Reimer.

Family Stichodactylidae

Radianthus crispa (Hemprich & Ehrenberg, 1834) (Figure 6; Figure S3)

The leathery sea anemone, *Radianthus crispa* (Figure 6; Figure S3), was originally described from the Red Sea. This species gets its common name from its thick body wall, which gives the animal a tough leathery texture. The tentacles in this species are all alike, elongate (up to 200 mm), tapering gradually to a pointed tip (Figure 6A; Figure S3). Tentacles are numerous (up to 800 in the largest individuals) and can be densely packed in some individuals. Tentacles frequently curl, yet only slightly, and not to the same degree as in *R. doreensis* (Figure 6C & E, Figure S3A, C). The body and tentacle color of this species range from white and light purple to tan/brown or yellow and may take on a matte appearance (Figure 6; Figure S3). Some individuals are bright pink/magenta, and it is not uncommon to encounter individuals with pink-tipped tentacles (Figure 6B; Figure S3C, E). Tentacle patterns vary, but generally have a mottled (Figure S3A, B, E), lightly striped (Figure 6E), or speckled appearance (Figure S3B). The column of *R. crispa* is typically white/gray/tan in color and dotted with conspicuous raised verrucae which form longitudinal rows and are the same color as the column (Figure 6D). Verrucae are strongly adherent to the surrounding substrate and regularly hold debris, shells, and other sediment that can be seen when the oral disc is folded back.

A morphological and microhabitat shift seems to occur in this species between Indian and Pacific Ocean populations, and although this is not unilateral across all individuals, it is noticeable. Generally, *R. crispa* in the Indian Ocean occupy sand pocket microhabitats that are found adjacent to hard reef substrate and have the pedal disc and column burrowed deeply in the sand (Figure 6C, E; Figure S3A, B). Indian Ocean specimens of *R. crispa* are typically found in calm patch reef or marginal reef habitats. In contrast, Pacific Ocean individuals more commonly occupy hard substrata directly in fore reef habitats and are more commonly found competing for space with stony corals (Figure 6A, B; Figure S3C, D). Indian Ocean members of *R. crispa* have tentacles that are fewer in number and less densely packed than those from the Pacific, and are smaller in their body size and maximum oral disc diameter. Finally, Pacific Ocean members of *R. crispa* are more colorful in general, often have pink tentacle tips, and are more likely to take on body colors with pinks and yellows whereas Indian Ocean *R. crispa* are typically tan or brown (Figure 6; Figure S3).

FIGURE 7. Confirmed geographic range of *Radianthus crispa* in the Indo-West Pacific. Red dots represent species observations from the Global Biodiversity Information Facility (GBIF). Blue shaded area represents shallow water habitat (60 m bathymetry).

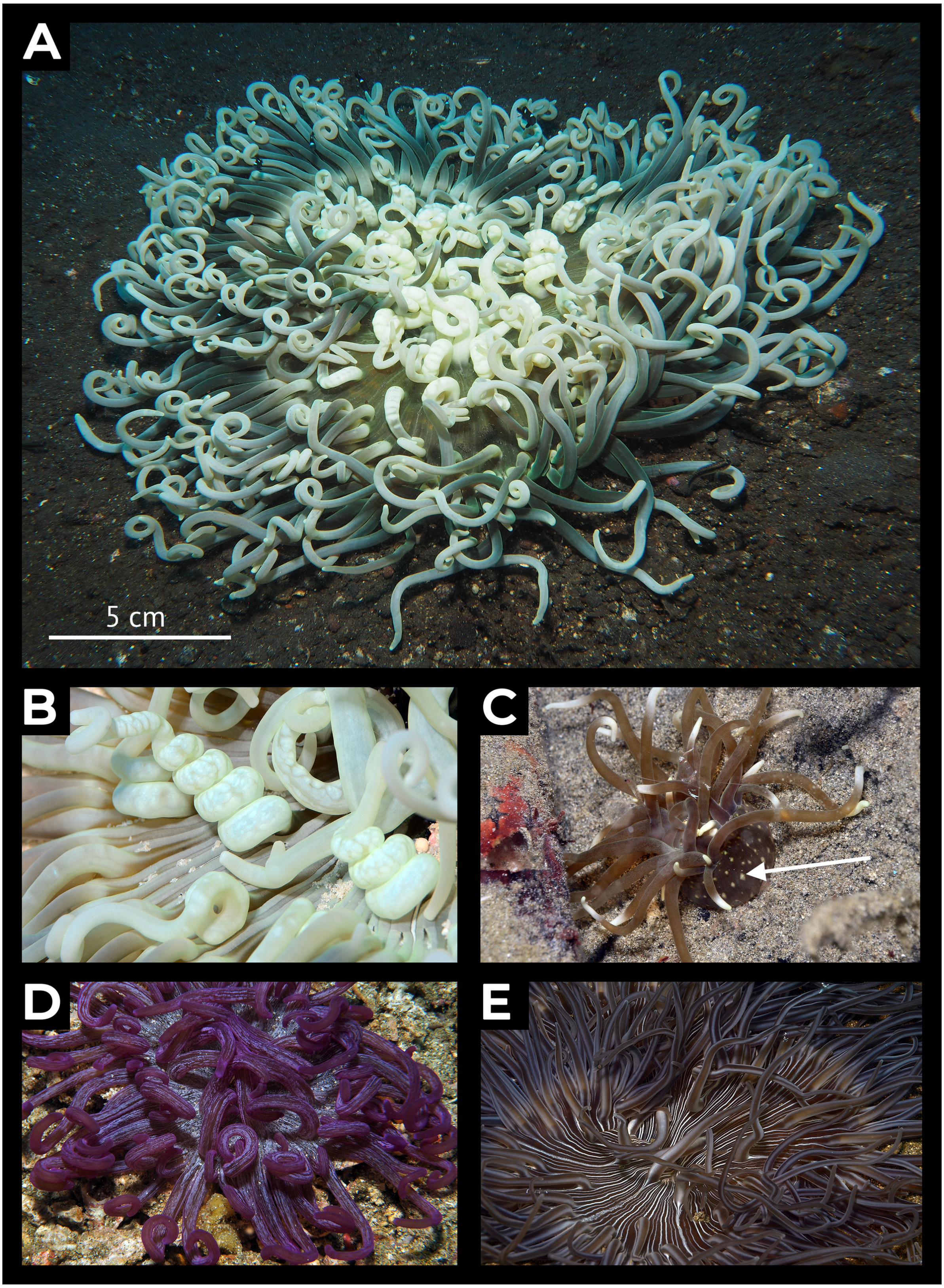

FIGURE 8. Representative images of the long-tentacled sea anemone *Radianthus doreensis* encompassing a broad range of geographic and phenotypic variation. A) Whole individual in typical sandy microhabitat (Bali, Indonesia). B) Macro photograph of characteristic curling/spiraling tentacle pattern (Kwajalein Atoll, Marshall Islands). C) Partially retracted individual revealing highly contrasting white verrucae on brown column (arrow; Anilao, Philippines). D) Small purple individual with longitudinally striped tentacles and oral disc (Anilao, Philippines). E) Large individual with longitudinal “zebra-stripe” tentacle and oral disc pattern (Anilao, Philippines). All photographs by Scott and Jeanette Johnson.

Geographically, *R. crispa* is the most widespread host anemone species, ranging from the Northern Red Sea throughout the entire Indian Ocean, Coral Triangle, and extending East all the way to French Polynesia (Figure 7). Like *E. quadricolor*, *R. crispa* extends into high latitudes, nearly reaching temperate habitats in the Japanese Archipelago to the North, as well as marginal reef habitats in Australia (Solitary Islands) and South Africa. Although this anemone forms associations with nearly as many clownfish species as *E. quadricolor*, in our experience, it is found without clownfish symbionts more frequently than *E. quadricolor*. Solitary individuals that do not host fishes are common in the Red Sea and around the Arabian Peninsula. This species regularly hosts juvenile rather than adult clownfishes. It is not known to reproduce asexually and does not form extensive aggregations, but it is not uncommon to find this species adjacent to other clownfish-hosting anemones.

Radianthus doreensis (Quoy & Gaimard, 1883) (Figure 8; Figure S4)

Radianthus doreensis, formerly in the genus *Macrodactyla*, is highly variable in terms of tentacle and oral disc color and pattern (Figure 8; Figure S4). It is commonly referred to as the "corkscrew anemone" or "long-tentacled anemone" in reference to the long (>150 mm), tapering tentacles that often curl or form spiral patterns (Figure 8A, B; Figure S4). The body and tentacle color of this species is often various shades of brown, yellow/white, or purple. Tentacles can be uniformly colored but are often longitudinally striped (Figure 8D, E). Tentacles are often sparse, but not always, leaving the oral disc highly visible (Figure 8E). The broad oral disc, up to 500 mm diameter in the largest individuals, typically lies flat on the surrounding sand or rubble and takes on a similar pattern to the tentacles. Individuals with longitudinally striped tentacles will also have highly striped oral discs, superficially resembling radially arranged zebra stripes (Figure 8; Figure S4C, E). Individuals without longitudinally striped tentacles will not display heavily striped oral discs (Figure 8A). Prominent, light-colored verrucae form longitudinal rows on the upper portion of the column, and contrast in color from the surrounding column, which is typically a purplish-gray or brown (Figure 8C; Figure S4). The light-colored verrucae are non-adhesive and are the most distinct feature in life that can be used for field identification. Verrucae are absent on the lower portion of the column which is typically bright orange and obscured from view by being burrowed deeply in the sediment.

Radianthus doreensis has a geographic range that is poorly resolved, likely due to this species being understudied (Figure 9). It is documented from Australia, through the Coral Triangle, and North to Japan, as far east as the Marshall Islands in the Central Pacific. Dunn (1981) lists the Red Sea as part of its native range, but this has not been confirmed through recent major surveys in the region (Bennett-Smith *et al.* 2021), and it has not been observed in the Indian Ocean outside of Western Australia.

