Article

A global coral phylogeny reveals resilience and vulnerability through deep time

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Claudia Francesca Vaga[1,2,3]✉, Andrea M. Quattrini[1], Isabela Galvão de Lossio e Seiblitz[2,3], Danwei Huang[4,5,6], Zheng Bin Randolph Quek[6,7], Jarosław Stolarski[8], Stephen Douglas Cairns[1] & Marcelo Visentini Kitahara[1,2,3]✉

Global climate change and its consequences for the symbiosis between corals and microalgae are impacting coral reefs worldwide—ecosystems that support more than one-quarter of marine species and sustain nearly one billion people[1–3]. Understanding how stony corals, the primary architects of both shallow and deep reef ecosystems, responded to past environmental challenges is key to predicting their future[4]. Here we describe a time-calibrated molecular phylogenetic analysis that includes hundreds of newly sequenced coral taxa, and sheds light on the deep-time evolution of scleractinian corals. We date the emergence of the most recent common ancestor of Scleractinia to about 460 million years ago and infer that it was probably a solitary, heterotrophic and free-living organism—or one that could reproduce through transverse division—thriving in both shallow and deep waters. Our analyses suggest that symbiosis with photosynthetic dinoflagellates was established around 300 million years ago and spurred coral diversification. However, only a few photosymbiotic lineages survived major environmental disruptions in the Mesozoic era. By contrast, solitary, heterotrophic corals with flexible depth and substrate preferences appear to have thrived in the deep sea despite these environmental disturbance events. Even though ongoing environmental changes are expected to severely affect shallow reefs[5], our finding that stony corals have shown resilience throughout geological history offers hope for the persistence of some lineages in the face of climate and other environmental changes.

Shallow and deep-water reef-based ecosystems occupy a small fragment of the ocean realm, but contain more than a quarter of all marine life[3]. However, current climatic changes are causing global mortality and decline of reef-building corals[1,2]. Increasing levels of atmospheric CO_2 are leading to ocean acidification (OA) and warming, and to a shallowing of the aragonite saturation horizon (ASH)[6]. Together, these processes impede calcification and, consequently, growth rates of coral reefs worldwide[4,5]. Understanding how different lineages of stony corals (Extended Data Fig. 1)—the main engineers of aragonitic reef ecosystems—have been affected by past environmental changes is of timely importance to inform current efforts in coral conservation and restoration. However, the evolutionary history of stony corals, along with their ecological and morphological traits through deep time, remains poorly understood[7] owing to the lack of a comprehensive global phylogeny.

Scleractinia have been hypothesized to have arisen between 479 and 383 million years ago (Ma)[8–10], suggesting that the order survived all major past global environmental adverse events, including mass extinctions and reef crises due to global warming, OA and ocean anoxic events (OAEs). Notably, the latter have been suggested to be major drivers of past losses of scleractinian diversity[11,12] and deep-water benthos in general[13]. However, several deep-water scleractinian corals, accounting for nearly half of the known extant scleractinian species[14], especially solitary forms, inhabit depths well below the ASH (>6,000 m for the deepest scleractinian record)[15] and are known to thrive in regions with oxygen-depleted concentrations[16]. If OAEs have had an important role in shaping the evolution of stony corals, we expect solitary and deep-water species to have fared better during these adverse conditions, serving as a repository for the following reappearance of their shallow-water counterparts.

In addition to OAEs, the marine realm has been subjected to multiple strong fluctuations in temperature and CO_2 concentrations since the beginning of the Palaeozoic era (~540 Ma)[4], leading to several reef crises. Shallow reef-building zooxanthellate corals are known to have been severely affected by the aforementioned crises[11]. Yet time-calibrated trees and skeleton microstructure data suggested that photosymbiosis arose in Scleractinia in the Palaeozoic era[17–19]. Together, these findings imply that some zooxanthellate lineages survived the multiple biotic crises during the Mesozoic and Cenozoic eras. Moreover, photosymbiosis and coloniality in stony corals have multiple independent origins from azooxanthellate and solitary ancestors, suggesting that these traits are relatively easy to acquire across the order[7,17]. Scleractinians have also

[1]Department of Invertebrate Zoology, Smithsonian Institution, Washington, DC, USA. [2]Center for Marine Biology, University of São Paulo, Sao Paulo, Brazil. [3]Graduate Program in Zoology, Department of Zoology, Institute of Biosciences, University of São Paulo, Sao Paulo, Brazil. [4]Lee Kong Chian Natural History Museum, National University of Singapore, Singapore, Singapore. [5]Tropical Marine Science Institute, National University of Singapore, Singapore, Singapore. [6]Department of Biological Sciences, National University of Singapore, Singapore, Singapore. [7]Yale-NUS College, National University of Singapore, Singapore, Singapore. [8]Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland. ✉e-mail: vagac@si.edu; kitahara@usp.br

survived periods of OA events and calcitic seas[10], during which conditions for the precipitation of aragonite were unfavourable[20]. Critically, which and how surviving lineages and the associated coral traits endured specific adverse events since the Palaeozoic remain unclear.

Broad phylogenies are being increasingly used to successfully infer the evolutionary history of a wide variety of organisms[18,21–23]. Thus, here, using a comprehensive time-calibrated phylogenomic reconstruction of the order (that is, balance between shallow/zooxanthellate (134) and deep-water/azooxanthellate (138) taxa), with representatives from all but two families, we address how past global (1) changes in temperature and CO_2 concentration; (2) OAEs; and (3) mass extinction events (MEEs) drove the diversification of scleractinian corals. Specific ancestral traits (that is, symbiosis, coloniality and relationship with substrate) and depth ranges that potentially enabled lineages to endure adverse events, as well as lineage-specific diversification rates and how the evolution of the aforementioned traits responded to past climatic events, were also tested. Moreover, the origin and traits of the scleractinian most-recent common ancestor (MRCA) were investigated. Together, the results illuminate the fate of stony corals under past and ongoing climatic changes.

Time-calibrated phylogeny

To elucidate patterns of stony coral diversification through time, we used target capture and genome skimming data to assemble a nuclear dataset (230,364 base pairs) of exon and ultraconserved element (UCE) loci from 274 scleractinian species (and 17 outgroup species) (Supplementary Table 1). The resulting maximum-likelihood (Fig. 1; ultrafast bootstrap (UFBoot) and SH-aLRT support values are shown in the Supplementary Fig. 1) and species tree phylogenies (Extended Data Fig. 2) show consistent topologies and general strong statistical support (>95% UFBoot and SH-aLRT values) at both deep and shallow nodes with two reciprocally monophyletic suborders: Vacatina, which also includes the 'Basal' clade[8], and Refertina. A molecular-clock estimate indicates an Ordovician period (460 Ma, 95% confidence interval (CI) = 405–519 Ma; Supplementary Fig. 2) MRCA of the order Scleractinia. The 95% CI is consistent with previous estimations (445 Ma (ref. 8), 479 Ma (ref. 9) and 415 Ma (ref. 17)) and it overlaps with the previous CI estimated with UCEs and exon loci (324–447 Ma)[10]. These results further support and improve date estimates, placing the origin of Scleractinia during a major period of marine animal diversification[24] and contemporary to the appearance of Rugosa and Tabulata—coral lineages with calcitic skeletons and different patterns of septal insertion[25] that went extinct at the Permian–Triassic period boundary. Furthermore, more than 65% of the calculated families' crown ages overlap with the fossil age of the oldest representative of the respective lineage (Supplementary Table 2, Extended Data Fig. 3, Supplementary Results and Supplementary Discussion).

