

Phylogenomics, Origin, and Diversification of Anthozoans (Phylum Cnidaria)

CATHERINE S. MCFADDEN^{1,*}, ANDREA M. QUATTRINI^{1,2}, MERCER R. BRUGLER^{3,4,5}, PETER F. COWMAN^{6,7}, LUISA F. DUEÑAS⁸, MARCELO V. KITAHARA^{9,10}, DAVID A. PAZ-GARCÍA¹¹, JAMES D. REIMER^{12,13}, AND ESTEFANÍA RODRÍGUEZ³

¹Department of Biology, Harvey Mudd College, 1250 N. Dartmouth Ave., Claremont, CA 91711 USA; ²Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, USA; ³Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA; ⁴Biological Sciences Department, NYC College of Technology, City University of New York, 285 Jay Street, Brooklyn, NY 11201, USA; ⁵Department of Natural Sciences, University of South Carolina Beaufort, 801 Carteret Street, Beaufort, SC 29902, USA; ⁶ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia; ⁷Biodiversity and Geosciences Program, Museum of Tropical Queensland, Queensland Museum, Townsville, QLD 4810, Australia; ⁸Departamento de Biología, Facultad de Ciencias, Universidad Nacional de Colombia-Sede Bogotá, Carrera 30 No.45-03 Edificio 421, Bogotá, D.C., Colombia; ⁹Department of Marine Science, Federal University of São Paulo, Santos, SP 11070-100 Brazil; ¹⁰Centre for Marine Biology, University of São Paulo, São Sebastião, SP 11612-109 Brazil; ¹¹CONACYT-Centro de Investigaciones Biológicas del Noroeste (CIBNOR). Laboratorio de Necton y Ecología de Arrecifes. Calle IPN 195, Col. Playa Palo de Santa Rita Sur, 23096 La Paz, B.C.S., México; ¹²Molecular Invertebrate Systematics and Ecology Laboratory, Department of Marine Science, Chemistry, and Biology, Faculty of Science, University of the Ryukyus, 1 Senbaru, Nishihara, Okinawa 903-0213, Japan; and ¹³Tropical Biosphere Research Center, University of the Ryukyus, 1 Senbaru, Nishihara, Okinawa 903-0213, Japan

*Correspondence to be sent to: Department of Biology, Harvey Mudd College, 1250 N. Dartmouth Ave., Claremont, CA 91711, USA; E-mail: mcfadden@g.hmc.edu

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Abstract.—Anthozoan cnidarians (corals and sea anemones) include some of the world's most important foundation species, capable of building massive reef complexes that support entire ecosystems. Although previous molecular phylogenetic analyses have revealed widespread homoplasy of the morphological characters traditionally used to define orders and families of anthozoans, analyses using mitochondrial genes or rDNA have failed to resolve many key nodes in the phylogeny. With a fully resolved, time-calibrated phylogeny for 234 species constructed from hundreds of ultraconserved elements and exon loci, we explore the evolutionary origins of the major clades of Anthozoa and some of their salient morphological features. The phylogeny supports reciprocally monophyletic Hexacorallia and Octocorallia, with Ceriantharia as the earliest diverging hexacorals; two reciprocally monophyletic clades of Octocorallia; and monophyly of all hexacorals orders with the exception of the enigmatic sea anemone *Relicanthus daphneae*. Divergence dating analyses place Anthozoa in the Cryogenian to Tonian periods (648–894 Ma), older than has been suggested by previous studies. Ancestral state reconstructions indicate that the ancestral anthozoan was a solitary polyp that had bilateral symmetry and lacked a skeleton. Colonial growth forms and the ability to precipitate calcium carbonate evolved in the Ediacaran (578 Ma) and Cambrian (503 Ma) respectively; these hallmarks of reef-building species have subsequently arisen multiple times independently in different orders. Anthozoans formed associations with photosymbionts by the Devonian (383 Ma), and photosymbioses have been gained and lost repeatedly in all orders. Together, these results have profound implications for the interpretation of the Precambrian environment and the early evolution of metazoans. [Bilateral symmetry; coloniality; coral; early metazoans; exon capture; Hexacorallia; Octocorallia photosymbiosis; sea anemone; ultraconserved elements.]

Anthozoan cnidarians (e.g., corals, sea anemones, and their relatives, Fig. 1) are an ecologically important and morphologically diverse clade of metazoans that occur worldwide in all marine habitats. They are among the oldest clades of animals (Erwin et al. 2011; Quattrini et al. 2020) and include some of the ocean's most important foundation species. Key morphological innovations that have led to their ecological success throughout the Phanerozoic include a modular, colonial growth form; the ability to precipitate a skeleton of crystalline aragonite or calcite; and the establishment of symbioses with photosynthetic dinoflagellates. When combined, these traits have allowed anthozoans to create massive biogenic structures that support entire reef-based ecosystems in both shallow and deep waters (Freiwald and Roberts 2005; Roberts et al. 2006). Yet the clade also includes ecologically important and diverse groups that lack one or all of these key traits, exemplified by the solitary, soft-bodied sea anemones. Studying their origin and diversification can help us to better

understand the evolutionary persistence of one of the earliest diverging groups of animals and shed additional light on the Precambrian world and the evolution of Metazoa.

Although textbooks often portray Cnidaria as a phylum characterized by radial symmetry, all anthozoan polyps exhibit bilateral symmetry, at least internally, either as adults or in earlier developmental stages (Manuel 2009; Gonçalves 2016; Genikhovich and Technau 2017). Whether or not bilateral symmetry is an ancestral trait in Cnidaria that is shared with Bilateria has profound implications for understanding the evolution of a feature that defines the vast majority of metazoans (Erwin 2020). The bilaterality of anthozoan polyps arises from the internal arrangement and developmental sequence of mesenteries (radial tissue sheets extending from the body wall to the pharynx), and also from the lateral compression of the pharynx. The numbers and arrangement of these mesenteries and other soft-tissue characters such as