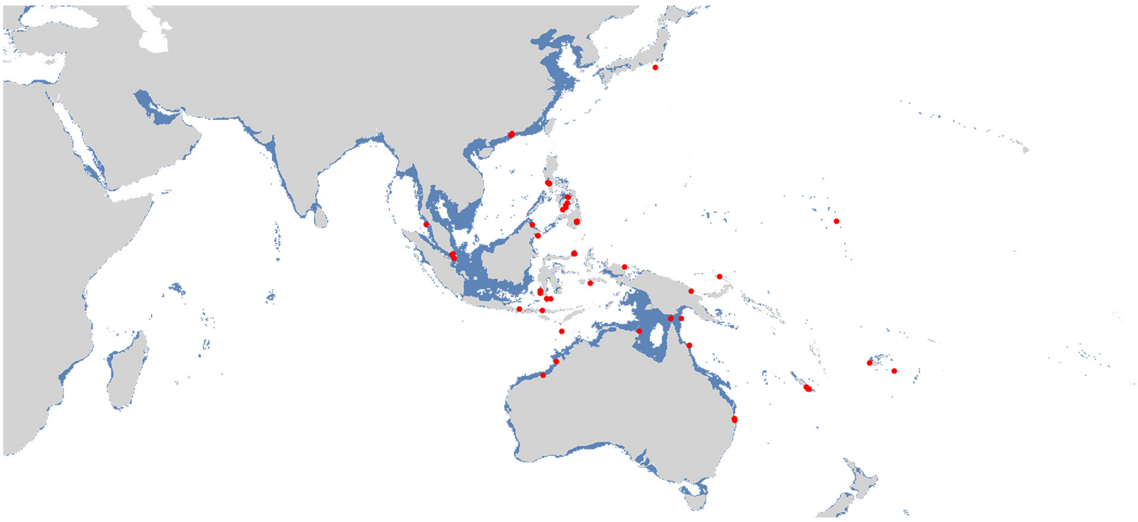

FIGURE 9. Confirmed geographic range of *Radianthus doreensis* in the Indo-West Pacific. Red dots represent species observations from the Global Biodiversity Information Facility (GBIF). Blue shaded area represents shallow water habitat (60 m bathymetry).

Radianthus doreensis is a sand/rubble dwelling species that occupies sand pockets in coral reef habitats or occupies sand flats adjacent to reefs. It is only known to reproduce sexually and does not form large aggregations. The geographic range, habitat, tentacle shape and color, orange base, and non-adhesive verrucae that contrast highly with surrounding column are also features partially shared by other clownfish hosting species such as *R. crispa, R. malu*, and *Heteractis aurora*. Thus, in the field this species can be easy to misidentify. *Radianthus crispa* has s long tentacles that can also curl or spiral but have adhesive verrucae that are the same color as the surrounding column. *Radianthus malu* also has orange bases/pedal discs, but does not have long curling tentacles. *Heteractis aurora* has white verrucae that contrast with a grayish column, but has beaded or semi-beaded tentacles that do not curl.

Radianthus magnifica **(Quoy & Gaimard, 1883) (Figure 10; Figure S5)**

The magnificent sea anemone *Radianthus magnifica,* formerly in the genus *Heteractis*, is one of the most iconic and heavily photographed clownfish-hosting sea anemones due to its prominent microhabitat, colorful and fully visible column, and a body size which can reach up to 1 m in oral disc diameter (Figure 10; Figure S5). In older literature and especially in the ornamental aquarium trade, this species is often colloquially referred to as the "Ritteri" sea anemone. The tentacles of this species are distinctive, all alike, densely packed, digitiform but some might be split at the tip (Y-shaped), elongate (up to 100 mm), or bluntly rounded (Figure 10C). Often a small dot is present in the center of the blunt tentacle tip (Figure 10C). Tentacles are typically tan, brown, or shade of green, but can also take on various shades of purple and have brightly colored tips (Figure 10). Tentacles contrast sharply with a brightly colored column, which is typically visible and vibrant shades of purple/magenta, red, and orange (Figure 10A, B), but can also be tan or brown and the same color as the tentacles (Figure S5B). Verrucae are present in longitudinal rows on the upper portion of the column only, are inconspicuous, and of the same color as the surrounding column. Verrucae typically do not hold debris.

This species occupies prominent positions on coral reef habitats, attaching its pedal disc directly to hard substrate. This is the only species that regularly has both its column and pedal disc fully exposed and visible (Figure 10A, B; Figure 5B). Due to its conspicuous placement on fore reef habitats, this species of anemone is the most encountered host anemone by SCUBA divers, and thus, the most heavily photographed. When disturbed, or possibly after capturing prey, *R. magnifica* will curl up into a distinctive ball, leaving only a small tuft of tentacles exposed (Figure 10B). In high wave energy environments *R. magnifica* often has a fully flared oral disc, which can obscure both the column and pedal disc (Figure 10D, E). Although this species occupies prominent positions, requires hard stable substrate, and is often common on fore reefs, *R. magnifica* is something of a habitat generalist in that it will also be common on calm patch reefs and even occurs on extremely shallow reef flats at less than 1m depth (Figure S5B, D, E). The shallowest individuals do not always host clownfishes (Figure S5B, D, E). *Radianthus magnifica* reproduces both sexually and asexually. It can thus be found as a solitary individual or in extensive clonal aggregations of dozens to hundreds of individuals (Figure 10; Figure S5).

Geographically, *R. magnifica* is widespread, ranging from the Northern Red Sea (but not in the Gulf of Aqaba), throughout the Indian Ocean, Coral Triangle, and the Central Pacific where it occurs at least as far east as French Polynesia (Moorea, Tahiti, and Tuomotu Archipelago) and the Line Islands (Figure 11). This species appears to require fully tropical waters and does not extend into high-latitude subtropical waters in the Japanese Archipelago or Australia. Interestingly, this species also appears to be absent from the Gulf of Aden, Gulf of Oman, and Persian/Arabian Gulf, and much of the Arabian Sea within the Northern stretches of the Indian Ocean (Figure 11).

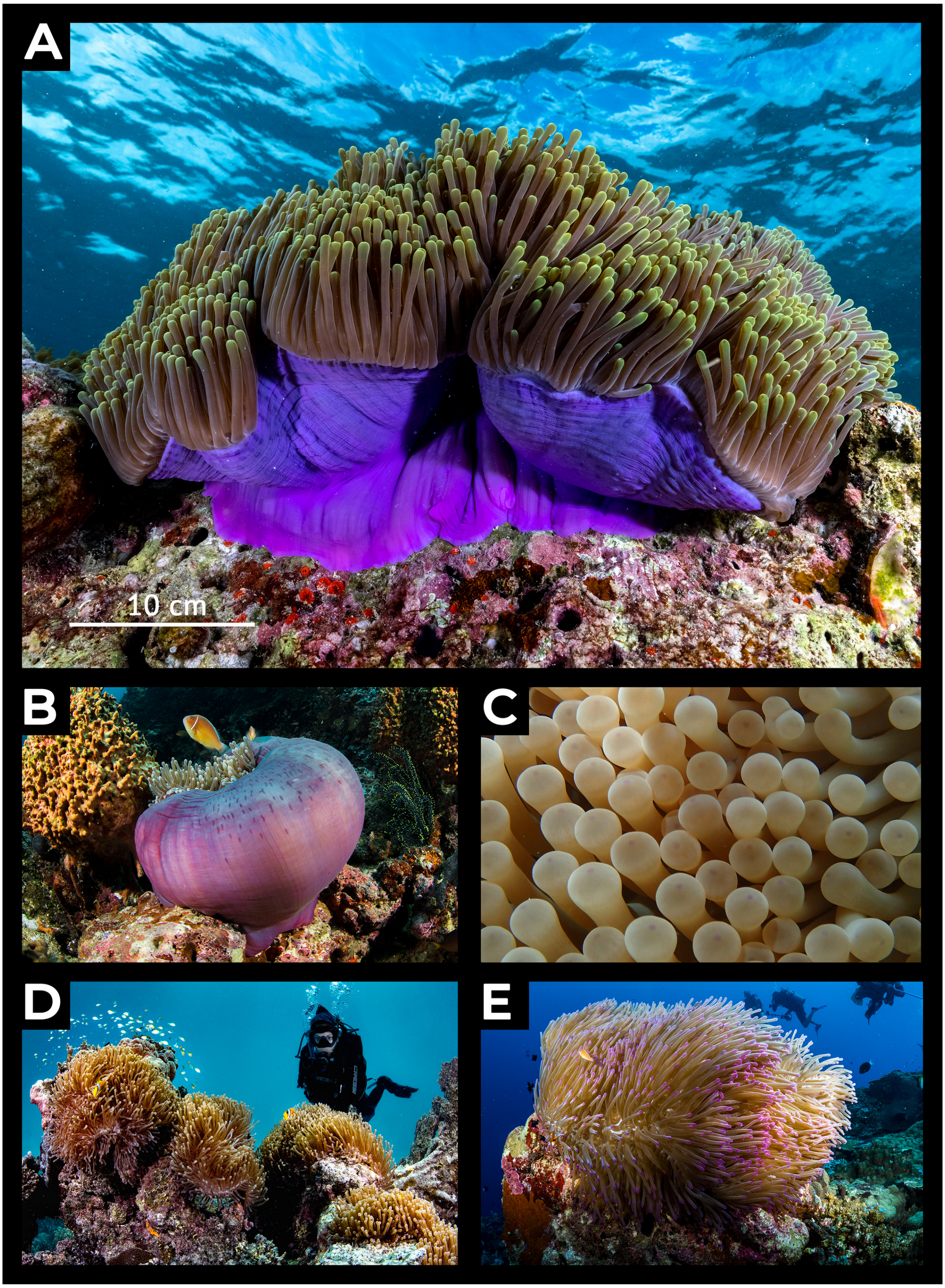

FIGURE 10. Representative images of the magnificent sea anemone *Radianthus magnifica* encompassing a broad range of geographic and phenotypic variation. A) Wide-angle photograph of stereotypical *R. magnifica* perched prominently on exposed rocky outcrop with fully visible purple column and pedal disc (Maldives). B) Retracted individual with column curled into a ball leaving only a small tuft of tentacles visible (Kimbe Bay, Papua New Guinea). C) Macro photograph of tentacles. Note the blunt-rounded ends that are all alike and the small "dot" present in the center of the tentacle tip (Fares-Maathodaa, Maldives). D) Cluster of at least four anemones on rocky outcrop (Saudi Arabia, Red Sea). E) Large solitary individual with pink tentacle tips. Note that the oral disc is fully expanded over the substrate obscuring the column and pedal disc from view (Kimbe Bay, Papua New Guinea. Photographs by Morgan Bennett-Smith and Benjamin Titus.