Scleractinia MRCA and fossil record

Our results show that the ancestral state of Scleractinia was solitary, azooxanthellate, either free-living (that is, unattached) or a species that could reproduce through transverse division, and a generalist across a broad depth range (Fig. 2). These characteristics, apart from the transverse division, correspond to those of the Palaeozoic scleractiniamorph fossils (*Kilbuchophyllia*[26] and *Numidiaphyllum*[27,28]). These fossils represent solitary and azooxanthellate species, and they are thought to have lived in shallow waters[26–28]. Nevertheless, it is possible that scleractinian Palaeozoic deep-water fossils, if not subducted under tectonic plates or not preserved due to their small dimension, have been overlooked as most Palaeozoic marine strata studied to date originate from shallow-water environments. Moreover, many of the extant deep-water species can, in fact, also be found in shallow waters (that is, depth generalists) (Supplementary Fig. 3 and Supplementary Table 1). Thus, it is possible that Palaeozoic solitary and azooxanthellate scleractinians were also able to survive and colonize deep-water environments. Previous studies have focused on onshore/offshore trend hypothesis to explain diversification pattern in scleractinians[29,30], stylasterids[31] and black corals[32]. Our result is of particular interest as it points at a different scenario in which Scleractinia arose from an azooxanthellate ancestor that was able to thrive in both shallow and deep waters, rather than restricted to a specific bathymetric range. Moreover, mesophotic ecosystems, long understudied, have been more recently explored and proved to contain a considerable diversity of scleractinian species[33], pointing to a continuum in their bathymetric distribution.

Diversification rates

Increased diversification rates appear at different geological times for zooxanthellate and azooxanthellate lineages within the Refertina and Vacatina groups (Fig. 1). In general, most of the extant families with increased rates began diversifying between 120 Ma and 90 Ma (Fig. 1). Such a time range succeeds the Triassic–Jurassic period MEE (around 200 Ma) and the Toarcian age OAE (T-OAE) (about 182 Ma), which also led to a reef crisis[11]. Furthermore, this time range corresponds with two major OAEs in the early Aptian age (around 120 Ma), and between the Cenomanian and Turonian (~93 Ma) age. In fact, several OAEs, which have been purported to be more deleterious for stony corals than MEEs[12], occurred throughout the Mesozoic. Yet, our data show that several azooxanthellate stony coral lineages persisted and even diversified in deep waters during and after these adverse events, perhaps because deep waters were not consistently anoxic[34] and/or because some deep-water species required lower levels of oxygen[16,35]. Regardless of the underlying mechanism, the intervals between OAEs are characterized by elevated diversification rates in stony coral lineages, whereas intervals between other MEEs show only modest increases or stable rates (Fig. 3).

Our results suggest that the MRCA of the oldest zooxanthellate lineages lived in the beginning of the Permian Period (~300 Ma); however, diversification rates did not increase until the beginning of the Cenozoic (~70 Ma). Zooxanthellate lineages that diversified in the Cenozoic either derived from few symbiotic descendants that survived the Mesozoic anoxic and acidification events or from azooxanthellate lineages by secondary acquisition of the zooxanthellae (similar to findings of a previous study[10]), whereas, based on the fossil record, a wide range of other shallow-water scleractinian families went extinct during Mesozoic adverse events[12]. On the other hand, most of the azooxanthellate taxa that arose between the mid to late Mesozoic diversified quickly after their appearance, further supporting resilience of azooxanthellate stony coral lineages to the anoxic and acidification events that occurred during this era.

Traits evolution through deep time

Our results show that coloniality was acquired and lost multiple times throughout the evolutionary history of Scleractinia, consistent with past studies[7,17] (Supplementary Fig. 4). Notably, whereas the ancestral state for the MRCA of the Vacatina group was most likely solitary, our phylogeny indicates that coloniality was the most probable ancestral state of the Refertina group. The diversification of these two forms was almost simultaneous, at about 400 Ma during a period of stable temperature and CO_2 concentration. This simultaneous origin might explain the appearance of an already highly morphologically diverse (both colonial and solitary forms) stony coral fossil fauna soon after the Permian–Triassic boundary[36].

The ancestral state of Scleractinia was azooxanthellate with the first zooxanthellate ancestor arising around 300 Ma (Supplementary Fig. 5). This result conflicts with previous studies[18,29] that retrieved the ancestral state for Scleractinia as zooxanthellate, although a limited number of azooxanthellate species were included in those studies. Our results showed that photosymbiosis was acquired near the end of the Palaeozoic period, which agrees with a previous study[19] that proposed