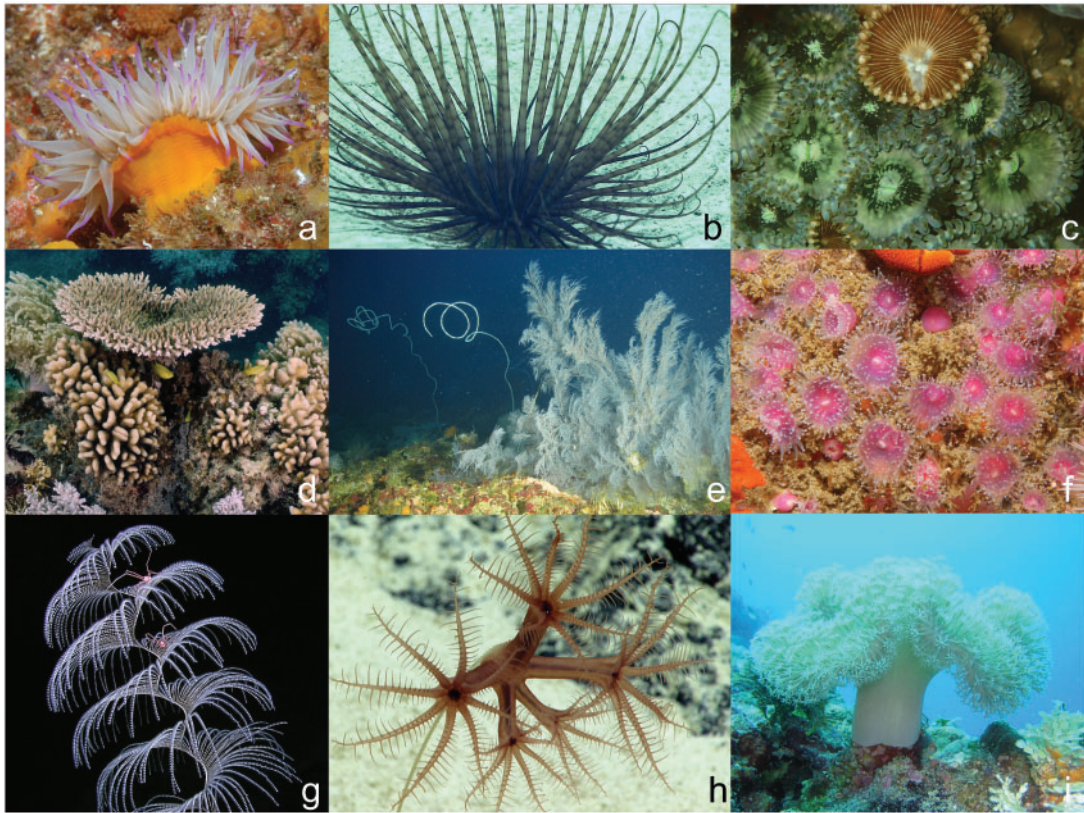


FIGURE 1. Representative anthozoans. a) *Pseudactinia* sp. (Actiniaria, true anemones); b) Ceriantharia (tube anemones); c) *Zoanthus giganteus* and *Palythoa heliodiscus* (Zoantharia, colonial anemones); d) *Acropora* sp. and *Pocillopora* sp. (Scleractinia, stony corals); e) *Stichopathes lutkeni* and *Plumapathes pennacea* (Antipatharia, black corals); f) *Corynactis* sp. (Corallimorpharia, mushroom anemones); g) *Iridogorgia* sp. (Alcyonacea, gorgonians); h) *Umbellula* sp. (Pennatulacea, sea pens); i) *Sarcophyton* sp. (Alcyonacea, soft corals). Photos by B. Pictou (a, f); J.D. Reimer (c); M.V. Kitahara (d); C.S. McFadden (i); or courtesy of NOAA Office of Ocean Exploration and Research (b, g, h) and Flower Garden Banks National Marine Sanctuary/UNCW-UVP (e).

tentacles, along with skeletal morphology and colony architecture, are the primary morphological characters that have traditionally been used for taxonomy and systematics of Anthozoa (Fautin and Mariscal 1991; Daly et al. 2007). Molecular phylogenetic studies have revealed widespread homoplasy in these traits and polyphyly at the ordinal, subordinal, and family levels within the class (e.g., Daly et al. 2003, 2008; Sinniger et al. 2005; McFadden et al. 2006; Fukami et al. 2008; Kitahara et al. 2010; Rodríguez et al. 2012, 2014; Brugler et al. 2013; Bo et al. 2018; Poliseño et al. 2020), and consequently deep flaws in our understanding of phylogenetic relationships and character evolution in Anthozoa.

Phylogenies reconstructed using rDNA (Berntson et al. 1999; Won et al. 2001) or complete mitochondrial genomes (Park et al. 2012; Kayal et al. 2013; Xiao et al. 2019) have provided conflicting evidence for such important inferences as the monophyly of Anthozoa, as well as the reciprocal monophyly of Hexacorallia and Octocorallia and the position of the early-diverging Ceriantharia (tube anemones) relative to those two clades (Stampar et al. 2014, 2019). Molecular phylogenetic analyses have been unable to resolve the basal relationships within Octocorallia (McFadden et al. 2006), and have offered weak or conflicting evidence for the

monophyly of and relationships among the recognized orders of Hexacorallia (Daly et al. 2003; Medina et al. 2006; Rodríguez et al. 2014; Xiao et al. 2019). Inferences about the evolution of morphological and other key traits within Anthozoa have been hindered not just by poor resolution and conflicting evidence of crucial nodes but also by limited taxon sampling. Recent phylogenomic studies have greatly expanded the numbers of loci used to address deep phylogenetic relationships within Cnidaria (Zapata et al. 2015; Kayal et al. 2018) but have been taxon-sparse, omitting entire orders.

Quattrini et al. (2020) recently published a robust, fossil-calibrated phylogeny for 234 anthozoans representing all orders and a majority of families (Table 1) using ultraconserved elements (UCEs) and exon loci captured with a targeted-enrichment approach (Faircloth et al. 2012; Quattrini et al. 2018). They addressed skeletal evolution in the group across paleoclimate conditions and geologic time. Here, we use the time-calibrated tree reconstructed in that study to explore the evolutionary history of Anthozoa in greater depth, focusing on the origins of major clades and the gains and losses of key morphological innovations, including bilateral symmetry, coloniality, and the acquisition of photosymbionts.

TABLE 1. Extant orders of Anthozoa and their defining morphological characters.

	Order	Common name	Families (# seq/n)	Polyp symmetry	Growth form	Skeleton	Mean Age Ma (95% HPD)
Hexacorallia	Ceriantharia	Tube anemones	3/3	Bilateral	Solitary	None	409 (283–534)
	Zoantharia	Colonial anemones	8/9	Bilateral	Colonial ^a	None ^b	436 (336–531)
	Actiniaria	True anemones	19/51	Bilateral, biradial	Solitary ^c	None	513 (424–608)
	Antipatharia	Black corals	4/7	Bilateral	Colonial	Scleroprotein	321 (249–407)
	Corallimorpharia	Mushroom anemones	3/4	Biradial	Solitary	None	359 (282–442)
Octocorallia	Scleractinia	Stony corals	14/33	Biradial	Solitary, colonial	Aragonite ^d	383 (324–447)
	Alcyonacea	Soft corals, sea fans, gorgonians	34/39	Bilateral	Colonial ^a	Calcite, protein (gorgonin) or none ^e	578 (483–685)
	Pennatulacea	Sea pens	7/14	Bilateral	Colonial	Calcite or none	329 (259–399)
	Heliopora	Blue corals	2/2	Bilateral	Colonial	Aragonite	155 (136–190)

n = number of families in order; # seq = number of families included in this study. Mean age of crown groups estimated from divergence dating analyses (HPD = highest posterior density interval).