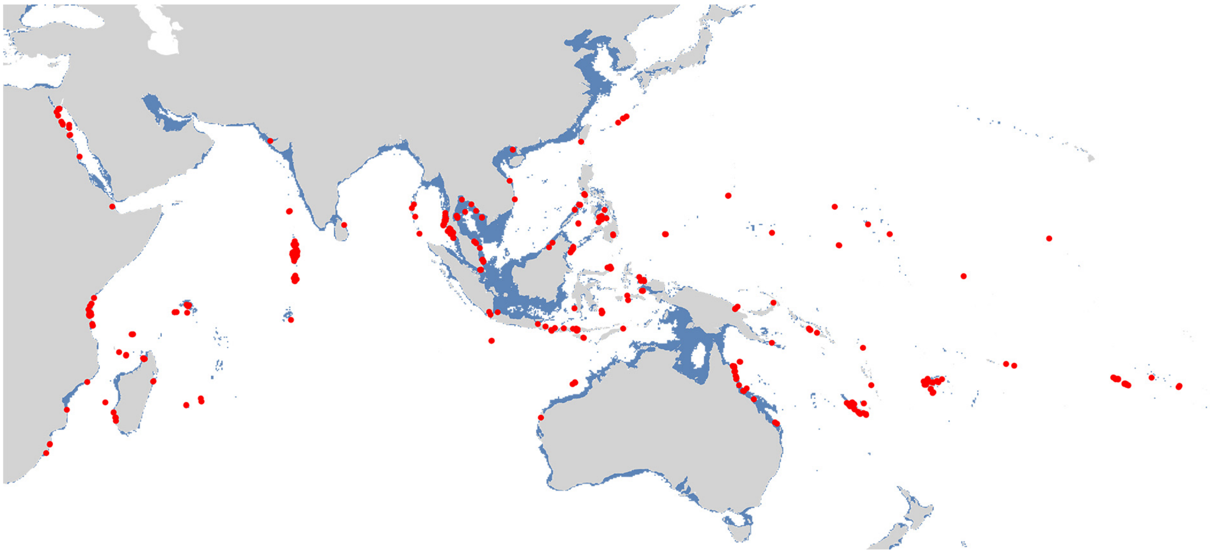

FIGURE 11. Confirmed geographic range of *Radianthus magnifica* in the Indo-West Pacific. Red dots represent species observations from the Global Biodiversity Information Facility (GBIF). Blue shaded area represents shallow water habitat (60 m bathymetry).

Radianthus malu **(Haddon & Shackleton, 1893) (Figure 12; Figure S6)**

The "malu" or "delicate" sea anemone, *Radianthus malu*, is the least well-known clownfish-hosting sea anemone species. Individuals are generally small, but can reach 200mm in oral disc diameter, and are characterized by stubby irregularly shaped tentacles (Figure 12; Figure S6). In general, tentacles are short (rarely exceeding 40mm in length) and bulbous, leading to a bluntly rounded tentacle tip. However, in some individuals, the bulbous swelling occurs lower on the tentacle leaving the tentacle tip to taper to a point (Figure 12D). As in *R. magnifica*, the tentacles often have a bright purple dot in the center of their bulbous tips (Figure 12A-C) but the tip can also be various shades of green (Figure 12E). Typical body and tentacle color for this species ranges from tan/cream to green and purple. Tentacles are typically sparse, leaving the oral disc visible in most individuals (Figure 12B, E). The oral disc is often radially striped (Figure 12B, E). Verrucae are present and form longitudinal rows on the upper portion of the column. Verrucae are strongly adhesive and often hold debris and sediment (Figure 12C). The lower portion of the column and pedal disc are buried in sediment and obscured from view.

This species occupies sand pockets in or adjacent to reefs as well as other calm sandy habitats. When disturbed, *R. malu* will retract completely into the sand. The reproductive mode for *R. malu* is thought to be sexual only. Individuals are typically found as solitary anemones but can be found adjacent to other anemones on occasion. This species is not always found hosting clownfishes, but when they do, they typically host juvenile fish. In life, this species can look like a cross between *Entacmaea quadricolor* and *R. crispa* and thus it is possible to confuse the three when making identifications in the field. Unlike *E. quadricolor, R. malu* has verrucae, and unlike *R. crispa*, the tentacles are stubby and sparse on the oral disc.

The geographic range of *R. malu* is centered in the Coral Triangle and extends South to Australia, North to Japan and West to the Southern Red Sea (Figure 13). However, this species does occur east to the Marshall Islands and all the way to the Hawaiian Islands where it does not host clownfish. This is the only clownfish-hosting sea anemone species to make it as far east as Hawaii.

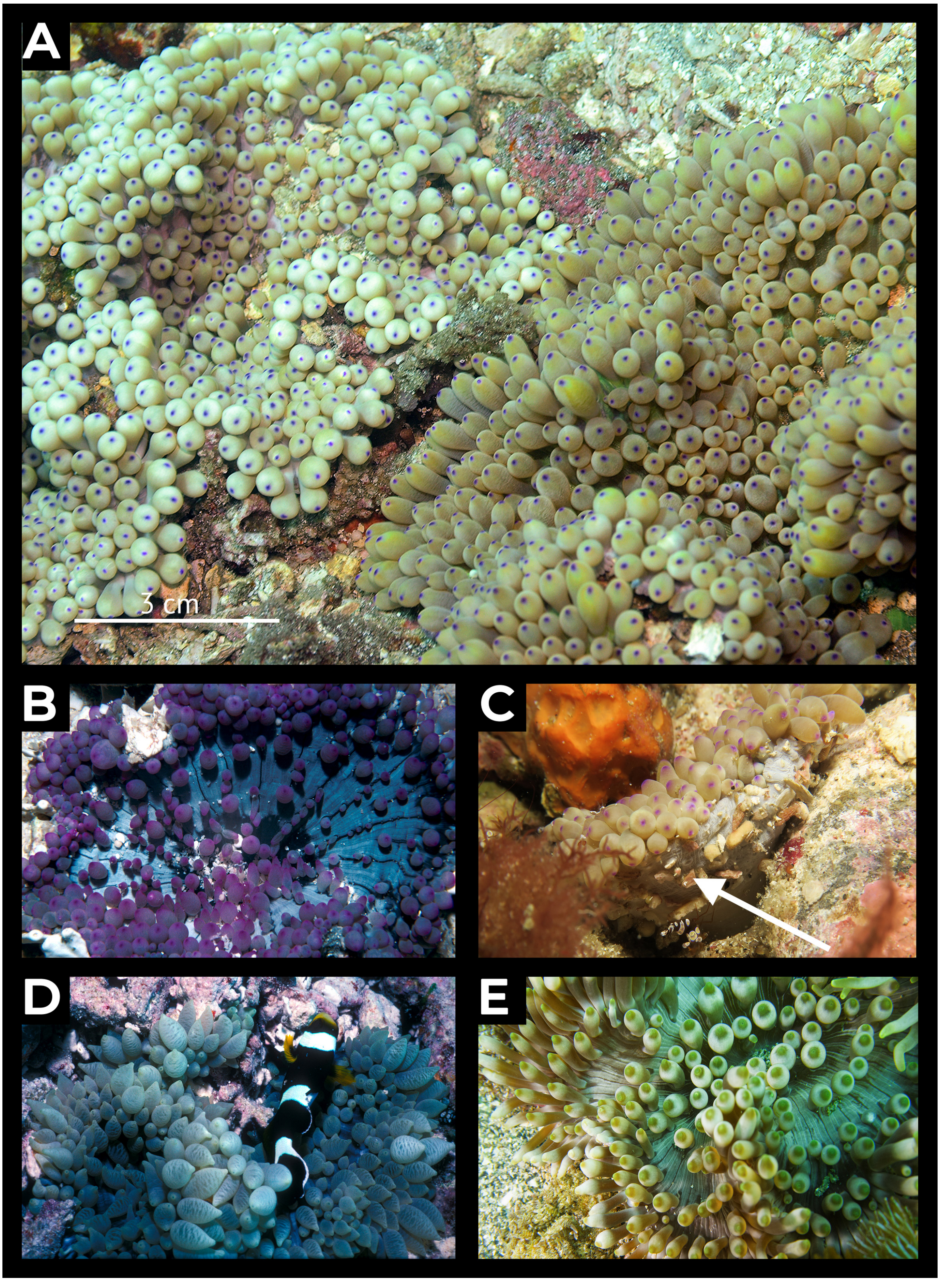

FIGURE 12. Representative images of *Radianthus malu* encompassing a broad range of geographic and phenotypic variation. A) Two *R. malu* individuals exhibiting typical morphology and coloration for the species (Japanese Archipelago). B) Purple individual with sparse tentacles displaying visible oral disc (Kwajalein Atoll, Marshall Islands). C) Retracted individual exposing upper column with strongly adhesive verrucae. Note the debris (arrow) attached to verrucae (Japanese Archipelago). D) Individual with pointed tentacle tips hosting juvenile *Amphiprion tricintus* (Kwajalein Atoll, Marshall Islands). E) Brownish/ green individual with sparse tentacles and radially striped oral disc (Japanese Archipelago). Photographs by Scott Johnson and Takuma Fuji.