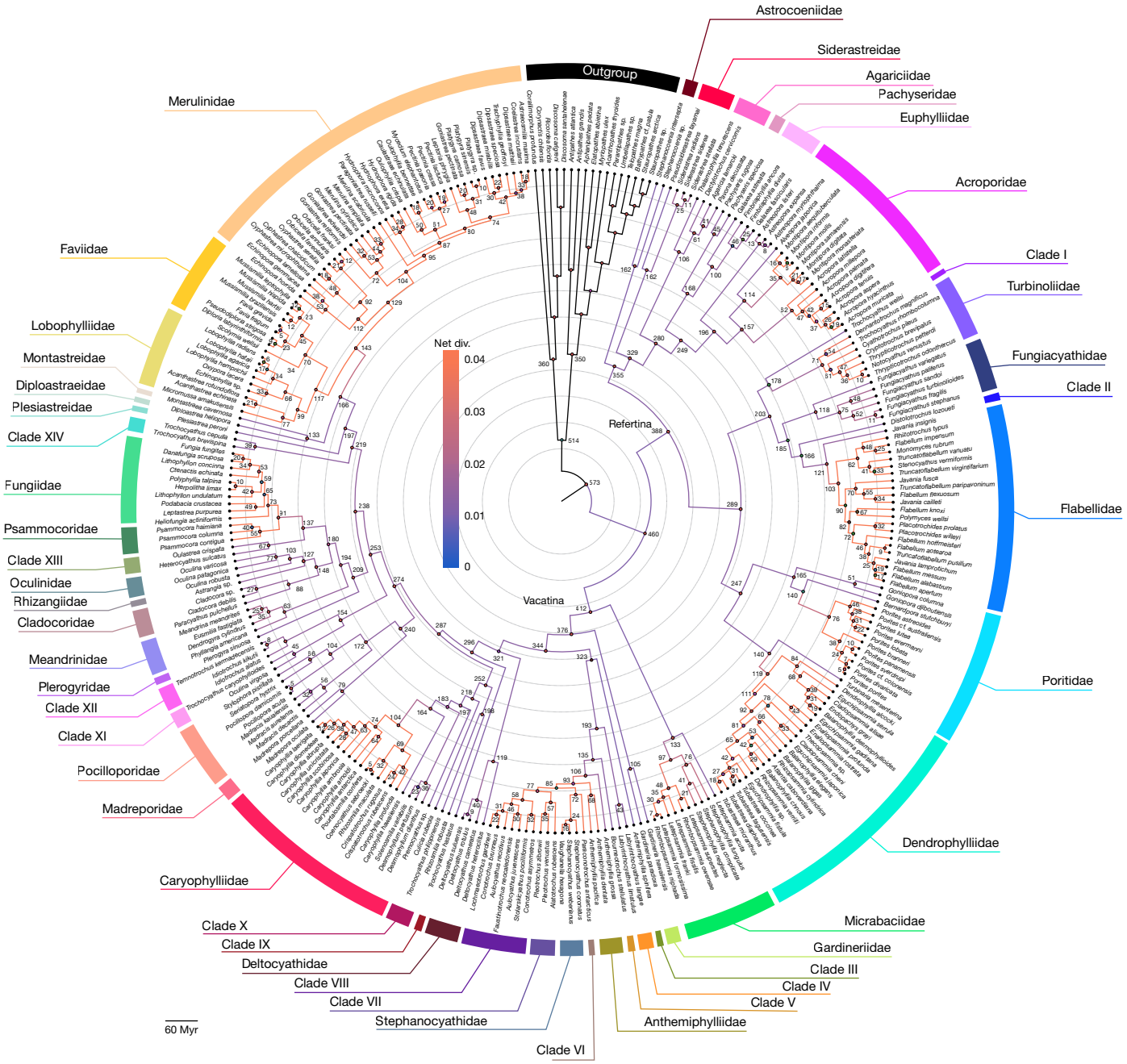

Fig. 1 | Time-calibrated phylogeny of Scleractinia with branch-specific diversification rates. Families are colour coded and names are indicated around the phylogeny. Clades labelled I–XIV represent lineages that do not correspond to any of the extant families. The values on the nodes correspond to the divergence time of each clade. The branches shown in orange indicate increased diversification (div.) rates. Topology was produced from maximum-likelihood analyses of a 50% data matrix (230,364 bp). Myr, million years.

that the Late Triassic coral fauna was predominantly zooxanthellate, including many solitary growth forms. In our phylogeny photosymbiosis was independently gained multiple times but very rarely lost. It has been hypothesized that lineages that acquired symbiosis with zooxanthellae can lose the capacity of producing some fundamental amino acids that are instead provided by the symbionts[37]. Together, these findings suggest that the loss of symbionts can be deleterious for zooxanthellate lineages, while azooxanthellate and/or deep-water lineages can easily acquire the symbioses after warming or OA events.

Analysis of corals' association with substrate show that attached and free-living species are often intermingled in the same family but, in both the Refertina and Vacatina clades, several early diverging lineages are free living (Supplementary Fig. 6 and Supplementary Table 3). Such a trend supports the hypothesis that the order Scleractinia arose from a soft-bodied ancestor[10,38] that lacks any form of skeleton and was therefore not firmly attached through a carbonate structure to the substrate—that is, corallimorpharian, sister group of stony corals[39,40]. The attached state is widespread in colonial and shallow-water lineages and rarely lost. On the contrary, solitary and azooxanthellate lineages retained the free-living state or occasionally gained it from attached ancestors.

Stony coral resilience and vulnerability

Our results show that Scleractinia diversified in the Ordovician while the suborders Refertina and Vacatina originated in the Devonian period.

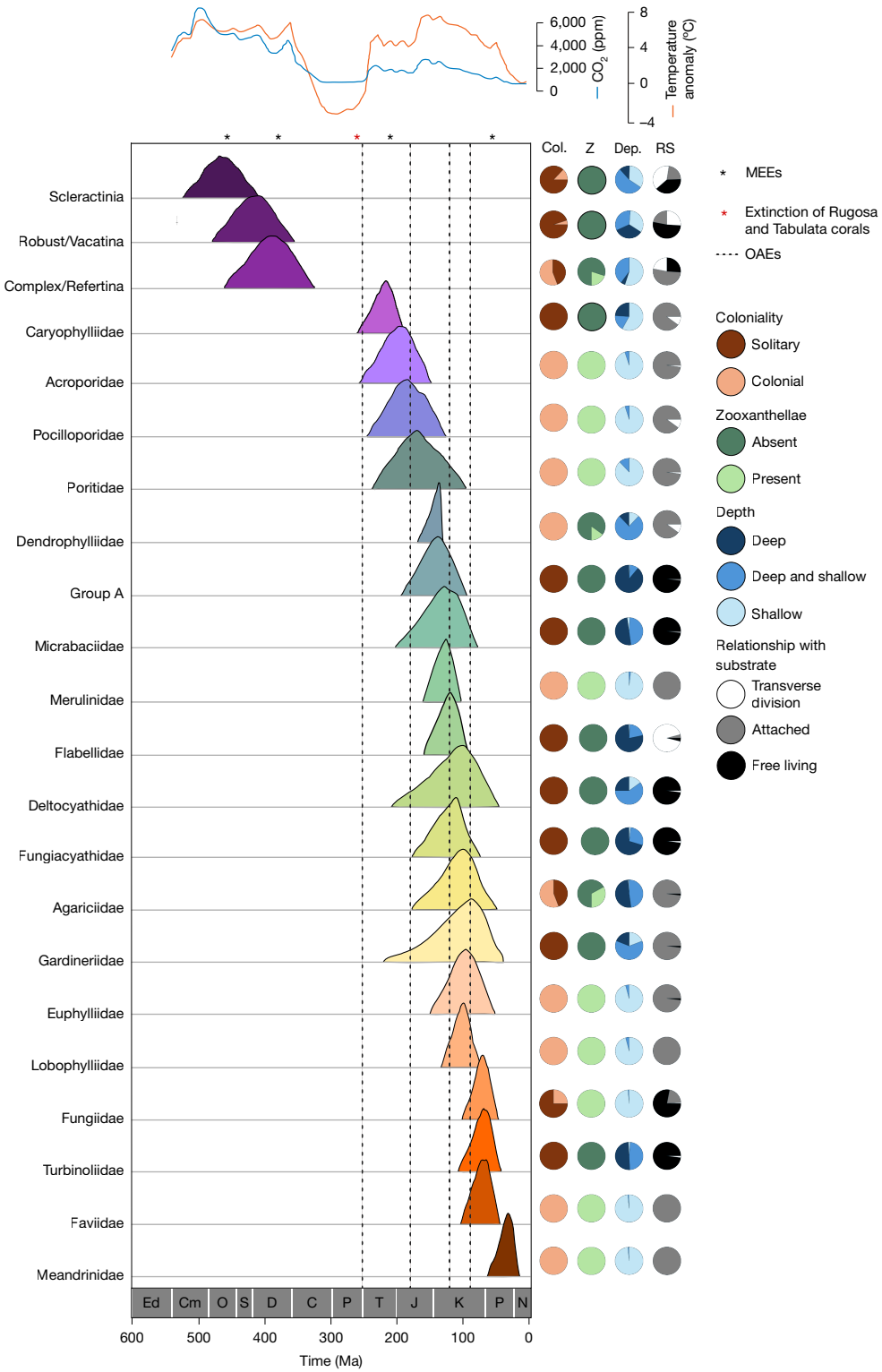

Fig. 2 | Timing of scleractinian families and traits of their MRCAs. The shapes indicate the 95% highest posterior densities for time of divergence of families within Scleractinia. Distributions were obtained from the divergence time estimation analyses run in BEAST. The dotted lines indicate OAEs and the asterisks indicate MEEs; the red asterisk also indicates the disappearance of Rugosa and Tabulata corals. The posterior probabilities of the traits of the MRCA of the corresponding family/group are shown on the right. Col., coloniality; dep., depth; RS, relationship with substrate; Z, zooxanthellae; Ed, Ediacaran; Cm, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; T, Triassic; J, Jurassic; K, Cretaceous; P, Palaeogene; N, Neogene. CO_2 and temperature curves were adapted with permission from ref. 4, AAAS. The bottom panel was reproduced from ref. 10, Springer Nature Limited.