^aOne or a few exceptions.

^bA few deep-sea species have a proteinaceous skeleton.

^cFor a possible exception see Häussermann and Försterra (2003).

^dOne species with a bimineralic (aragonite, calcite) skeleton (Stolarski et al. 2021).

^eOccasionally aragonite in axis or holdfast.

MATERIALS AND METHODS

As described in detail in Quattrini et al. (2020), phylogenies were constructed from 50% and 75% concatenated data matrices for 1729 UCE and exon loci sequenced using a target-enrichment approach. Trees generated using maximum likelihood (RAxML v8, Stamatakis 2014; including hexacorals and octocorals separately), Bayesian (ExaBayes, Aberer et al. 2014), and species tree (ASTRAL III, Zhang et al. 2018) approaches were congruent at all deeper nodes but varied in support values (Supplementary Table S1 available on Dryad at <https://doi.org/10.5061/dryad.d51c5b00j>). The tree produced by the RAxML analysis of the 50% data matrix (Fig. 2) had the highest support values and a topology that reflected the consensus across analyses and was therefore chosen for divergence dating (Quattrini et al. 2020). All tree and alignment files can be found on figshare (<https://doi.org/10.6084/m9.figshare.12363953>), and the code that generated results used in the present paper are included herein (Supplementary File S1 available on Dryad).

Divergence-Dating Analyses

Divergence-dating analyses were described in detail in Quattrini et al. (2020), but we also include them here. Analyses were conducted in BEAST v 2.5 (Bouckaert et al. 2019) on CIPRES (Miller et al. 2010). We used seven fossil calibration points for dating (Quattrini et al. 2020; Fig. 2, Supplementary Table S2 available on Dryad). Six anthozoan fossils whose identities had been validated from diagnostic morphological characters were selected after confirming that their morphological characters unequivocally matched extant lineages. We also included a calibration at the root of the phylogeny for the earliest confirmed Cambrian fossil of a cnidarian (Hou and Bergström 2003; Li et al. 2007). For each fossil

calibration point, exponential priors were used because they assign the highest probability toward the minimum bound while allowing some probability for an earlier divergence (Ho and Phillips 2009). Exponential priors are preferred over others (e.g., lognormal) particularly when there is an inadequate paleontological record. For each fossil point, the minimum fossil ages were set as offset constraints with mean constraints set at 10–20% of those ages, allowing for a distribution encompassing known minimum and maximum fossil ages as well as a diminished probability toward older ages (following Ho and Phillips 2009, see Supplementary Table S2 available on Dryad).

Other priors for the BEAST analysis included a relaxed clock model to account for varying rates of sequence evolution across the phylogeny along with a Birth–Death tree prior to allow for the probability that a lineage will go extinct. A lognormal distribution on the ucl.d.mean (initial 0.0002, 0-infinity bounds, following Stolarski et al. 2011) and uniform distribution on the ucl.d.stdev (initial 0.1, 0–1 bounds) were used for the relaxed clock models. For the Birth–Death tree prior, uniform priors on the birth rate (initial 1.0, 0–1000 bounds) and death rate (initial 0.5, 0–1 bounds) were set. Following Oliveros et al. (2019), we included a fixed topology (RAxML tree) and 25 clock-like loci as determined using SortaDate (Smith et al. 2018) that were each checked for substitution bias using the Xia saturation test on fully resolved sites (Xia et al. 2003; Xia and Lemey 2009) in DAMBE7 (Xia 2018). Only one locus had saturation bias at fully resolved sites, but this locus was kept in the dating analysis because the RAxML gene tree constructed from this locus (see Quattrini et al. 2020) exhibited low root to tip variation and had discernible information content (Smith et al. 2018). Loci were partitioned and a GTRGAMMA model was applied to each locus separately. Three separate runs of 250M generations were conducted and log and tree files from each run were combined in LogCombiner (10% burnin). The combined log file was assessed for convergence