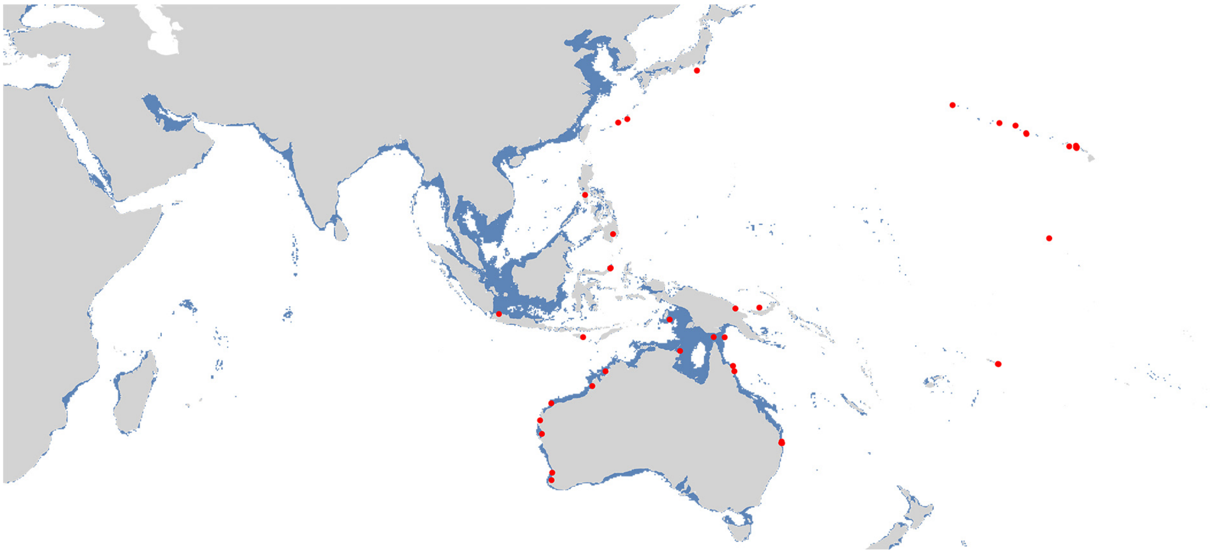

FIGURE 13. Confirmed geographic range of *Radianthus malu* in the Indo-West Pacific. Red dots represent species observations from the Global Biodiversity Information Facility (GBIF). Blue shaded area represents shallow water habitat (60 m bathymetry).

Stichodactyla gigantea **(Forsskål, 1775) (Figure 14; Figure S7)**

Contrary to its name, the "giant carpet" anemone *Stichodactyla gigantea* is not the largest clownfish-hosting anemone species, and not even the largest of the "carpet" anemones in the genus *Stichodactyla*. Although large-bodied, this species rarely reaches 500 mm in oral disc diameter and is generally exceeded in size by *S. mertensii* and *R. magnifica*. This species is characterized by a deeply folded oral disc, which is covered by densely packed tentacles. Tentacles are typically short (10-20 mm in length), thin, and taper to a blunt point (Figure 14, Figure S7). The tapered tentacle tips represent one important diagnostic character to differentiate *S. gigantea* from *S. haddoni, S. mertensii,* and *R. magnifica*. The density and thickness of the tentacles give the anemone a "furry" appearance like a shag carpet. Tentacle color is typically tan but can also be tipped with purple or blue. Some individuals are a vibrant blue or violet color (Figure 14B). Tentacles are most densely packed surrounding the margin of the oral disc, and typically stop just shy of the mouth (Figure 14A; Figure S7D). Tentacles are extremely sticky to the touch and will tear off easily, some always twitching even in calm waters. The column is usually short and can contrast in color with the tentacles. Column color typically ranges from tan to yellow to pink but can also take on brownish-green hues. Longitudinal rows of verrucae occupy the upper portion of the column only, and contrast in color from the surrounding column (Figure 14C). Verrucae are not strongly adherent and do not hold debris. Verrucae color is typically blue, maroon, or purple. The pedal disc and lower portion of column are typically obscured from view and burrowed in sand pockets or reef crevices.

This species occupies calm, shallow-water habitats and may become exposed at low tides. It occupies both sandy and rocky microhabitats. Molecular evidence suggests this species is capable of asexual reproduction (Gatis 2014). Among the three species of clownfish-hosting sea anemones in the genus *Stichodactyla*, *S. gigantea* can be easily differentiated from *S. mertensii* and *S. haddoni* by its tapered tentacle tips, more deeply folded/wavy oral disc, and shallow-water habitat.

Geographically, this species ranges from the Andaman and Nicobar Islands in the Eastern Indian Ocean, throughout the Coral Triangle, Northern Australia, Taiwan and Southern Japanese Archipelago, and as far east as New Caledonia and Vanuatu in the South Pacific and Micronesia in the North Pacific (Figure 15). It does not reach Fiji or the Marshall Islands.

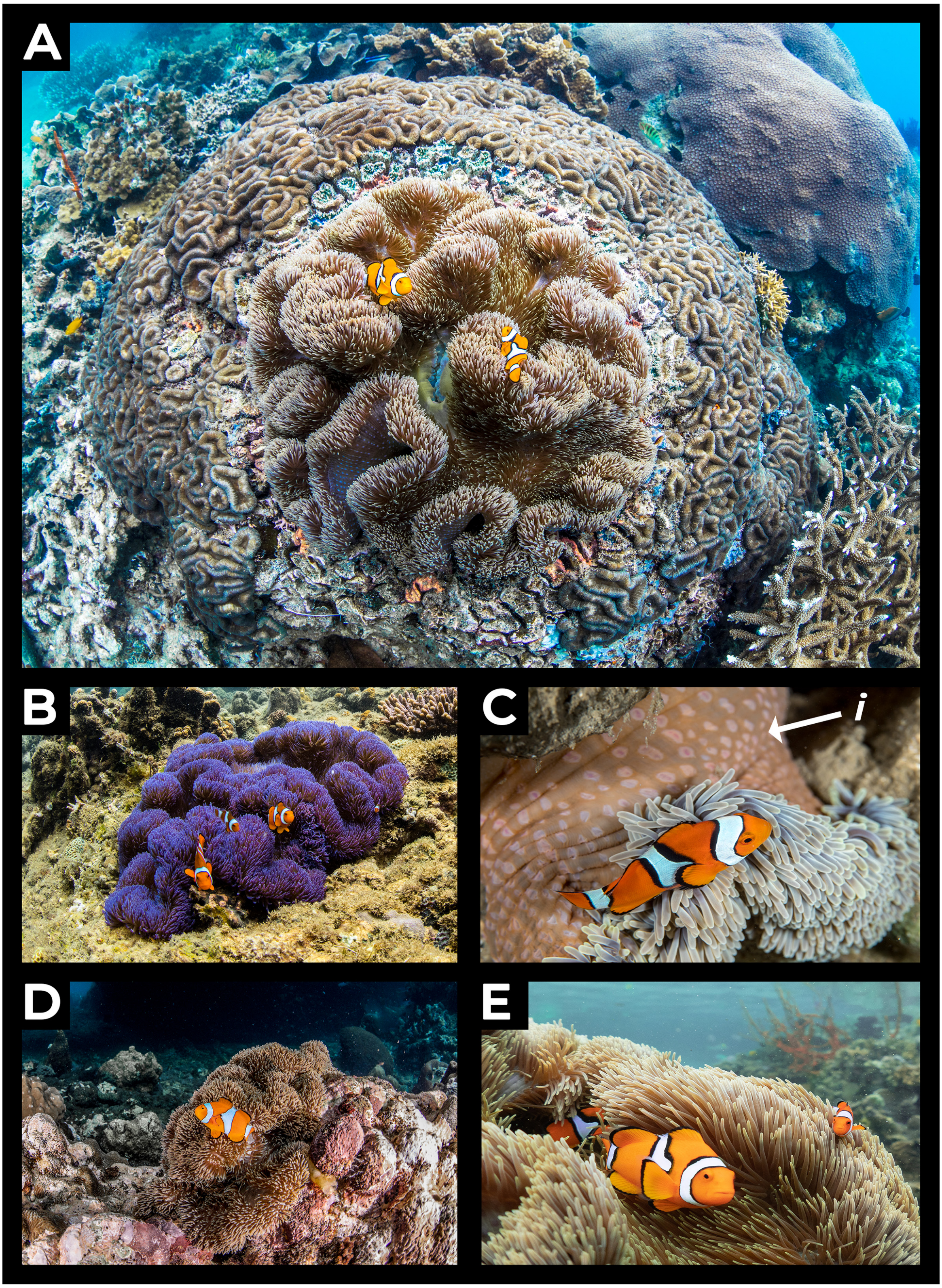

FIGURE 14. Representative images of *Stichodactyla gigantea* encompassing a broad range of geographic and phenotypic variation. A) Wide-angle photograph of *S. gigantea* in shallow water habitat surrounded by stony corals. Note the strongly wavy oral disc and visible mouth (Kimbe Bay, Papua New Guinea). B) Individual with rare vibrant blue/violet body coloration (Kimbe Bay, Papua New Guinea). C) Macro photograph of *S. gigantea* column, tentacles, and verrucae. Note the thin tentacles, slightly tapered tentacle tips, and verrucae (arrow) that contrast in color with surrounding column (Kimbe Bay, Papua New Guinea. D) Common tan colored individual (Kimbe Bay, Papua New Guinea). E) Macro photograph of *S. gigantea* tentacles highlighting tapered tentacle tips (Palawan, Philippines). Photographs by Morgan Bennett-Smith.