Both periods are known for the origins and diversification of a wide range of metazoans[41], and are characterized by decreasing global temperatures and CO_2 concentrations[4,42]. During these periods, rugose and tabulate corals, which occupied the majority of the shallow-water niches[43], coexisted with mostly deep-water scleractinian corals (Fig. 2). However, rugose and tabulate corals disappeared near the

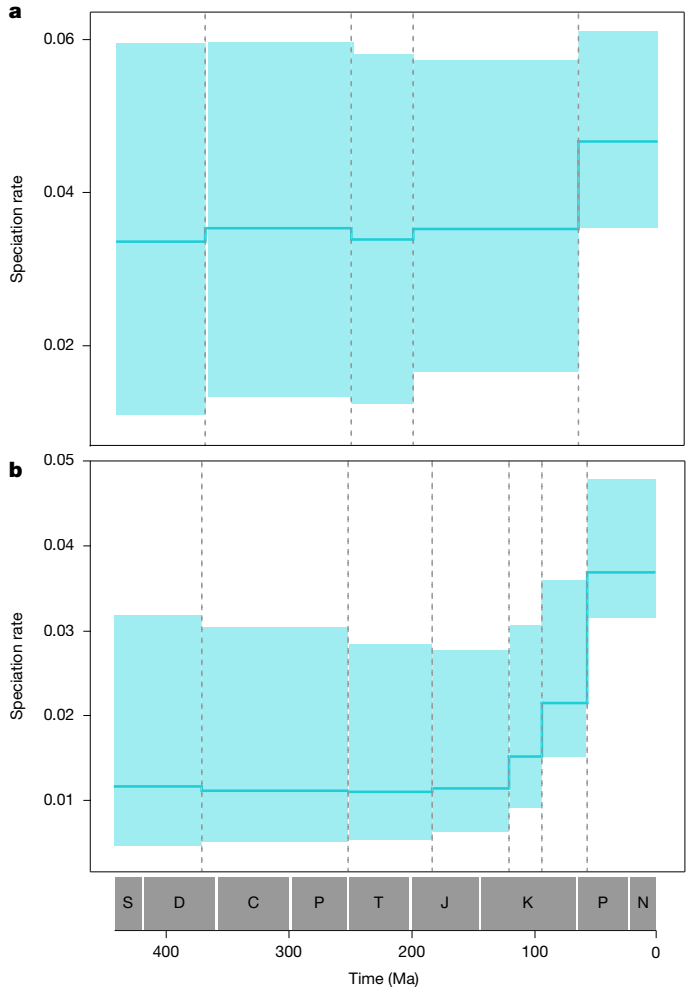

Fig. 3 | Speciation rates across deep time. a,**b**, The speciation rates across deep time calculated between MEEs (**a**) and between OAEs (**b**). The dotted lines in both figures indicate the MEEs and anoxic events.

Permian–Triassic MEE[44] (around 250 Ma), which was characterized by strong OA and ocean anoxia. Scleractinian lineages that survived this event capitalized on the resulting evolutionary opportunity and diversified, colonizing shallow-water habitats[10]. This diversification is supported by the fossil record[45,46] as well as by our calibrated phylogeny, which shows that families emerging shortly after the Permian–Triassic boundary—except for Caryophylliidae—had MRCAs that were shallow-water, colonial, substrate-attached and zooxanthellate (Fig. 2). At the same time, scleractinian corals lineages also occupied deeper habitats as supported by the MRCA depth range results and absence of photosymbionts (Fig. 2). Thus, deep-water coral lineages were probably more resilient to the Permian–Triassic MEE and OA, while colonial and symbiotic lineages that arose in the Triassic showed resilience to the subsequent Triassic–Jurassic (around 200 Ma) MEE—characterized by strong OA and global warming[11]—and the T-OAE event (about 180 Ma).

The Triassic–Jurassic MEE and T-OAE have been hypothesized to have caused a global decrease of the deep-water benthos[13]. This decrease was followed by the colonization and diversification of coral lineages with adaptive traits in deep-water environments (Fig. 2). Our data suggest that solitary and azooxanthellate lineages persisted during OAEs, perhaps because they needed less oxygen[35]. Moreover, most of the species examined here—both solitary and colonial—can upregulate their calcifying fluid internal pH, enabling calcification of the skeleton in waters below the ASH[47,48]. Most recovered MRCAs that arose after the Triassic–Jurassic and T-OAE events were solitary, azooxanthellate, deep sea or depth generalist, and either free-living or characterized by transverse division. Notably, unattached forms can move from their position—a behaviour known as automobility that is shared with some Rugosa and Tabulata corals[49]—by inflating their tissues, serving as a mechanism to escape stressful events[50,51]. Overall, free-living and transverse division character states, coupled with azooxanthellate and solitary lifestyles, probably facilitated the resilience of scleractinians against the Triassic–Jurassic and T-OAE adverse events.

Fossil records show well-diversified colonial and photosymbiotic Triassic (250–200 Ma) stony-coral lineages, the majority of which became extinct in the following adverse events (Triassic–Jurassic MEE and T-OAE)[12], showing great vulnerability to OA and OAEs. Concurrently, azooxanthellate and solitary lineages simply persisted in the deep or arose from colonial, shallow-water lineages as they invaded the deep sea (for example, ancestor lineages of the family Agariciidae) during the ongoing adverse events (Supplementary Figs. 3 and 4). Together, deep-water lineages and the few colonial and photosymbiotic families that arose in the Triassic and persisted through adverse events showed resilience against the following Aptian OAE (around 120 Ma). Additional families with a colonial and zooxanthellate MRCA arose again starting 100 Ma, after the end of major adverse events and in a period of decreasing global temperature and CO_2 concentration.

Summary

Our analyses show that the scleractinian MRCA was solitary and azooxanthellate, and that the appearance of scleractinian families with specific traits followed past palaeoclimate conditions and OAEs. First, colonial lineages with newly acquired symbiosis with zooxanthellae arose in a period of stable global temperature and CO_2 concentration, taking advantage of newly available niches vacated by the rugose and tabulate corals. Families mainly represented by solitary, azooxanthellate, free-living and deep-water species arose during or after two adjacent OAEs that severely impacted shallow-water counterparts. Increased diversification rates followed the last two Mesozoic OA and OAEs. As also shown for other aragonitic animals (such as pteropods[52]), some lineages of stony corals endured past ocean chemistry and climate changes[10]. We show that coloniality was repeatedly gained and lost while photosymbionts were independently gained, but rarely lost, in several lineages. This level of trait lability was fundamental for past survival and enabled the persistence of scleractinians across deep time. Overall, solitary and deep-sea lineages can easily acquire photosymbiosis and coloniality under the right conditions and, therefore, serve as a refugia for following recolonization of shallow-water habitats. Colonial and shallow-water species are more vulnerable to adverse events as they probably cannot survive the loss of photosymbionts. Future projections of climate change coupled with the results here show that shallow-water coral reefs will be highly impacted, but the order Scleractinia will probably survive as they have in the past with the persistence of deep-water lineages.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-025-09615-6.