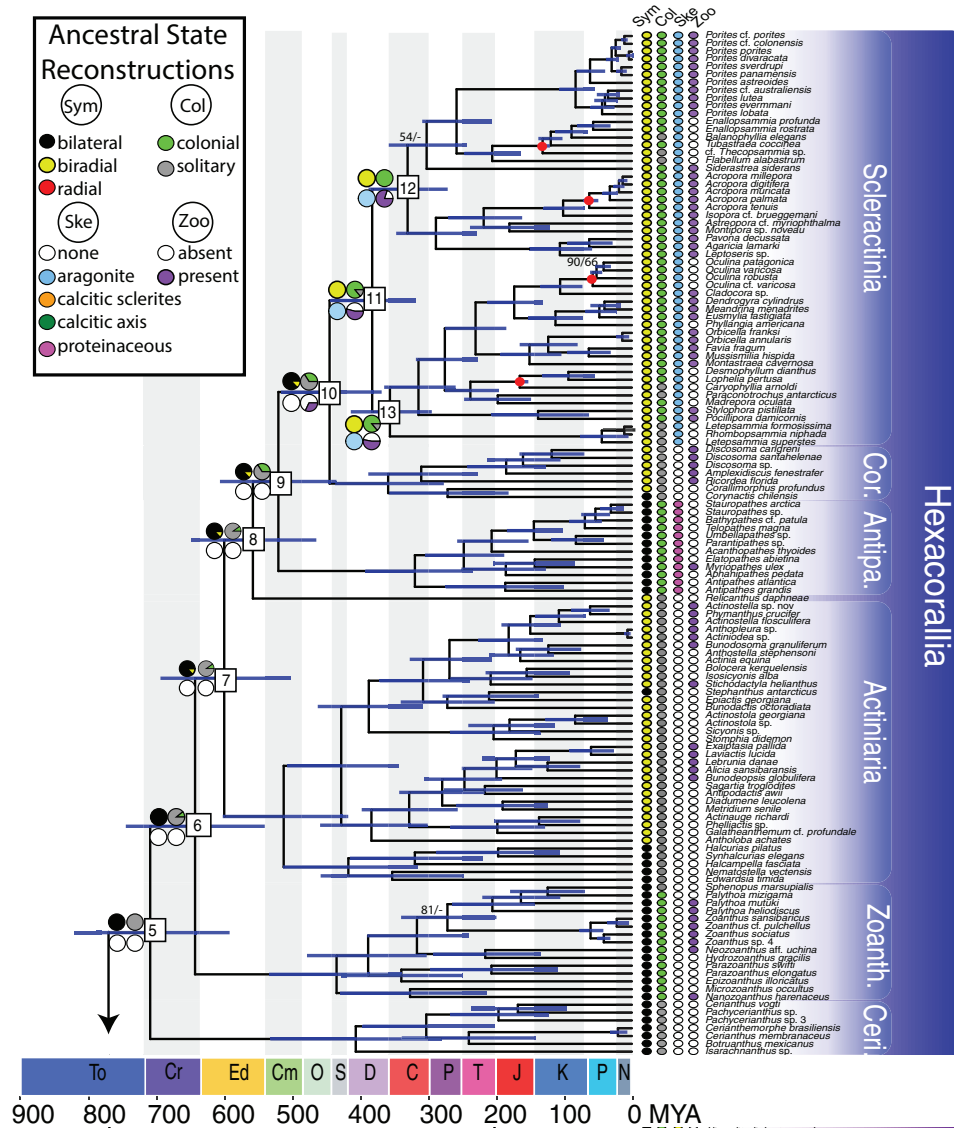


FIGURE 2. Maximum likelihood tree for Anthozoa based on 933 UCE and exon loci (RaxML, 50% data matrix). Tree is scaled to time (million years ago) and rooted to Medusozoa. Bootstrap support was > 95% at nodes in one or both of the phylogenies constructed with the 50% or 75% data matrices, unless indicated (b.s. support from 50/75% data matrices). Support values for numbered nodes based on other analyses presented in Quattrini et al. (2020) can be found in Supplementary Table S1 available on Dryad (for other nodes see Quattrini et al. 2020 and figshare). Blue bars show 95% highest posterior density (HPD) intervals for divergence dating analyses with six fossil calibration points shown as red circles on nodes. Character states for symmetry, coloniality, skeletal composition, and photosymbioses (Table 1) shown as colored circles adjacent to tip labels. Ancestral state reconstruction (ASR) for each trait illustrated with pie diagrams at numbered nodes (see Supplementary Figs. S1–S3 available on Dryad and Quattrini et al. 2020 for all nodes). Coding of octocoral skeletal types has been simplified with solid calcitic (calcaxonian) and consolidated and unconsolidated scleritic (scleraxonian) axes all shown as “calcitic axis”; skeletal axes that are entirely proteinaceous (scleroprotein or gorgonin) or that may contain a small amount of calcareous material (holaxonian) have been coded as “proteinaceous” (see Quattrini et al. 2020 for more detailed ASR of skeletal traits). Antipath = Antipatharia; Ceri = Ceriantharia; Cor = Corallimorpharia; Zoanth = Zoantharia.

of parameter values and age estimates by inspecting traces and effective sample sizes in Tracer v1.7 (Rambaut et al. 2018). TreeAnnotator (Rambaut and Drummond 2013) was then used to produce a maximum clade credibility tree. We compared Yule and Birth–Death tree priors, which resulted in similar age estimates, and we conducted an analysis (250M generations) without data by “Sampling from the Prior,” in order to ensure that

the results were driven by the data and not solely by the prior information (Brown and Smith 2018).

Ancestral State Reconstruction

Ancestral states of morphological characters were calculated using stochastic character mapping, which samples ancestral states from their posterior probability

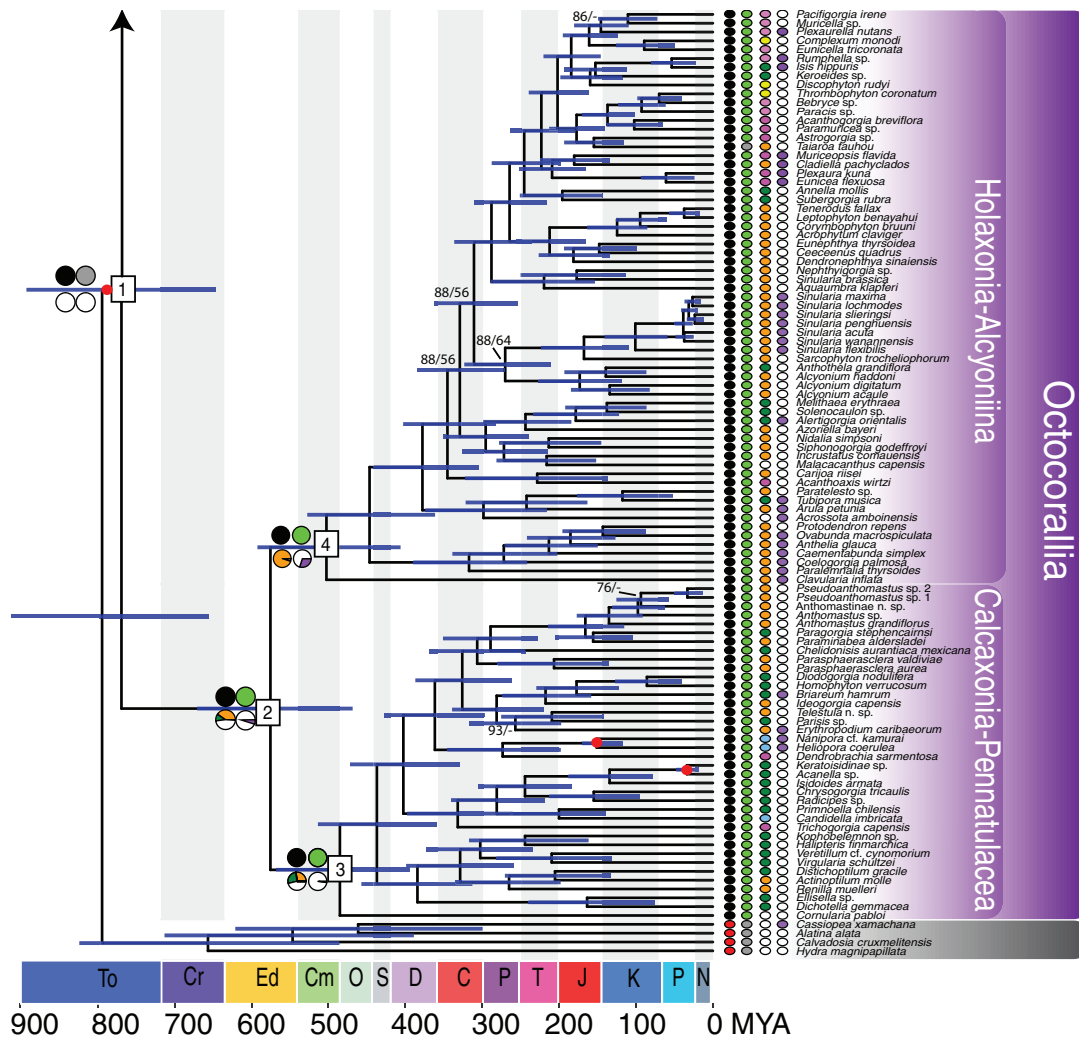


FIGURE 2. (Continued)

distribution using an MCMC approach (Huelsenbeck et al. 2003). Following methods in Kayal et al. (2018), we examined the presence/absence of coloniality and photosymbionts (e.g., zooxanthellae), which are important reef-building traits. We also included body plan symmetry (bilateral, biradial, radial) and type of skeleton (none, aragonite, calcite, free calcitic sclerites, proteinaceous as in Quattrini et al. 2020). All traits are key characters in anthozoan systematics (Table 1). Posterior probabilities were generated from 100 stochastic character maps for each trait using the make.simap function in the R package phytools (Revell 2012) (code provided in Supplementary File S1 available on Dryad). For each trait, one stochastic character map was plotted on the time-calibrated phylogeny. We also plotted the posterior probabilities generated from 100 stochastic maps as pie charts at each node using phytools (Supplementary Figs. S1–S3 available on Dryad).