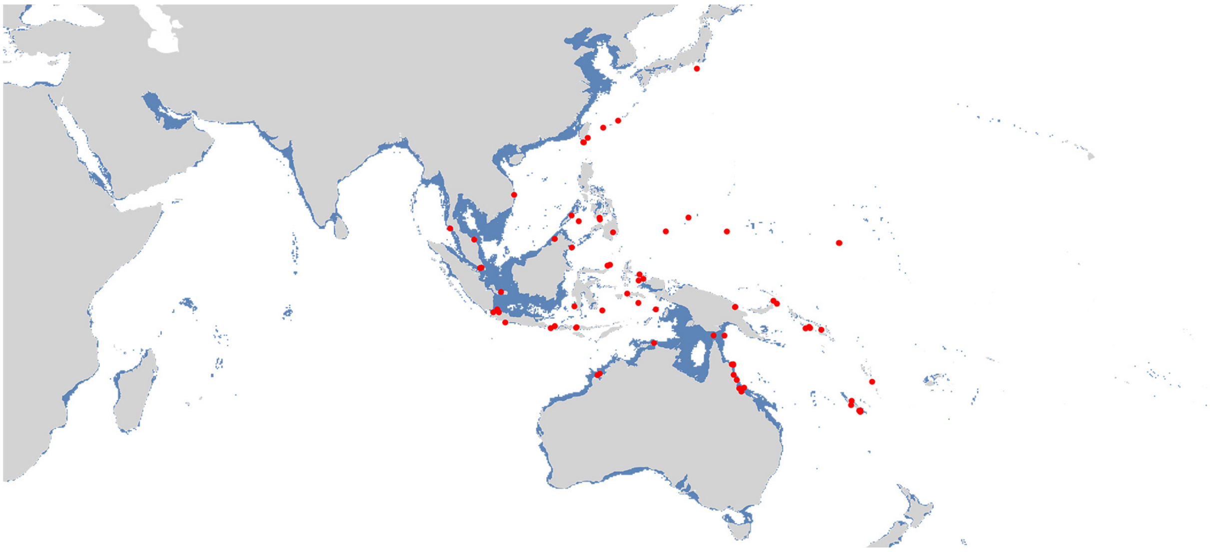

FIGURE 15. Confirmed geographic range of *Stichodactyla gigantea* in the Indo-West Pacific. Red dots represent species observations from the Global Biodiversity Information Facility (GBIF). Blue shaded area represents shallow water habitat (60 m bathymetry).

Stichodactyla haddoni (Saville-Kent, 1893) (Figure 16; Figure S8)

Haddon's carpet anemone, *Stichodactyla haddoni*, is a sand dwelling species and the most heavily collected carpet sea anemone in the ornamental aquarium trade (Figure 16; Figure S8). Although not small (potentially reaching up to 800 mm in oral disc diameter), the overall body size of this species is smaller than the other clownfish-hosting species in the genus *Stichodactyla*, making them more suited for home aquaria than their congenrs. The tentacles of this species are short, rounded, and globular in shape. They are also densely packed, leaving little of the oral disc visible. Endocoelic tentacles are often white, giving the anemone a radially striped pattern (Figure 16A-E). This pattern is common in *S. haddoni*, but also seen occasionally in *S. mertensii* and thus should not be used as a diagnostic character for this species. The most important diagnostic character for *S. haddoni* is the enlarged exocoelic tentacles that protrude from the margin of oral disc (Figure 16A). These tentacles are typically 2-3 times longer in total length than endocoelic tentacles. Tentacle color is typically various shades of dull green, tan, and brown, but can also be bright red, blue, or green (Figure 16; Figure S8). The brightest individuals are typically targeted by the aquarium trade.

The oral disc of this species is flared widely and often lays flat over the surrounding sandy substrate (Figure 16; Figure S8). This species can also form deep folds in the oral disc similar to *S. gigantea*, but in general, the oral disc of *S. haddoni* is much more circular in shape than those of any other carpet anemone species (Figure 16; Figure S8). The column of *S. haddoni* is smooth, typically pale, and lacks the conspicuous verrucae seen in other carpet anemones (Figure 16B; Figure S8B, E). The combination of enlarged exocoelic tentacles and lack of conspicuous verrucae are the two most important characters for identifying *S. haddoni* in the field. As a sand-dwelling species, the column and pedal disc are burrowed deeply in the sediment and typically obscured from view (Figure 16; Figure S8). Upon disturbance, this species can retract entirely into the sand. *Stichodactyla haddoni* is often found on calm sand flats and seagrass beds away from fore reef habitats, at depth rangin from 0.5-30 m. This species is only found as solitary anemones (it does not form aggregations) and it is expected to sexually reproduce only.

Stichodactyla haddoni is widespread throughout the Indo-West Pacific, and ranges from the Red Sea, throughout the Indian ocean, Coral Triangle, and into the Central Pacific at least to the Marshall Islands (Figure 17). This species extends north to the Japanese Archipelago, and south to Australia and South Africa.

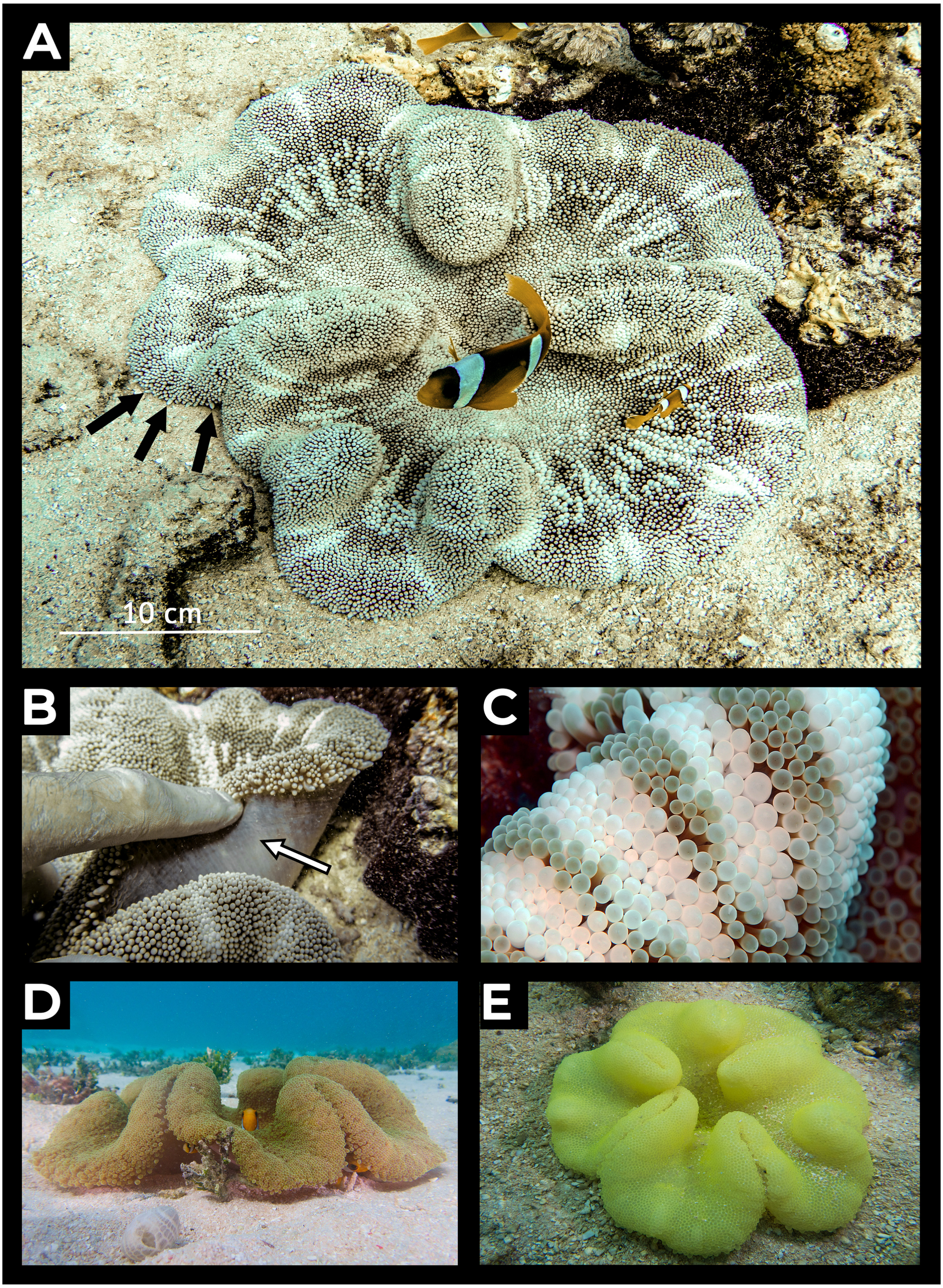

FIGURE 16. Representative images of *Stichodactyla haddoni* encompassing a broad range of geographic and phenotypic variation. A) Tan/olive individual in sandy microhabitat with enlarged exocoelic tentacles (black arrows; Saudi Arabia, Red Sea). B) Exposed upper column revealing pale color and lack of distinctive verrucae (white arrow; Saudi Arabia, Red Sea). C) Macro photograph of striped endocoelic tentacles. Note the rounded globular shape (Kwajalein Atoll, Marshall Islands). D) Individual in typical microhabitat (Majuro Atoll, Marshall Islands). E). Bright yellow individual likely experiencing bleaching stress (Majuro Atoll, Marshall Islands). Photographs by Morgan Bennett-Smith and Benjamin M. Titus.