1. Hoegh-Guldberg, O. et al. Coral reefs under rapid climate change and ocean acidification. *Science* **318**, 1737–1742 (2007).
2. Carpenter, K. E. et al. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science* **321**, 560–563 (2008).
3. Knowlton, N. Coral reef biodiversity-habitat size matters. *Science* **292**, 1493–1495 (2001).
4. Pandolfi, J. M., Connolly, S. R., Marshall, D. J. & Cohen, A. L. Projecting coral reef futures under global warming and ocean acidification. *Science* **333**, 418–422 (2011).

5. Mellin, C. et al. Cumulative risk of future bleaching for the world's coral reefs. *Sci. Adv.* **10**, eadn9660 (2024).
6. Kleypas, J. A. et al. Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science* **284**, 118–120 (1999).
7. Gault, J. A., Bentlage, B., Huang, D. & Kerr, A. M. Lineage-specific variation in the evolutionary stability of coral photosymbiosis. *Sci. Adv.* **7**, eabh4243 (2021).
8. Stolarski, J. et al. The ancient evolutionary origins of Scleractinia revealed by azooxanthellate corals. *BMC Evol. Biol.* **11**, 316 (2011).
9. Arrigoni, R. et al. A new sequence data set of SSU rRNA gene for Scleractinia and its phylogenetic and ecological applications. *Mol. Ecol. Resour.* **17**, 1054–1071 (2017).
10. Quattrini, A. M. et al. Palaeoclimate ocean conditions shaped the evolution of corals and their skeletons through deep time. *Nat. Ecol. Evol.* **4**, 1531–1538 (2020).
11. Kiessling, W. & Simpson, C. On the potential for ocean acidification to be a general cause of ancient reef crises. *Glob. Change Biol.* **17**, 56–67 (2011).
12. Vasseur, R. et al. Major coral extinctions during the early Toarcian global warming event. *Glob. Planet. Change* **207**, 103647 (2021).
13. Jacobs, D. K. & Lindberg, D. R. Oxygen and evolutionary patterns in the sea: onshore/offshore trends and recent recruitment of deep-sea faunas. *Proc. Natl Acad. Sci. USA* **95**, 9396–9401 (1998).
14. Cairns, S. D. Deep-water corals: an overview with special reference to diversity and distribution of deep-water scleractinian corals. *Bull. Mar. Sci.* **81**, 311–322b (2007).
15. Roberts, J. M., Wheeler, A., Freiwald, A. & Cairns, S. (eds) *Cold-Water Corals: The Biology and Geology of Deep-Sea Coral Habitats* (Cambridge University Press, 2009).
16. Orejas, C. et al. *Madrepora oculata* forms large frameworks in hypoxic waters off Angola (SE Atlantic). *Sci. Rep.* **11**, 15170 (2021).
17. Campoy, A. N. et al. The origin and correlated evolution of symbiosis and coloniality in scleractinian corals. *Front. Mar. Sci.* **7**, 461 (2020).
18. McFadden, C. S. et al. Phylogenomics, origin, and diversification of Anthozoans (phylum Cnidaria). *Syst. Biol.* **70**, 635–647 (2021).
19. Frankowiak, K. et al. Photosymbiosis and the expansion of shallow-water corals. *Sci. Adv.* **2**, e1601122 (2016).
20. Ries, J. B. Geological and experimental evidence for secular variation in seawater Mg/Ca (calcite-aragonite seas) and its effects on marine biological calcification. *Biogeosciences* **7**, 2795–2849 (2010).
21. Misof, B. et al. Phylogenomics resolves the timing and pattern of insect evolution. *Science* **346**, 763–767 (2014).
22. Shao, Y. et al. Phylogenomic analyses provide insights into primate evolution. *Science* **380**, 913–924 (2023).
23. Zuntini, A. R. et al. Phylogenomics and the rise of the angiosperms. *Nature* **629**, 843–850 (2024).
24. Erwin, D. H., Valentine, J. W. & Sepkoski, J. J. Jr A comparative study of diversification events: the early Paleozoic versus the Mesozoic. *Evolution* **41**, 1177–1186 (1987).
25. Scrutton, C. T. The Palaeozoic corals, I: origins and relationships. *Proc. York. Geol. Soc.* **51**, 177–208 (1997).
26. Scrutton, C. T. & Clarkson, E. N. K. A new scleractinian-like coral from the Ordovician of the Southern Uplands, Scotland. *Palaeontology* **34**, 179–194 (1991).
27. Ezaki, Y. The Permian coral *Numidiaphyllum*: new insights into anthozoan phylogeny and Triassic scleractinian origins. *Palaeontology* **40**, 1–14 (1997).
28. Ezaki, Y. Paleozoic Scleractinia: progenitors or extinct experiments? *Paleobiology* **24**, 227–234 (1998).
29. Barbeitos, M. S., Romano, S. L. & Lasker, H. R. Repeated loss of coloniality and symbiosis in scleractinian corals. *Proc. Natl Acad. Sci. USA* **107**, 11877–11882 (2010).
30. Campoy, A. N., Rivadeneira, M. M., Hernández, C. E., Meade, A. & Venditti, C. Deep-sea origin and depth colonization associated with phenotypic innovations in scleractinian corals. *Nat. Commun.* **14**, 7458 (2023).
31. Lindner, A., Cairns, S. D. & Cunningham, C. W. From offshore to onshore: multiple origins of shallow-water corals from deep-sea ancestors. *PLoS ONE* **3**, e2429 (2008).
32. Horowitz, J. et al. Bathymetric evolution of black corals through deep time. *Proc. R. Soc. B* **290**, 20231107 (2023).
33. Rocha, L. A. et al. Mesophotic coral ecosystems are threatened and ecologically distinct from shallow water reefs. *Science* **361**, 281–284 (2018).
34. Meyer, K. M. & Kump, L. R. Oceanic euxinia in Earth history: causes and consequences. *Annu. Rev. Earth Planet. Sci.* **36**, 251–288 (2008).
35. Buhl-Mortensen, L., Mortensen, P. B., Armsworthy, S. & Jackson, D. Field observations of *Flabellum* spp. and laboratory study of the behavior and respiration of *Flabellum alabastrum*. *Bull. Mar. Sci.* **81**, 543–552 (2007).
36. Veron, J. E. N. *Corals in Space and Time: the Biogeography and Evolution of the Scleractinia* (Cornell Univ. Press, 1995).
37. Ying, H. et al. Comparative genomics reveals the distinct evolutionary trajectories of the robust and complex coral lineages. *Genome Biol.* **19**, 175 (2018).
38. Stanley, Jr. G. D. & Fautin, D. G. The origins of modern corals. *Science* **291**, 1913–1914 (2001).
39. Chadwick, N. E. & Adams, C. in *Coelenterate Biology: Recent Research on Cnidaria and Ctenophora* (eds Williams, R. B. et al.) 263–269 (Springer, 1991).
40. Daly, M. et al. The phylum Cnidaria: a review of phylogenetic patterns and diversity 300 years after Linnaeus. *Zootaxa* **1668**, 127–182 (2007).
41. Minter, N. J. et al. Early bursts of diversification defined the faunal colonization of land. *Nat. Ecol. Evol.* **1**, 0175 (2017).
42. Judd, E. J. et al. A 485-million-year history of Earth's surface temperature. *Science* **385**, eadk3705 (2024).
43. Hongzhen, W. & Jianqiang, C. Late Ordovician and early Silurian rugose coral biogeography and world reconstruction of palaeocontinents. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **86**, 3–21 (1991).
44. Fedorowski, J. Extinction of Rugosa and Tabulata near the Permian Triassic boundary. *Acta Palaeont. Polonica.* **34**, 47–70 (1989).
45. Stanley, G. D. Jr. The evolution of modern corals and their early history. *Earth Sci. Rev.* **60**, 195–225 (2003).
46. Roniewicz, E. & Morycowa, E. Evolution of the Scleractinia in the light of microstructural data. *Cour. Forsch. Senckenberg* **164**, 233–240 (1993).
47. Anagnostou, E., Huang, K. F., You, C. F., Sikes, E. L. & Sherrell, R. M. Evaluation of boron isotope ratio as a pH proxy in the deep sea coral *Desmophyllum dianthus*: evidence of physiological pH adjustment. *Earth Planet. Sci. Lett.* **349**, 251–260 (2012).
48. McCulloch, M. et al. Resilience of cold-water scleractinian corals to ocean acidification: boron isotopic systematics of pH and saturation state up-regulation. *Geochim. Cosmochim. Acta* **87**, 21–34 (2012).
49. Plusquellec, Y., Webb, G. E. & Hoeksema, B. W. Automobility in Tabulata, Rugosa, and extant scleractinian analogues: stratigraphic and paleogeographic distribution of Paleozoic mobile corals. *J. Paleontol.* **73**, 985–1001 (1999).
50. Hoeksema, B. W. & Bongaerts, P. Mobility and self-righting by a free-living mushroom coral through pulsed inflation. *Mar. Biodivers.* **46**, 521–524 (2016).
51. Sentoku, A., Tokuda, Y. & Ezaki, Y. Burrowing hard corals occurring on the sea floor since 80 million years ago. *Sci. Rep.* **6**, 24355 (2016).
52. Peijnenburg, K. T. et al. The origin and diversification of pteropods precede past perturbations in the Earth's carbon cycle. *Proc. Natl Acad. Sci. USA* **117**, 25609–25617 (2020).