RESULTS AND DISCUSSION

Phylogenetic Analyses and Systematics

All phylogenetic analyses presented by Quattrini et al. (2020) recovered reciprocally monophyletic Hexacorallia and Octocorallia, with strong support for Ceriantharia sister to all other hexacorals (Fig. 2, Supplementary Table S1 available on Dryad). Previous phylogenomic studies have found the position of Ceriantharia to be unstable (Zapata et al. 2015; Quattrini et al. 2018), while some analyses based on mt genomes or rDNA have recovered Ceriantharia outside of Hexacorallia, either sister to Octocorallia (Park et al. 2012; Kayal et al. 2013; Xiao et al. 2019) or to all anthozoans (Stampar et al. 2014, 2019). It has been suggested that substitution saturation and evolutionary biases in mitochondrial and rDNA sequences respectively could lead to the different topologies recovered in studies based on those sources of molecular evidence (Nosenko et al. 2013; Pratlong et al. 2016). In addition, all of our analyses support Zoantharia (colonial anemones) as the next group to

diverge, followed by Actiniaria (true anemones) (Fig. 2). These results also contrast with studies using rDNA that have placed the divergence of Actiniaria earlier than Zoantharia (Berntson et al. 1999; Daly et al. 2003; Rodríguez et al. 2014) but are congruent with other phylogenomic (Kayal et al. 2018) and some mitogenome phylogenies (Park et al. 2012; Kayal et al. 2013). Some inconsistency in support values for nodes 7–9 in Fig. 2 (Supplementary Table S1 available on Dryad) is perhaps related to the position of the anemone, *Relicanthus daphneae*, a species whose ordinal status has remained uncertain (Rodríguez et al. 2014). This species did not group with other solitary anemones in Actiniaria, but was instead recovered as sister to Antipatharia–Corallimorpharia–Scleractinia in a majority of analyses (Supplementary Table S1 available on Dryad). In a recent study using mitochondrial genomes, Xiao et al. (2019) recovered a monophyletic Actiniaria (with moderate support) with *R. daphneae* as the earliest diverging member of the clade, and suggested that this enigmatic deep-sea species represents a new sub-order of Actiniaria. It should be noted, however, that Xiao et al. (2019) also recovered some phylogenetic relationships that have not been supported by phylogenomic analyses (Zapata et al. 2015; Kayal et al. 2018).

Despite its former classification with Ceriantharia in Ceriantipatharia, to date molecular phylogenetic studies (but see Rodríguez et al. 2014) have recovered Antipatharia (black corals) sister to the clade of Scleractinia (stony corals) plus Corallimorpharia (mushroom anemones). Although the node uniting Antipatharia–Corallimorpharia–Scleractinia was poorly supported in the RAxML analyses using the 50% data matrix (Fig. 2), higher support values were recovered in all other analyses (Supplementary Table S1 available on Dryad). Results also support a monophyletic Scleractinia, similar to other studies that have incorporated nuclear DNA into phylogenetic analyses (e.g., Kitahara et al. 2014; Lin et al. 2016), but in contrast to some mitogenome analyses that have recovered Scleractinia paraphyletic with Corallimorpharia (Medina et al. 2006; Xiao et al. 2019). Furthermore, there is strong support across the majority of analyses for two reciprocally monophyletic clades of scleractinians, the Robust and the Complex clades (*sensu* Romano and Palumbi 1996). The analyses included three species of Micrabaciidae, a family that has been recovered within a third, “Basal” clade, sister to all other scleractinians in previous studies that have either used mtDNA alone or a combination of mtDNA and nuclear rDNA (Kitahara et al. 2010; Stolarski et al. 2011; Campoy et al. 2020; Seiblitiz et al. 2020). The results presented here suggest instead that Micrabaciidae is the earliest diverging lineage in the Robust clade. Although Quattrini et al. (2020) sampled widely within both Robust and Complex clades, they were unable to include the early diverging scleractinian family, Gardineriidae, in their analyses. Adding this taxon as well as other members of Micrabaciidae will

help to confirm the position of the Basal clade within Scleractinia.

The phylogeny recovered for Octocorallia is largely congruent with results that have been obtained previously from analyses of mtDNA or nuclear rDNA, but with much better resolution of deep nodes that have been poorly supported in past studies (Berntson et al. 2001; McFadden et al. 2006; Brockman and McFadden 2012). Two reciprocally monophyletic clades of Alcyonacea were recovered with strong support. One of these clades corresponds to the Holaxonia–Alcyoniina clade that has also been well-supported in previous analyses (McFadden et al. 2006). The second clade corresponds to the Calcaxonia–Pennatulacea clade whose monophyly has been poorly supported previously. Notably, the analyses presented here place the stoloniferan family Cornulariidae within Calcaxonia–Pennatulacea, while analyses based on mtDNA have supported Cornulariidae as the earliest diverging octocoral, sister to both major clades (Brockman and McFadden 2012; McFadden and Ofwegen 2012). As in these previous molecular analyses, monophyletic Helioporacea (blue corals) and Pennatulacea (sea pens) were recovered nested within Calcaxonia–Pennatulacea, the latter as sister to the gorgonian family Ellisellidae (Fig. 2).

Divergence-Dating Results

Cnidarians are some of the earliest evolving metazoans, with our analyses placing them in the Cryogenian to Tonian periods (Fig. 2). We constrained the age at the root node with a cnidarian fossil from the Cambrian (520 Ma) with an exponential prior distribution to weight the probability toward the minimum bound (see Ho and Phillips 2009); nonetheless, we still recovered an older age for Cnidaria (798 Ma, CI 668–935 Ma) than the minimum age constraint on the node. Other molecular studies have also suggested that cnidarians arose during the Precambrian Eon, with age estimates ranging from the Ediacaran (595 Ma, Peterson et al. 2004) to the Cryogenian (700 Ma, Erwin et al. 2011) and Tonian (741–842 Ma, Park et al. 2012; 800–1000 Ma, Waggoner and Collins 2004). Although putative (not confirmed) cnidarian macrofossils support the phylum’s presence in the Ediacaran (560 Ma; Liu et al. 2014), most of the confirmed physical record of the group does not extend to these much earlier molecular age estimates. More data from Medusozoa are needed for confirmation of our result as an inadequate sampling of major lineages can bias age estimates (Beaulieu et al. 2015), and we included only a few medusozoan taxa (and no other phyla) as outgroups to Anthozoa.