FIGURE 17. Confirmed geographic range of *Stichodactyla haddoni* in the Indo-West Pacific. Red dots represent species observations from the Global Biodiversity Information Facility (GBIF). Blue shaded area represents shallow water habitat (60 m bathymetry).

Stichodactyla mertensii Brandt, 1835 (Figure 18; Figure S9)

Merten's carpet anemone, *Stichodactyla mertensii*, is among the largest sea anemone species in the world (clownfish-host or otherwise), regularly reaching oral disc diameters of one meter (Figure 18; Figure S9). *Stichodactyla mertensii* has tentacles that are variable in length, with the inner tentacles around the mouth considerably longer (50-80 mm) than marginal ones (6-12 mm; Figure 18C). This difference in tentacle morphology is unique among the carpet anemones and serves as one diagnostic character that can be used to differentiate *S. mertensii* from *S. haddoni* or *S. gigantea.* Regardless of length, all tentacles are digitiform and otherwise alike (Figure 18B). Tentacles are less densely packed than *S. haddoni*, leaving the oral disc more exposed in some individuals. Tentacle color is almost exclusively browns and greens. Endocoelic tentacles can form radial striping patterns as in *S. haddoni* (Figure 18E). The column is typically pale in color and contains bright and highly contrasting verrucae in longitudinal rows that are orange, red, and purple. Spots that are similarly colored to the verrucae extend the entire length of the column; this is unique among the carpet anemone host species (Figure S9B).

This species is the only carpet anemone to be found draped prominently over hard substrate on fore reef environments (Figure 18; Figure S9). It attaches its column deeply into crevices in the reef substrate (Figure S9B). Weak column musculature prohibits the anemone from fully retracting. The combination of longer tentacles around the mouth, reddish non-adhesive verrucae, and hard reef microhabitat form three important characters for identifying this species in the field.

Geographically, this species is widespread throughout the Indo-West Pacific. It ranges from the Northern Red Sea, Indian Ocean, Coral Triangle, and into the Central Pacific at least to the Marshall Islands (Figure 19). It is found north into the Japanese Archipelago, south to Australia and Mozambique Channel. Its range in the South Pacific appears to stop at Tonga and does not extend to the Cook Island or French Polynesia.

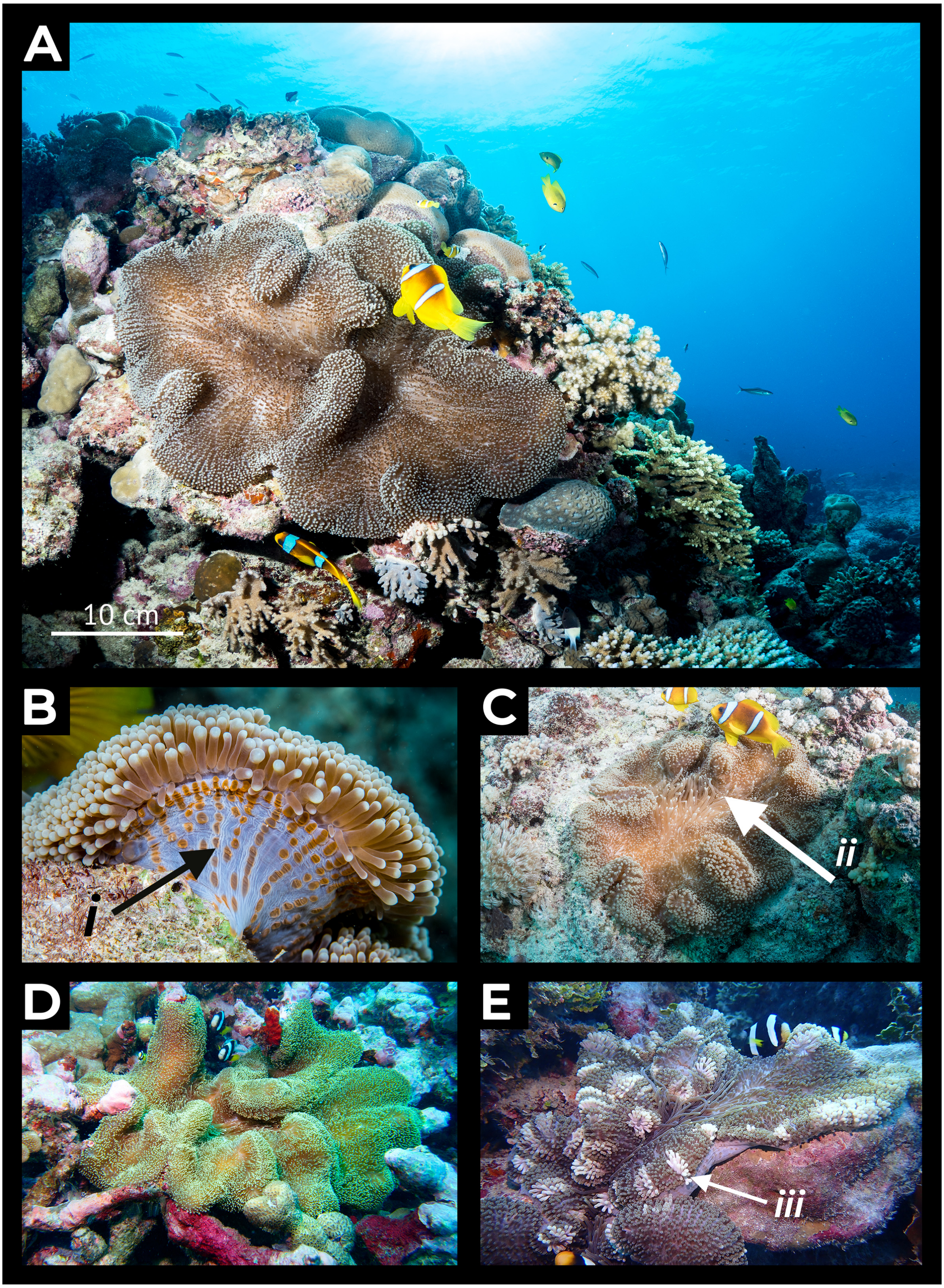

FIGURE 18. Representative images of *Stichodactyla mertensii* encompassing a broad range of geographic and phenotypic variation. A) Wide angle photograph of a brown individual highlighting fore reef habitat (Saudi Arabia, Red Sea). B) Macro photograph of rounded, digitiform tentacles, pale column color, and (i) highly contrasting reddish verrucae (Saudi Arabia, Red Sea). C) Tan individual with (ii) long tentacles surrounding the mouth (Saudi Arabia, Red Sea). D) Green individual draped over hard reef substrate (Fares-Maathodaa, Maldives). E) Partially retracted individual with (iii) endocoelic tentacle striping pattern (Fares-Maathoda, Maldives). Photographs by Morgan Bennett-Smith and Benjamin M. Titus.

FIGURE 19. Confirmed geographic range of *Stichodactyla mertensii* in the Indo-West Pacific. Red dots represent species observations from the Global Biodiversity Information Facility (GBIF). Blue shaded area represents shallow water habitat (60 m bathymetry).

Family Thalassianthidae

Cryptodendrum adhaesivum (Klunzinger, 1877) (Figure 20; Figure S10)

Among the most spectacularly colored and morphologically distinct host anemones, *Cryptodendrum adhaesivum* is hard to misidentify in the field and the only host anemone within the family Thalassianthidae (Figure 20; Figure S10). Commonly referred to as the "pizza anemone" or "adhesive anemone" *C. adhaesivum* bears multiple tentacle types that are highly adhesive (Figure 20B). The outer marginal tentacles are densely packed and bulbous, and contrast strongly with the inner tentacles which are slender and may branch into five or more projections, giving the anemone an appearance that resembles a pizza with a thick crust (Figure 20; Figure S10). Marginal and inner tentacles may be uniformly colored or highly contrasting in color. Immediately adjacent to the bulbous marginal tentacles are a row of branched nematospheres (spherical modified tentacles co-located with exocoelic tentacles at the oral disc margin; Figure 20B) that attach directly to the oral disc and give the anemone a frilly appearance when exposed. Verrucae are present, non-adhesive, and form longitudinal rows on upper column. Verrucae color is variable and can range from red, purple, or orange that may contrast highly with the column. Oral disc is usually flat and round when expanded (Figure 20A), reaching up to 600 mm in diameter, but may also be wavy when wedged into crevices in the reef (Figure 20C and D).

Cryptodendrum adhaesivum has a broad geographic distribution and is known to occur from the Red Sea, continental Africa in the Western Indian Ocean, throughout the Coral Triangle, North to Japan, and as far east in the South Pacific as the Marquesas (but not making it to Hawaii; Figure 21). This species has a broad depth range and can be found in near-intertidal rocky reef habitats to depths of at least 25 m. On reefs, *C. adhaesivum* always attaches its pedal disc deep within hard stable substrate and is commonly found wedged in boulder fields. The column is never exposed. When disturbed, *C. adhaesivum* will retract rapidly into crevices and holes in the reef. This species has the most rapid contraction of any host anemone species and will completely disappear into the reef matrix.

This species is thought to sexually reproduce only and does not form aggregations of individuals on reefs. Although one of ten documented clownfish hosting anemones, it does not host fish in much of its range and has only ever been documented in association with Clark's anemonefish *Amphiprion clarki* (Figure S10). In the far western and eastern edges of its range, including the Red Sea, Western Indian Ocean, French Polynesia, and Marshall Islands, this species has never been documented hosting clownfishes.