Methods

DNA extraction and genome sequencing

Specimens used here were sourced from previously published taxonomic studies[53–55], or identified by M.V.K., S.D.C. or D.H. according to approaches described previously[56,57]. Total DNA was extracted from specimens (Supplementary Table 1) using the Qiagen DNeasy Blood and Tissue kit according to the manufacturer's animal tissue protocol, except for *Anthemiphyllia patera costata*, *Cladocora* sp., *Desmophyllum pertusum*, *Paracyathus pulchellus*, *Premocyathus* sp., *Trochocyathus caryophylloides* for which the total DNA was extracted using the Qiagen Gentra Puregene Tissue kit. DNA purification was performed for samples that did not yield good DNA quality using the Genomic DNA Clean and Concentrator kit (Zymo Research). DNA quality and integrity were assessed on a microvolume spectrophotometer (Nanodrop, Thermo Fisher Scientific) and 1% agarose gel electrophoresis, respectively. Libraries were prepared using the TruSeq DNA Nano Library Preparation kit (Illumina) with modifications in index adapter concentration and the number of PCR cycles (details were reported previously[58]). For 50 specimens (Supplementary Table 1) the MyBaits protocol v.IV (Arbor BioSciences) was used to target and enrich UCEs and exons with a combination of the hexacoral/scleractinian baits sets developed previously[59–61]. The DNA concentration before and after library preparation was quantified using the Qubit fluorometer (Thermo Fisher Scientific), and the size distributions were assessed on the Bioanalyzer (Agilent). Libraries were then sequenced on multiple Illumina platforms at the (1) Human Genome and Stem Cell Research Center (CEGH-CEL, USP); (2) Genome Investigation and Analysis Laboratory (GENIAL, CEFAP/USP); and (3) Macrogen South Korea in multiple runs (Supplementary Table 1).

Bioinformatic and phylogenetic analyses

Quality control and adapter removal of demultiplexed Illumina reads was performed on Trimmomatic (v.0.39)[62]. Trimmed sequences were assembled into contigs using SPAdes (v.3.1)[63] (with the --careful parameters). Assembled reads were processed using the Phyluce (v.1.6.8) pipeline[64]. At this stage, previously published genomic and transcriptomic scleractinian data—plus Corallimorpharia and Antipatharia representatives as outgroup—were included in the analyses (Supplementary Table 1). UCEs and exon loci that matched the aforementioned combined scleractinian bait set were identified using 'phyluce_assembly_match_contigs_to_probes'; only assembled contigs with a minimum coverage of 70% and a minimum identity of 70% were retained. Loci were then extracted into separate FASTA files using 'phyluce_assembly_get_fastas_from_match_counts' and aligned with the default parameters using 'phyluce_align_seqcap_align' in MAFFT[65]. Loci were internally trimmed with 'phyluce_align_get_gblocks_trimmed_alignments_from_untrimmed', which uses GBlocks[66]. A data matrix of locus alignments was created using 'phyluce_align_get_only_loci_with_min_taxa', in which each locus had 50% data occupancy. Finally, all locus alignments were then concatenated, and the partition charset explicit using 'phyluce_align_format_nexus_files_for_raxml'.

Before the phylogenetic analyses, a saturation test was run on the nuclear loci (PhyloMad, v.1.2)[67], using entropy models on all sites. All loci displaying substitution saturation were removed from further analyses. Phylogenetic analyses were conducted using maximum-likelihood and species tree methods. For the maximum-likelihood analysis, a partitioned phylogenomic analyses was conducted in IQTree (v.2.1)[68]. The best-fit models and best partition scheme were selected by ModelFinder[69] under the Bayesian information Criterion as implemented in IQTree (v.2.1). Ultrafast bootstrapping[70] (-B 1000) was conducted as well as the SH-like approximate likelihood ratio test[71] (-alrt 1000). Phylogenetic reconstruction was rooted with Corallimorpharia and Antipatharia. The species tree analysis was conducted using ASTRAL III[72]. First, 238 gene trees (75% data occupancy alignments, loci displaying substitution saturation excluded) were constructed using IQTree with the best-fit models selected by ModelFinder. Trees were then concatenated into one file and branches with low bootstrap support (<30%) were removed using a newick utility (nw_ed)[73]. Finally, TreeShrink (v.1.3.9)[74] was used to remove long branches from gene trees before input in ASTRAL III.

Divergence time estimation

Major challenges in reliably determining the calibration points for the divergence of scleractinian clades stem, on one hand, from the limited fossil record especially of deep-water—potentially ancestral—forms and, on the other, from the profound shifts that have occurred in coral taxonomy, which substantially hinder the correlation between, for example, early Mesozoic and modern taxa. Historically, scleractinian taxonomy was based on macromorphological characteristics and specific microstructural features[75]. However, the advent of molecular phylogenetics has fundamentally reshaped our understanding of scleractinian evolution, rejecting the monophyly of several traditionally recognized lineages[76–78]. Integrating molecular data with detailed skeletal analyses has since demonstrated the taxonomic significance of previously overlooked morphological traits (for example, the arrangement patterns of skeletal fibres, referred to as thickening deposits), which have been found to be informative for molecularly defined clades[79,80]. While correlations between skeletal microstructure and molecular phylogeny for some extant coral lineages are now established, applying these criteria to fossil taxa remains a major challenge. The taxonomy of extinct scleractinians requires revision using modern criteria, but this effort is hindered by the often-poor preservation of skeletal material in many fossil groups. In this scenario, we have prioritized fossil forms that can be unambiguously assigned to extant clades: five fossil calibration points (genus *Acropora* (56 Ma)[81,82]; genus *Caryophyllia* (160 Ma)[8]; family Dendrophylliidae (127 Ma)[8]; genus *Madrepora* (71 Ma)[83]; and genus *Oculina* (100 Ma)[84]) were selected for dating the scleractinian phylogeny. These selected taxa provide the most reliable calibration points for molecular phylogenetic analyses, ensuring a robust framework for reconstructing scleractinian evolutionary history.