Our results also suggest that Anthozoa evolved in the Cryogenian to Tonian periods, with an estimated age of 771 Ma (CI 648–894 Ma, Fig. 2), much older than what has been documented previously using molecular data. Erwin et al. (2011) found that anthozoans arose during the Ediacaran; their study, however, did not

include the early-diverging hexacorals (e.g., Zoantharia, Ceriantharia) and had only a single representative of octocorals. The only other time-calibrated phylogeny with a broad sampling of the class was constructed using mitochondrial genome data and resulted in a paraphyletic Anthozoa with younger ages for both major clades (Park et al. 2012). Park et al. (2012) estimated Hexacorallia to have arisen in the Ediacaran (549 Ma, CI 540–574 Ma), compared to our analyses which place it in the Cryogenian (711 Ma), although there is quite a wide distribution around the mean age (CI: 599–828 Ma). They also recovered a younger age for Octocorallia (499 Ma, CI 320–647 Ma), whereas our analyses place Octocorallia in the Ediacaran (578 Ma, CI 483–685 Ma, Fig. 2). As acknowledged by Park et al. (2012), those younger ages may have been driven by incomplete taxon sampling, including the omission of Ceriantharia. In contrast to these other studies, we sampled widely from all major lineages of anthozoans; used calibration points from both major clades (Hexacorallia and Octocorallia) based on fossils whose morphology was confirmed unequivocally to match extant clades; and used only the most clock-like loci to estimate rates. With the exception of the lower bound placed on Cnidaria, however, all of the calibration points we used are relatively recent (<200 Ma; Supplementary Table S2 available on Dryad), which adds uncertainty to estimates of deep divergence times (see Mello and Schrago 2014). Unfortunately, with the exception of Scleractinia, the fossil record of extant anthozoans is, in general, very poor; the earliest-diverging groups are soft-bodied; the affinities of the oldest anthozoan fossils to crown groups are very uncertain (Scrutton 1997); and homoplasy of skeletal characters (e.g., Fukami et al. 2008; Quattrini et al. 2020) complicates the interpretation of even recent fossil lineages. These constraints limit our ability to include much older calibration points in the analysis.

Despite the surprisingly old estimated ages of Anthozoa, Hexacorallia, and Octocorallia, the divergence times we recovered for some of the early-diverging orders of hexacorals are nonetheless supported by the fossil record of putative anthozoan fossils. Our analyses place Actiniaria in the Cambrian with an estimated age of 513 Ma (95% CI 424–608 Ma); putative actiniarian fossils have been found in the Lower Cambrian (Han et al. 2010). We estimated zoantharians to have diverged in the Silurian (436 Ma, CI 336–531 Ma). Based on shared morphological features, it has been suggested that Rugosa, an extinct clade of corals with an extensive fossil record starting in the mid-Ordovician, either evolved from or shared a common ancestor with the soft-bodied zoantharians (Scrutton 1997), a theory that would validate a Silurian (or earlier) origin of Zoantharia.

Our estimate that Scleractinia originated 383 Ma (CI 324–447 Ma) pre-dates their first appearance in the fossil record of the early Triassic and is older than that of Park et al. (2012) based on complete mitogenomes [CodonRates: 204 Ma, (CI 203–286); Multidivtime: 243 Ma (CI 158–259 Ma)]. The analysis of Park et al. (2012)

did not include a broad sampling of Scleractinia or Micrabaciidae, which has been suggested in a few prior studies to be the sister lineage to Robust and Complex Scleractinia (Stolarski et al. 2011; Campoy et al. 2020), nor were the oldest confirmed, crown scleractinian fossils (Dendrophylliidae, Caryophylliidae) included for time-calibration of their phylogeny. Our divergence time estimate is, however, slightly younger than the ages estimated by Stolarski et al. (2011) (425 Ma) and Campoy et al. (2020) (406 Ma) from nuclear and mitochondrial rDNA sequences, and Stolarski et al. (2021) (389 Ma) from complete mitogenomes. Each of these time-calibrated phylogenies was based on a wide sampling of Scleractinia including early-diverging micrabaciid and gardineriid lineages. Gardineriidae was not included in our study, which could be the reason for the difference between our (383 Ma) and their (389–425 Ma) divergence time estimates. However, in addition to taxon sampling, these differences could also be driven by differences in topology or loci between the studies. Errors in tree topology and variation in rates among lineages can lead to biased age estimates (Sanderson and Doyle 2001; Beaulieu et al. 2015). Mitochondrial DNA evolves notoriously slowly in anthozoans (Shearer et al. 2002; Hellberg 2006), and as Stolarski et al. (2011) also noted, might not be optimal for addressing deep divergence events. Topology differences between our phylogeny and theirs might also contribute to divergence time differences, as we recovered a Micrabaciidae lineage sister to the Robust clade, rather than a sister to all other scleractinians.

Incomplete taxon sampling may also bias our estimates of the ages of other crown groups towards younger dates. The black coral family Leiopathidae, which is hypothesized to be the oldest member of that clade (Opresko 1998), is not included in our analyses, nor is the divergent zoantharian family Abysoanthidae, whose phylogenetic position within that order remains uncertain (Poliseno et al. 2020). The long branches leading to the crown clades of Antipatharia and Zoantharia (Fig. 2) could be artifacts of those missing lineages. Alternatively, long branches in those groups, as well as those of Ceriantharia and *Relicanthus*, may be evidence of the extinction of early-diverging lineages (Trewick and Morgan-Richards 2016), a hypothesis that is difficult to test in the virtual absence of a fossil record for these soft-bodied animals.