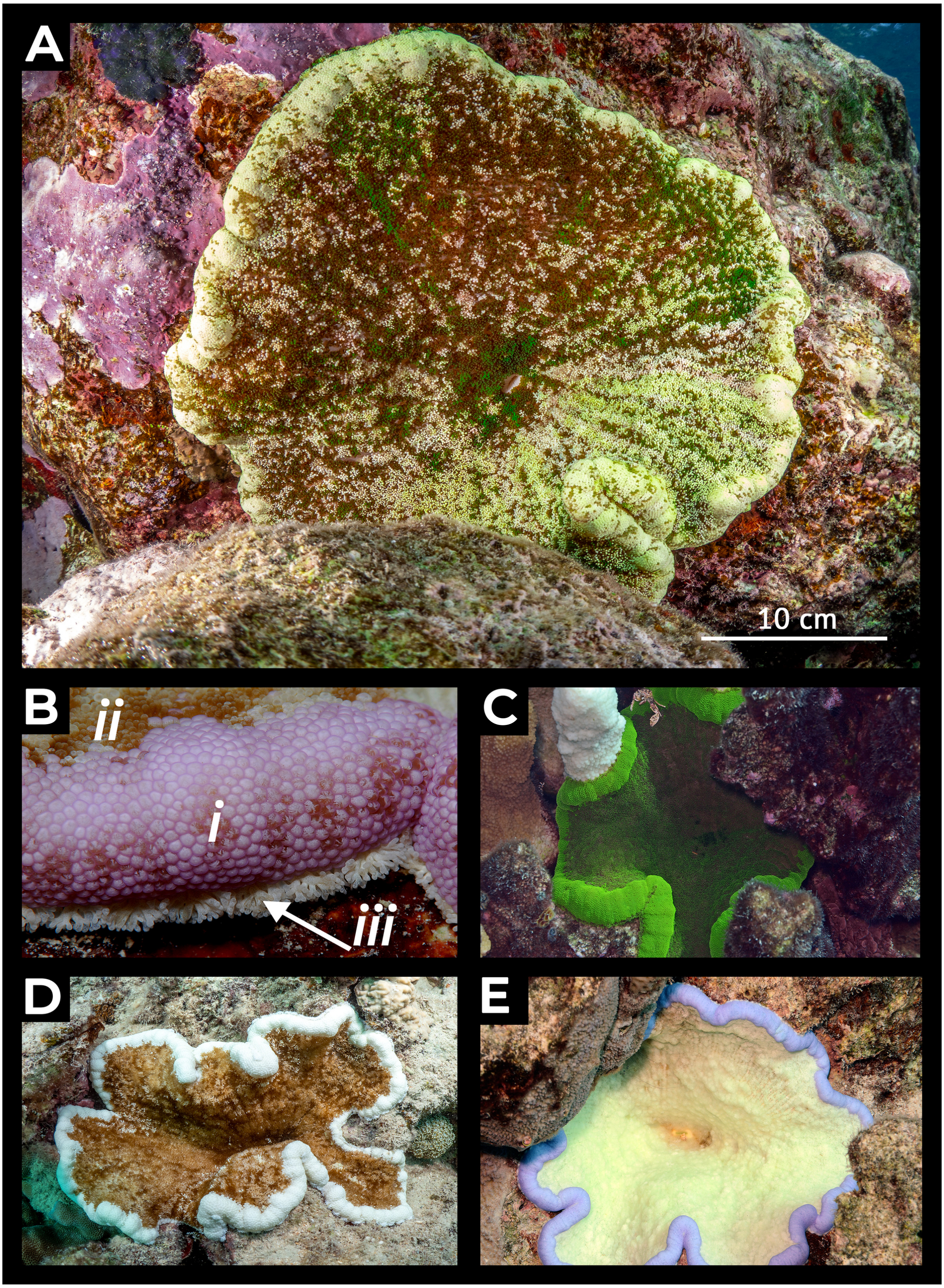

FIGURE 20. Representative images of *Cryptodendrum adhaesivum* encompassing a broad range of geographic and phenotypic variation. A) Wide angle photograph capturing hard substrate microhabitat (Saudi Arabia, Red Sea). B) Macro photograph highlighting distinct tentacle types (*i*) bulbous outer tentacles, (*ii*) branched inner tentacles, and (*iii*) branched fringing nematospheres (Kwajalein Atoll, Marshall Islands). C) Green individual with all tentacles similar in color (Kwajalein Atoll, Marshall Islands). D) Individual with white peripheral tentacles (Saudi Arabia, Red Sea). E) Individual with purple peripheral tentacles (Kwajalein Atoll, Marshall Islands). Photographs by Morgan Bennett-Smith and Scott Johnson.

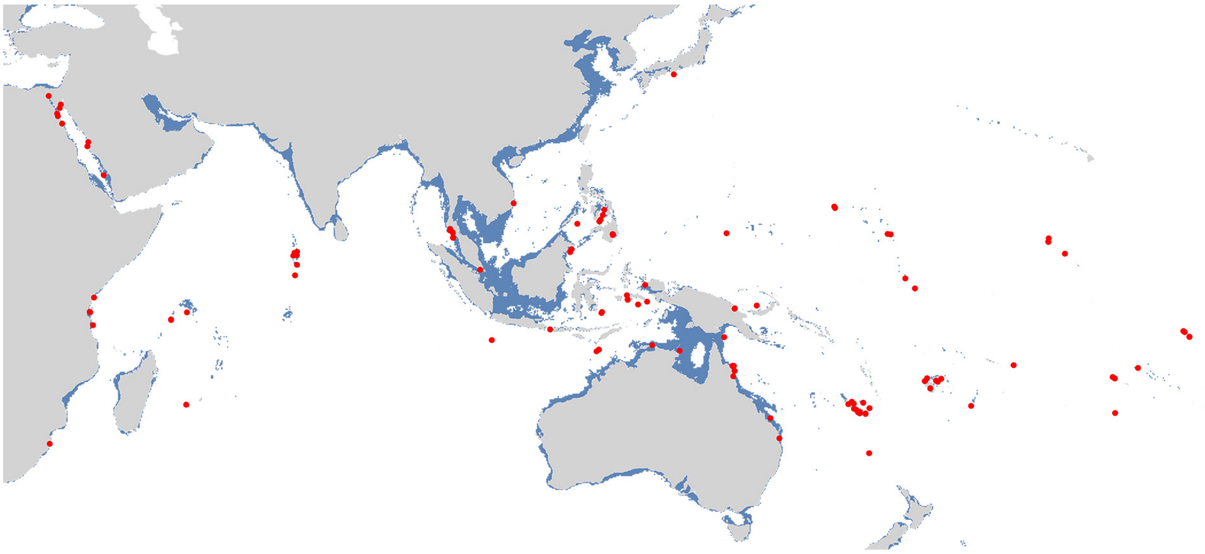

FIGURE 21. Confirmed geographic range of *Cryptodendrim adhaesivum* in the Indo-West Pacific. Red dots represent species observations from the Global Biodiversity Information Facility (GBIF). Blue shaded area represents shallow water habitat (60 m bathymetry).

Acknowledgements

We are grateful to those who contributed photographs of the clownfish-hosting sea anemones used here, especially Scott and Jeanette Johnson, Sara Heim, Takuma Fuji, Richard Smith, and James Reimer. We thank Gustav Paulay, Nicholas Yap, Ricardo Gonzalez-Muñoz, and Marymegan Daly for comments that greatly improved this manuscript. This work was funded by National Science Foundation grant DEB-1934274 to BMT and ER.

References

Abadi, M., Agarwal, A., Barham, P., Brevdo, E., Chen, Z., Citro, C., Corrado, G.S., Davis, A., Dean, J., Devin, M. & Ghemawat, S. (2016) Tensorflow: Large-scale machine learning on heterogeneous distributed systems. arXiv preprint arXiv, 1603.04467. Available from: https://arxiv.org/abs/1603.04467 (accessed 17 June 2024)

Assis, J., Tyberghein, L., Bosch, S., Heroen, V., Serrão, E., De Clerck, O. & Tittensor, D. (2018) Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. *Global Ecology and Biogeography*, 27 (3), 277–284. https://doi.org/10.1111/geb.12693

Barragán, Y., Sánchez, C., Hooker, Y. & Rodríguez, E. (2019) First inventory of sea anemones (Cnidaria: Actiniaria) from La Paz Bay, Southern Gulf of California (Mexico). *Zootaxa*, 4559 (3), 501–549. https://doi.org/10.11646/zootaxa.4559.3.4

Bennett-Smith, M.F., Majoris, J.E., Titus, B.M. & Berumen, M.L. (2021) Clownfish hosting anemones (Anthozoa, Actiniaria) of the Red Sea: new associations and distributions, historical misidentifications, and morphological variability. *Marine Biodiversity Records*, 14 (1), 1–15. https://doi.org/10.1186/s41200-021-00216-6

Bennett-Smith, M.F., Justo, M.S., Berumen, M.L., Peixoto, R. & Titus, B.M. (2022) Novel *in situ* observations of asexual reproduction in the carpet sea anemone, *Stichodactyal mertensii* (Stichodactylidae, Actiniaria). *ZooKeys*, 1103, 57–63. https://doi.org/10.3897/zookeys.1103.84415

Buston, P.M. (2004) Territory inheritance in clownfish. *Proceedings of the Royal Society of London*, Series B: Biological Sciences, 271 (Supplement 4), S252–S254. https://doi.org/10.1098/rsbl.2003.0156

Branconi, R., Barbasch, T.A., Francis, R.K., Srinivasan, M., Jones, G.P. & Buston, P.M. (2020) Ecological and social constraints combine to promote evolution of non-breeding strategies in clownfish. *Communications Biology*, 3 (1), 649. https://doi.org/10.1038/s42003-020-01380-8