Divergence dating was performed in BEAST2 (v.2.5)[85]. Exponential priors were used for calibration points with minimum age constraints set as the offset values and mean values set as 10% of the offsets. A relaxed clock model with a lognormal distribution on the ucld.mean (initial 0.0002, 0-infinity bounds; following ref. 8) and the uniform distribution on the ucld.stdev (initial 0.1, 0–1 bounds) was calculated. A birth–death tree prior was also used, with uniform priors on the birth rate (initial 1.0, 0–1,000 bounds) and death rate (initial 0.5, 0–1 bounds). Following ref. 86, we used a fixed topology in BEAST2. This topology was first time-calibrated with the above-mentioned fossils (no root calibration) using a penalized likelihood method[87] in the R package ape. We included 30 loci in the BEAST2 analysis[10] selected to be the most represented in terms of number of taxa. Locus data were partitioned so that a GTRGAMMA model (initial 1.0, 0 to infinity bounds) was applied to each of them. Three separate runs of 200 million generations were conducted. Log and tree files from each run were combined in LogCombiner[85] using a 10% burn-in. The combined log file was assessed for convergence of parameter values and age estimates by inspecting traces and effective sample sizes in Tracer (v.1.7)[88]. TreeAnnotator[85] was then used to produce a maximum clade credibility tree. A separate analysis (two separate runs of 250 million generations) was also conducted without data by sampling from the prior, to ensure that the results were driven by the data and not solely by the prior information[89] (Supplementary Fig. 7).

The combined tree file was resampled to randomly select 11,995 trees to obtain the 95% highest posterior distribution of node ages (crown age) for particular clades (crown groups). Clades for which 95% highest posterior distributions were calculated included the following: main families (if monophyletic); the two main clades at the subordinal level (that is, Refertina and Vacatina); and also, for the order. Group A is a

monophyletic lineage of species with congruent traits in the process of being described (Supplementary Results and Discussion). Families represented by equal to or less than three branches (and it was therefore not possible to calculate properly their crown age) were not included. The plotting of the posterior distributions was conducted in R (https://github.com/johnjschenk/Rcode/blob/master/NodeAgeDensity.R).

Finally, the crown ages retrieved for the main families (Supplementary Table 4) and coloniality trait were compared with the ages and traits of the oldest fossil for each group. Literature data were leveraged to compile a table with information about the oldest fossil for all the families included in the study. Fossil age, coloniality trait and related references were populated in the table including some remarks regarding the reliability of the fossil information and/or the systematics of each considered group.

Ancestral state reconstruction

Ancestral states of coloniality (colonial or solitary), symbiosis (zooxanthellate, azooxanthellate or facultative) and relationship to substrate (attached, free-living, or transverse division species) were calculated using stochastic character mapping, which samples ancestral states from their posterior probability distribution (term definitions are provided in Supplementary Table 3). The best fit model (between equal rates (ER), all-rates-different (ARD) and symmetric (SYM)) was calculated for each trait using the Akaike information criterion method (the model with the lowest Akaike information criterion value was chosen). Posterior probabilities were generated under the best model from 100 stochastic character maps for each trait using the make.simap function in the R package phytools[90]. Character maps for each trait were plotted on the time-calibrated tree. The ancestral ranges (deep (species only found at >200 m), shallow (species only found at <200 m) or deep and shallow (species that can be found at both bathymetric ranges) waters) were calculated using a dispersal–extirpation–cladogenesis model in RevBayes (v.1.0.12)[91]. The resulting ancestral ranges were plotted using the RevGadgets function (https://github.com/revbayes/RevGadgets) in R.

Diversification rate analyses

Episodic speciation rates were calculated in RevBayes (v.1.2.2)[91] to determine whether they shifted across past adverse events. Speciation rates were calculated between mass extinction and anoxic events. A uniform taxon sampling strategy was used, with incomplete taxon sampling accounted for by dividing the number of tips by the total number of scleractinian species (rho). Two MCMC runs were conducted for 500,000 generations (tuning interval 200). Speciation rates were plotted using the RevGadgets[92] function (https://github.com/revbayes/RevGadgets) in R with the weighted average rate computed in each of 100 time intervals. Branch-specific diversification rates[93] were also calculated on the time-calibrated tree in RevBayes (v.1.2.2)[91] to determine whether branch rates ($k = 6$ discrete branch-rate categories) varied across the phylogeny. The extinction rate was kept constant, and a uniform incomplete taxon strategy was used with incomplete taxon sampling accounted for by dividing the number of tips by the total number of scleractinian species (rho). Two MCMC runs were conducted for 30,000 generations. Trace files were examined for convergence in Tracer (v.1.7)[88]. The resulting diversification rates were plotted using the RevGadgets function in R.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Nuclear UCEs and exon locus sequences were deposited as a Targeted Locus Study at DDBJ, ENA and GenBank under BioProject accession PRJNA1294964, BioSamples SAMN50172845–SAMN50173024 and accession numbers KJBF00000000–KJIC00000000 (Supplementary Table 1). Scleractinia bait set and tree files are available at Figshare[94] (https://doi.org/10.6084/m9.figshare.29242487).