Ancestral State Reconstruction

Stochastic character mapping revealed that, despite the distinct external radial symmetry of anthozoan polyps, the ancestral character state of class Anthozoa is bilateral symmetry (i.e., a single plane of symmetry orthogonal to the oral–aboral axis that gives rise to mirror images) (Fig. 2; Supplementary Fig. S1 available on Dryad). The biradial symmetry (i.e., two planes of symmetry orthogonal to the oral–aboral axis) of some hexacorals is therefore a secondarily and independently

derived trait not homologous to the n-radial symmetry (i.e., multiple planes of symmetry) of the Medusozoa and the earliest metazoan lineages, Ctenophora and Porifera (Manuel 2009). Bilateral symmetry in anthozoan polyps arises internally from the arrangement of mesenteries and their associated retractor muscles as well as the development in some taxa of a single siphonoglyph (ciliated groove in the actinopharynx). All octocorals, cerianthids, zoantharians, antipatharians, and an early diverging clade of actinarians have retained this ancestral bilateral symmetry, as did the extinct rugosans (Scrutton 1997). While scleractinians, corallimorpharians, and actinarians pass through bilaterally symmetric phases during development, the majority of the adult polyps in these lineages are characterized by internal biradial symmetry (Gonçalves 2016). Those anthozoans that have retained bilateral symmetry internally have nonetheless evolved to exhibit radial symmetry externally (viz. a cylindrical polyp with a 360° cycle of tentacles), which may be selectively advantageous in sessile filter-feeders whose food sources may come from any direction (Shick 1991). The ancestral bilateral symmetry of Anthozoa supports the hypothesis that the Most Recent Common Ancestor (MRCA) of Cnidaria and its sister clade Bilateria was also a bilaterally symmetrical organism, as suggested by the analysis of shared developmental genes and patterns of gene expression (Finnerty et al. 2004; Malakhov 2016; Genikhovich and Technau 2017). Despite being the most parsimonious explanation, however, it has also been argued that the bilateral symmetries of Anthozoa and Bilateria are not homologous, and that both bilateral and radial symmetries have evolved independently multiple times among the early metazoan phyla (Manuel 2009). Ctenophores also display elements of bilateral symmetry (Tamm 2015).

The MRCA of Anthozoa lacked a skeleton, an ancestral state that has been retained in Ceriantharia, Zoantharia, Actinaria, and Corallimorpharia (Fig. 2). A diversity of different skeletal types was gained independently in each of the other orders, as discussed in detail in Quattrini et al. (2020). Briefly, within Hexacorallia, a proteinaceous skeletal axis was gained once in Antipatharia, and the ability to produce a massive skeleton of aragonite was gained once in Scleractinia (Fig. 2); there have been no evolutionary losses of either of those skeletal types (Quattrini et al. 2020). The fossil record also supports one or more independent gains of calcitic skeletons among the extinct Rugosa and Tabulata, two clades of hexacorals that were diverse from the mid-Ordovician to the end-Permian. In contrast to Hexacorallia, calcareous skeletal elements (i.e., sclerites) were gained early in the history of Octocorallia (503 Ma; Quattrini et al. 2020), and there have been multiple subsequent gains and losses of a variety of different types of skeletons in this subclass, including proteinaceous, aragonitic, and consolidated or unconsolidated calcitic skeletons (Fig. 2). Evolutionary lability of skeletal form in octocorals and diversification rates that are correlated with paleoclimate variables suggest that this clade may

exhibit greater adaptability and evolutionary flexibility in the face of past and future environmental instability than scleractinians with aragonite skeletons (Quattrini et al. 2020).

Like a skeleton, coloniality is widely viewed as an adaptation that allows organisms to attain larger size, conferring a competitive advantage on hard, stable substrata (Jackson 1977), as well as protection from predation. Throughout geological history, periods of reef-building by corals have been accompanied by diversification of colonial forms with high levels of integration (Coates and Jackson 1985), a body plan that is also significantly associated with the acquisition of photosymbionts (Coates and Jackson 1987; Campoy et al. 2020). The ancestral anthozoan was a solitary polyp (Fig. 2, Supplementary Fig. S2 available on Dryad), suggesting that colonial growth forms arose independently in Anthozoa and Medusozoa (Kayal et al. 2018). Within Anthozoa, coloniality has also evolved multiple times. Among hexacorals, Ceriantharia, Actinaria, and Corallimorpharia are exclusively solitary organisms; although they may reproduce clonally, no physiological connection is maintained between genetically identical daughter polyps. The lack of coloniality is also associated with the lack of a skeleton in these orders, and they have evolved alternative ways to increase their body size other than skeletogenesis or coloniality (Grebelyni 1982). In contrast, Antipatharia, Zoantharia, and Octocorallia are almost exclusively colonial (with small polyps), and each of those clades represents a single, independent gain of that character state (Fig. 2, Supplementary Fig. S2 available on Dryad). Once gained, loss of coloniality in these groups is rare, with only a single documented case in Alcyonacea and a few cases in Zoantharia (Table 1). Our time-calibrated tree places the origin of Octocorallia in the Ediacaran (578 Ma, Table 1), suggesting that a modular, colonial growth plan has Precambrian origins. Among extant Hexacorallia, coloniality first appears in Zoantharia, a group with a Silurian origin (436 Ma) (Table 1; Fig. 2; Supplementary Fig. S2 available on Dryad). The extinct tabulate and rugosan corals also provide ample fossil evidence of skeletonized, colonial growth forms among hexacorals that first appear in the early Ordovician (Scrutton 1997; Copper 2002).

Scleractinia is the only extant anthozoan order to include many colonial and solitary taxa. Although it has been widely assumed that the MRCA of Scleractinia was solitary (Wells 1956; Stolarski et al. 2011), most previous attempts at ancestral state reconstruction have lacked the phylogenetic resolution and broad taxon sampling of other anthozoans necessary to rigorously test that assumption (Barbeitos et al. 2010; Kayal et al. 2018). A recent analysis based on a tree inferred from mt and rDNA genes, however, finds strong support for a solitary MRCA of Scleractinia (Campoy et al. 2020). In conjunction with the placement of Micrabaciidae sister to the Robust clade rather than a sister to all other scleractinians, we recover coloniality as the ancestral state within the order (Fig. 2). This conclusion will