Brandt, J.F. (1835) Polypos, acalephas discophoras et siphonophoras, nec non echinodermata continens. *Prodromus Descriptionis Animalium AB H. Mertensio in Orbis Terrarum Circumnavigatione Observatorum.* Sumptibus Academiae, Petropoli, 75

pp.
GBIF (2023) Derived dataset GBIF.org. 30 March 2023. Filtered export of GBIF occurrence data. https://doi.org/10.15468/dd.u2yyzx
Duchassaing de Fombressin, P. & Michelotti, G. (1864) *Supplément au mémoire sur les Coralliaires des Antilles*. Imprimerie Royale, Turin, 112 pp. https://doi.org/10.5962/bhl.title.105196
Dunn, D.F. (1981) The clownfish sea anemones: Stichodactylidae (Coelenterata: Actiniaria) and other sea anemones symbiotic with pomacentrid fishes. *Transactions of the American Philosophical Society*, 71 (1), 3–115. https://doi.org/10.2307/1006382
England, K.W. (1987) *Certain Actiniaria (Cnidaria, Anthozoa) from the Red Sea and tropical Indo-Pacific Ocean*. *Bulletin of the British Museum (Natural History)*, 53, 205–292.
England, K.W. (1988) Redefinitions and systematics of *Heteractis aurora*, the genera *Heteractis* and *Radianthus*, and the family Heteractidae (Cnidaria: Actinaria). *Indo-Malayan Zoology*, 5 (1), 45–55.
Ehrenberg, C.G. (1834) Beitrage zur physiologischen Kenntniss der Corallenthiere im allgemeinen, und besonders des rothen Meeres, nebst einem Versuche zur physiologischen Systematik derselben. *Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin*, 1, 225–380.
Fautin, D.G. & Allen, G.R. (1992) *Field guide to anemonefishes and their host sea anemones*. Western Australian Museum, Perth, 78 pp.
Fautin, D.G. (2016) Catalog to families, genera, and species of orders Actiniaria and Corallimorpharia (Cnidaria: Anthozoa). *Zootaxa*, 4145 (1), 1–449. https://doi.org/10.11646/zootaxa.4145.1.1
Forsskål, P. (1775*) Descriptiones Animalium.* Mölleri, Hauniae, 164 pp.
Gatins, R. (2014) *Fine-scale population structure of two anemones (Stichodactyla gigantea and Heteractis magnifica) in Kimbe Bay, Papua New Guinea*. Master's Thesis, King Abdullah University of Science and Technology, Thuwal. [published online]
Haguenauer, A., Zuberer, F., Siu, G., Cortese, D., Beldade, R. & Mills, S.C. (2021) Deep heat: A comparison of water temperature, anemone bleaching, anemonefish density and reproduction between shallow and mesophotic reefs. *Fishes*, 6 (3), 37. https://doi.org/10.3390/fishes6030037
Haddon, A.C. & Shackleton, A.M. (1893) Description of some new species of Actiniaria from Torres Straits*. Scientific Proceedings of the Royal Dublin Society*, 8 (1), 116–131.
Hill, R. & Scott, A. (2012) The influence of irradiance on the severity of thermal bleaching in sea anemones that host anemonefish. *Coral Reefs*, 31, 273–284. https://doi.org/10.1007/s00338-011-0848-x
Huebner, L.K., Dailey, B., Titus, B.M., Khalaf, M. & Chadwick, N.E. (2012) Host preference and habitat segregation among Red Sea anemonefish: effects of sea anemone traits and fish life stages. *Marine Ecology Progress Series*, 464, 1–15. https://doi.org/10.3354/meps09964
Jones, G.P., Srinivasan, M., Galbraith, G.F., Berumen, M.L. & Planes, S. (2022) Saving Nemo: Extinction Risk, Conservation Status, and Effective Management Strategies for Anemonefishes. *In*: *Evolution, Development and Ecology of Anemonefishes*. CRC Press, Boca Raton, Florida, pp. 285–298. https://doi.org/10.1201/9781003125365-30
Kashimoto, R., Tanimoto, M., Miura, S., Satoh, N., Laudet, V. & Khalturin, K. (2022) Transcriptomes of giant sea anemones from Okinawa as a tool for understanding their phylogeny and symbiotic relationships with anemonefish. *Zoological Science*, 39 (4), 1–15. https://doi.org/10.2108/zs210111
Klunzinger, C.B. (1877) *Die Korallthiere des rothen Meeres. Erster Theil: Die Alcyonarien und Malacodermen.* Gutmann'schen Buchhandlung, Berlin, 98 pp.
Laudet, V. & Ravasi, T. (Eds.) (2022) *Evolution, development and ecology of anemonefishes: model organisms for marine science*. CRC Press, Boca Raton, Florida, 328 pp. https://doi.org/10.1201/9781003125365
Litsios, G., Sims, C.A., Wüest, R.O., Pearman, P.B., Zimmermann, N.E. & Salamin, N. (2012) Mutualism with sea anemones triggered the adaptive radiation of clownfishes. *BMC Evolutionary Biology*, 12 (1), 1–15. https://doi.org/10.1186/1471-2148-12-212
Marcionetti, A. & Salamin, N. (2023) Insights into the genomics of clownfish adaptive radiation: the genomic substrate of the diversification. *Genome Biology and Evolution*, 15 (7), evad088. https://doi.org/10.1093/gbe/evad088
Neave S.A. (1940) *Nomenclator Zoologicus*. *Vol. III*. Zoological Society of London, London, 1065 pp.
Quoy, J.R.C. & Gaimard, J.P. (1833) *Voyage de Découvertes de l'Astrolabe Exécuté par Ordre du Roi, Pendant les Années 1826–1827–1828–1829, sous le Commandement de M. J. Dumont D'Urville*. J. Tastu, Paris, 390 pp.
R Core Team (2022) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna. Available from: https://www.R-project.org/ (accessed 17 June 2024)
Rodríguez, E., Fautin, D. & Daly, M. (2024) World List of Actiniaria. Available from: https://www.marinespecies.org/actiniaria

(accessed 7 March 2024)
https://doi.org/10.14284/568
Rodríguez, E., Titus, B.M. & Lauretta, D. (2024) Case 3885: *Priapus giganteus* Forsskål, 1775 (currently *Stichodactyla gigantea*) (Cnidaria, Actiniaria): proposed conservation of prevailing usage of the specific names by the designation of a non-topotypic neotype for *Priapus giganteus*. *Bulletin of Zoological Nomenclature*. [in press]
Rodríguez, E., Barbeitos, M.S., Brugler, M.R., Crowley, L.M., Grajales, A., Gusmão, L., Häussermann, V., Reft, A. & 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 (5), e96998.
https://doi.org/10.1371/journal.pone.0096998
Rowlett, J. (2020) *Indo-Pacific Corals*. Independently Published, Rowlett, 809 pp.
Rüppell, E. & Leuckart, F.S. (1828) *Atlas zu der Reise im Nördlichen Afrika von Eduard Rüppell, Neue Wirbellose Thiere des Rothen Meers.* Heinr. Ludw. Brvnner, Frankfurt am Main, 47 pp.
Saville-Kent, W. (1893) *The Great Barrier Reef of Australia; its Products and Potentialities.* W. H. Allen & Co., London, 387 pp.
https://doi.org/10.5962/bhl.title.58247
Shick, J.M. (1991) A Functional Biology of Sea Anemones. *In*: Calow, P. (Ed.), *Functional Biology Series*. Chapman & Hall, London, New York, Tokyo, Melbourne and Madras, pp. 1–395.
https://doi.org/10.1007/978-94-011-3080-6
Steinberg, R.K., Dafforn, K.A., Ainsworth, T. & Johnston, E.L. (2020) Know thy anemone: A review of threats to octocorals and anemones and opportunities for their restoration. *Frontiers in Marine Science*, 7, 590.
https://doi.org/10.3389/fmars.2020.00590
Steinberg, R.K., Ainsworth, T.D., Moriarty, T., Bednarek, T., Dafforn, K.A. & Johnston, E.L. (2022) Bleaching Susceptibility and Resistance of Octocorals and Anemones at the World's Southern-Most Coral Reef. *Frontiers in Physiology*, 13, 726.
https://doi.org/10.3389/fphys.2022.804193
Scott, A. & Hoey, A.S. (2017) Severe consequences for anemonefishes and their host sea anemones during the 2016 bleaching event at Lizard Island, Great Barrier Reef. *Coral Reefs*, 36 (3), 873–873.
https://doi.org/10.1007/s00338-017-1577-6
Titus, B.M., Benedict, C., Laroche, R., Gusmão, L.C., Van Deusen, V., Chiodo, T., Meyer, C.P., Berumen, M.L., Bartholomew, A., Yanagi, K., Reimer, J.D., Fujii, T., Daly, M. & Rodríguez, E. (2019) Phylogenetic relationships among the clownfish-hosting sea anemones. *Molecular Phylogenetics and Evolution*, 139, 106526.
https://doi.org/10.1016/j.ympev.2019.106526
Titus, B.M., Laroche, R., Rodríguez, E., Wirshing, H. & Meyer, C.P. (2020) Host identity and symbiotic association affects the taxonomic and functional diversity of the clownfish-hosting sea anemone microbiome. *Biology Letters*, 16 (2), 20190738.
https://doi.org/10.1098/rsbl.2019.0738
Wäldchen, J. & Mäder, P. (2018) Machine learning for image based species identification. *Methods in Ecology and Evolution*, 9 (11), 2216–2225.
https://doi.org/10.1111/2041-210X.13075
Yap, N.W.L., Mitchell, M.L., Quek, Z.B.R., Tan, R., Tan, K.S. & Huang, D. (2023) Taxonomy and molecular phylogeny of the sea anemone *Macrodactyla* (Haddon, 1898) (Cnidaria, Actiniaria), with a description of a new species from Singapore. *Zoological Studies*, 62, 1–25.