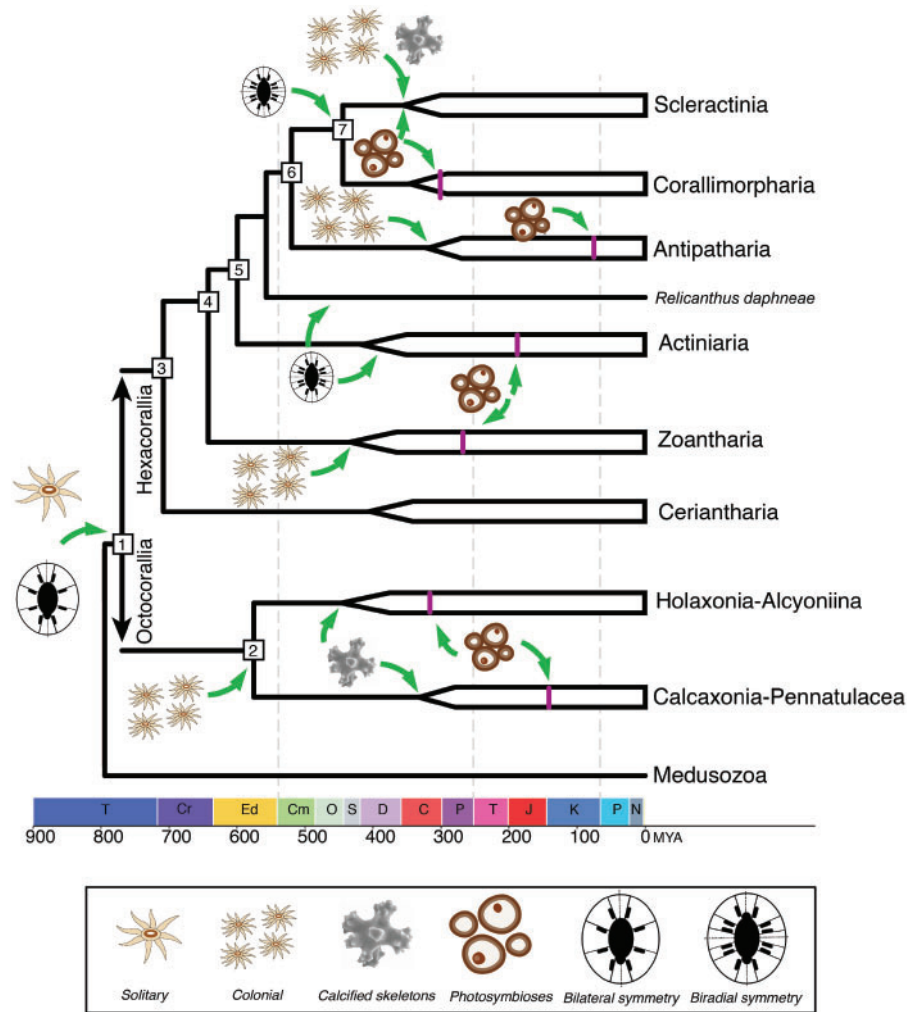


FIGURE 3. Simplified phylogeny of class Anthozoa illustrating independent gains of key character states in different lineages inferred from ancestral character state reconstruction (see [Supplementary Figs. S1–S3](#), [Table S2](#) available on Dryad). 1) The Most Recent Common Ancestor (MRCA) of class Anthozoa was a solitary polyp with bilateral symmetry that lacked a skeleton and photosymbioses. 2) A colonial growth form and calcified skeletal elements were gained early in the evolution of subclass Octocorallia. Photosymbioses were gained independently multiple times in multiple clades of octocorals. 3) In subclass Hexacorallia, the earliest diverging order Ceriantharia retains the ancestral character states of Anthozoa. 4) Among Hexacorallia, colonial growth forms were first gained in Zoantharia. All lineages except Ceriantharia and *Relicanthus* have evolved photosymbioses independently, with the earliest acquisitions in the Devonian. 5) Biradial symmetry was gained independently in some Actiniaria, in *Relicanthus*, and in the MRCA of Scleractinia + Corallimorpharia. 6) Colonial growth forms were gained independently in Antipatharia and Scleractinia. 7) Calcified skeletons evolved in Scleractinia.

need to be confirmed, however, by broader taxonomic sampling of Scleractinia. Our analysis supports several subsequent losses of coloniality in scleractinians but no secondary gains. This result is also likely to change with increased taxon sampling, as molecular phylogenetic analyses of scleractinian families that include colonial and solitary forms have found evidence for both evolutionary transitions ([Gittenberger et al. 2011](#); [Arrigoni et al. 2014](#)).

Associations with photosymbionts have been gained and lost repeatedly throughout the phylogenetic history of Anthozoa (Fig. 2; [Supplementary Fig. S3](#) available on Dryad). While the MRCA of Anthozoa lacked photosymbionts (Fig. 2), zooxanthellate species have evolved subsequently within all extant orders except

Ceriantharia. Our time-calibrated tree suggests that photosymbioses arose in the Devonian ([Supplementary Table S3](#) available on Dryad), appearing first in Scleractinia (383 Ma), followed by alcyonacean octocorals (318 Ma) and corallimorpharians (312 Ma). Additional independent gains of the trait in zoantharians, actiniarians, and other clades of alcyonaceans occurred from the Permian (273 Ma) through the Jurassic (199–151 Ma) ([Supplementary Table S3](#) available on Dryad). In conjunction with the tree topology they recovered that supported a Basal clade of azooxanthellate, deep-water corals, [Campoy et al. \(2020\)](#) estimated a later origin (282 Ma) of photosymbioses in scleractinians, closer in time to the trait's appearance in other anthozoan lineages.

Fossil evidence suggests that most upper Triassic scleractinian corals had photosymbionts (Frankowiak et al. 2016; Stolarski et al. 2011), and there is indirect morphological and isotope evidence of photosymbioses in the extinct tabulates and rugosans of the Silurian and Devonian (Coates and Jackson 1987; Copper 2002; Zapalski 2014). Recent molecular clock estimates suggest the diversification of Symbiodiniaceae, the family of dinoflagellate photosymbionts hosted by most extant anthozoans, only occurred in the Jurassic (~160 Ma; Lajeunesse et al. 2018), considerably more recently than the origins of zooxanthellate clades of anthozoans. It is likely, therefore, that anthozoan photosymbioses evolved first in partnership with earlier clades of photosymbionts that may later have been replaced by Symbiodiniaceae. Indeed, some extant actiniarians maintain symbioses with other photosymbionts such as green algae (Chlorellaceae) (Muscatine 1971; Clavijo et al. 2018).

In summary, our time-calibrated phylogeny—based on phylogenomic data with comprehensive taxon sampling across all orders—places the origin of class Anthozoa (and by extension phylum Cnidaria) in the Cryogenian to Tonian periods, far earlier than the first physical evidence for the group appears in the fossil record. The ancestral anthozoan was a solitary polyp that lacked a skeleton but shared bilateral symmetry with the common ancestor of Bilateria (Fig. 3). Colonial growth forms as exemplified by the exclusively colonial octocorals date to the Ediacaran, and associations with photosymbionts were present by the Devonian. In combination with the ability to precipitate skeletons of calcium carbonate, these traits have allowed some groups of anthozoans to engineer massive reef structures that support entire, complex ecosystems in both shallow and deep ocean environments. Although the fossil record documents the sensitivity of these reef-building forms to past environmental instability evidenced by mass extinctions, periods of history not conducive to reef-building have witnessed the evolution and diversification of equally successful and resilient groups of anthozoans such as the octocorals and the non-calcified orders of hexacorals (Quattrini et al. 2020). Although the future of reef-builders once again appears grim (Pandolfi et al. 2011), anthozoans have survived, diversified and ecologically dominated diverse marine ecosystems since the Precambrian.

SUPPLEMENTARY MATERIAL

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.d51c5b00j>.

The data associated with this paper are available for review via Dryad. The following is a temporary direct download link. Please copy and paste it directly into a web browser to download the data files to your computer (unfortunately this may not work as a link to click on) <https://datadryad.org/stash/share/7ZxiBae3fq5zEATfcdXM9yraYQjO-U7PIb62FxFjGzk>.

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