53. Kitahara, M. V. Species richness and distribution of azooxanthellate Scleractinia in Brazil. *Bull. Mar. Sci.* **81**, 497–518 (2007).
54. Capel, K. C. et al. *Atlantia*, a new genus of Dendrophylliidae (Cnidaria, Anthozoa, Scleractinia) from the eastern Atlantic. *PeerJ* **8**, e8633 (2020).
55. Kitahara, M. & Cairns, S. *Tropical Deep-Sea Benthos* Vol. 32 (Publications Scientifiques du Muséum, 2021).
56. Cairns, S. D. *The Marine Fauna of New Zealand: Scleractinia (Cnidaria: Anthozoa)* (NIWA, 1995).
57. Wong, J. S. Y. et al. Comparing patterns of taxonomic, functional and phylogenetic diversity in reef coral communities. *Coral Reefs* **37**, 737–750 (2018).
58. Seiblitz, I. G. et al. Caryophylliids (Anthozoa, Scleractinia) and mitochondrial gene order: insights from mitochondrial and nuclear phylogenomics. *Mol. Phylogenet. Evol.* **175**, 107565 (2022).
59. Quattrini, A. M. et al. Universal target-enrichment baits for anthozoan (Cnidaria) phylogenomics: new approaches to longstanding problems. *Mol. Ecol. Resour.* **18**, 281–295 (2018).
60. Cowman, P. F. et al. An enhanced target-enrichment bait set for Hexacorallia provides phylogenomic resolution of the staghorn corals (Acroporidae) and close relatives. *Mol. Phylogenet. Evol.* **153**, 106944 (2020).
61. Quek, Z. B. R., Jain, S. S., Neo, M. L., Rouse, G. W. & Huang, D. Transcriptome-based target-enrichment baits for stony corals (Cnidaria: Anthozoa: Scleractinia). *Mol. Ecol. Resour.* **20**, 807–818 (2020).
62. Bolger, A. M., Lohse, M. & Usadel, B. Trimmomatic: a flexible trimmer for Illumina sequence data. *Bioinformatics* **30**, 2114–2120 (2014).
63. Bankevich, A. et al. SPAdes: a new genome assembly algorithm and its applications to single-cell sequencing. *J. Comput. Biol.* **19**, 455–477 (2012).
64. Faircloth, B. C. PHYLUCE is a software package for the analysis of conserved genomic loci. *Bioinformatics* **32**, 786–788 (2016).
65. Katoh, K., Misawa, K., Kuma, K. & Miyata, T. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Res.* **30**, 3059–3066 (2002).
66. Castresana, J. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Mol. Biol. Evol.* **17**, 540–552 (2000).
67. Duchêne, D. A., Mather, N., van der Wal, C. & Ho, S. Y. W. Excluding loci with substitution saturation improves inferences from phylogenomic data. *Syst. Biol.* **71**, 676–689 (2021).
68. Nguyen, L. T., Schmidt, H. A., Von Haeseler, A. & Minh, B. Q. IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Mol. Biol. Evol.* **32**, 268–274 (2015).
69. Kalyaanamoorthy, S., Minh, B. Q., Wong, T. K. F., von Haeseler, A. & Jermiin, L. S. ModelFinder: fast model selection for accurate phylogenetic estimates. *Nat. Methods* **14**, 587–589 (2017).
70. Hoang, D. T., Chernomor, O., von Haeseler, A., Minh, B. Q. & Vinh, L. S. UFBoot2: improving the ultrafast bootstrap approximation. *Mol. Biol. Evol.* **35**, 518–522 (2018).
71. Anisimova, M., Gil, M., Dufayard, J.-F., Dessimoz, C. & Gascuel, O. Survey of branch support methods demonstrates accuracy, power, and robustness of fast likelihood-based approximation schemes. *Syst. Biol.* **60**, 685–699 (2011).
72. Zhang, C., Rabiee, M., Sayyari, E. & Mirarab, S. ASTRAL-III: polynomial time species tree reconstruction from partially resolved gene trees. *BMC Bioinform.* **19**, 15–30 (2018).
73. Junier, T. & Zdobnov, E. M. The Newick utilities: high-throughput phylogenetic tree processing in the UNIX shell. *Bioinformatics* **26**, 1669–1670 (2010).
74. Mai, U. & Mirarab, S. TreeShrink: fast and accurate detection of outlier long branches in collections of phylogenetic trees. *BMC Genom.* **19**, 23–40 (2018).
75. Wells, J. W. in *Treatise on Invertebrate Paleontology, Part F. Coelenterata* (ed. Moore, R. C.) F328–F444 (Geological Society of America, 1956).
76. Romano, S. L. & Palumbi, S. R. Evolution of scleractinian corals inferred from molecular systematics. *Science* **271**, 640–642 (1996).
77. Kitahara, M. V. et al. A comprehensive phylogenetic analysis of the Scleractinia (Cnidaria, Anthozoa) based on mitochondrial CO1 sequence data. *PLoS ONE* **5**, e11490 (2010).
78. Huang, D., Licuanan, W. Y., Baird, A. H. & Fukami, H. Cleaning up the 'Bigmessidae': molecular phylogeny of scleractinian corals from Faviidae, Merulinidae, Pectiniidae and Trachyphylliidae. *BMC Evol. Biol.* **11**, 37 (2011).
79. Stolarski, J. et al. A unique coral biomineralization pattern has resisted 40 million years of major ocean chemistry change. *Sci. Rep.* **6**, 27579 (2016).
80. Janiszewska, K. et al. Microstructural disparity between basal micrabaciids and other scleractinia: new evidence from Neogene *Stephanophyllia*. *Lethaia* **48**, 417–428 (2015).
81. Carbone, F., Matteucci, R., Rosen, B. R. & Russo, A. Recent coral facies of the Indian Ocean coast of Somalia with an interim check list of corals. *Facies* **30**, 1–13 (1994).
82. Vecsei, A. & Moussavian, E. Paleocene reefs on the Maiella platform margin, Italy: an example of the effects of the Cretaceous/Tertiary boundary events on reefs and carbonate platforms. *Facies* **36**, 123–139 (1997).
83. Stolarski, J. & Vertino, A. First Mesozoic record of the scleractinian *Madrepora* from the Maastrichtian siliceous limestones of Poland. *Facies* **53**, 67–78 (2007).
84. Squires, D. F. *The Cretaceous and Tertiary Corals of New Zealand* Paleontological Bulletin 29 (New Zealand Geological Survey, 1958).
85. Bouckaert, R. et al. BEAST 2.5: an advanced software platform for Bayesian evolutionary analysis. *PLoS Comput. Biol.* **15**, e1006650 (2019).
86. Oliveros, C. H. et al. Earth history and the passerine superradiation. *Proc. Natl Acad. Sci. USA* **116**, 7916–7925 (2019).
87. Sanderson, M. J. Estimating absolute rates of molecular evolution and divergence times: a penalized likelihood approach. *Mol. Biol. Evol.* **19**, 101–109 (2002).

88. Rambaut, A., Drummond, A. J., Xie, D., Baele, G. & Suchard, M. A. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Syst. Biol.* **67**, 901–904 (2018).
89. Brown, J. W. & Smith, S. A. The past sure is tense: on interpreting phylogenetic divergence time estimates. *Syst. Biol.* **67**, 340–353 (2018).
90. Revell, L. J. phytools 2.0: an updated R ecosystem for phylogenetic comparative methods (and other things). *PeerJ* **12**, e16505 (2024).
91. Höhna, S. et al. RevBayes: Bayesian phylogenetic inference using graphical models and an interactive model-specification language. *Syst. Biol.* **65**, 726–736 (2016).
92. Tribble, C. M. et al. RevGadgets: an R package for visualizing Bayesian phylogenetic analyses from RevBayes. *Methods Ecol. Evol.* **13**, 314–323 (2022).
93. Höhna, S. et al. A Bayesian approach for estimating branch-specific speciation and extinction rates. Preprint at *BioRxiv* https://doi.org/10.1101/555805 (2019).
94. Vaga, C. F. et al. Data for 'A global coral phylogeny reveals resilience and vulnerability through deep time'. *Figshare* https://doi.org/10.6084/m9.figshare.29242487 (2025).
95. Bosellini, F. R., Papazzoni, C., A. & Vescogni, A. Exceptional development of dissepimental coenosteum in the new Eocene scleractinian coral genus Nancygyra (Ypresian, Monte Postale, NE Italy). *Boll. Soc. Paleontol. Ital.* **59**, 291–298 (2020).
96. Stolarski, J. On Cretaceous *Stephanocyathus* (Scleractinia) from the Tatra Mts. *Acta Palaeontol. Pol.* **35**, 31–39 (1990).

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Author contributions The project was conceived by C.F.V. and M.V.K. with input from A.M.Q and D.H. C.F.V, Z.B.R.Q. and I.G.d.L.e.S. conducted the molecular laboratory work. C.F.V. analysed the genetic data and conducted all bioinformatic and phylogenetic analyses with guidance from A.M.Q. and M.V.K. J.S. helped with the divergent time estimation analyses. C.F.V., A.M.Q., D.H., S.D.C., J.S. and M.V.K. aided in interpretation of results. C.F.V., M.V.K. and A.M.Q. wrote the manuscript with input from all of the other authors. All of the authors contributed to and approved the final version of the manuscript.

Competing interests The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to Claudia Francesca Vaga or Marcelo Visentini Kitahara.

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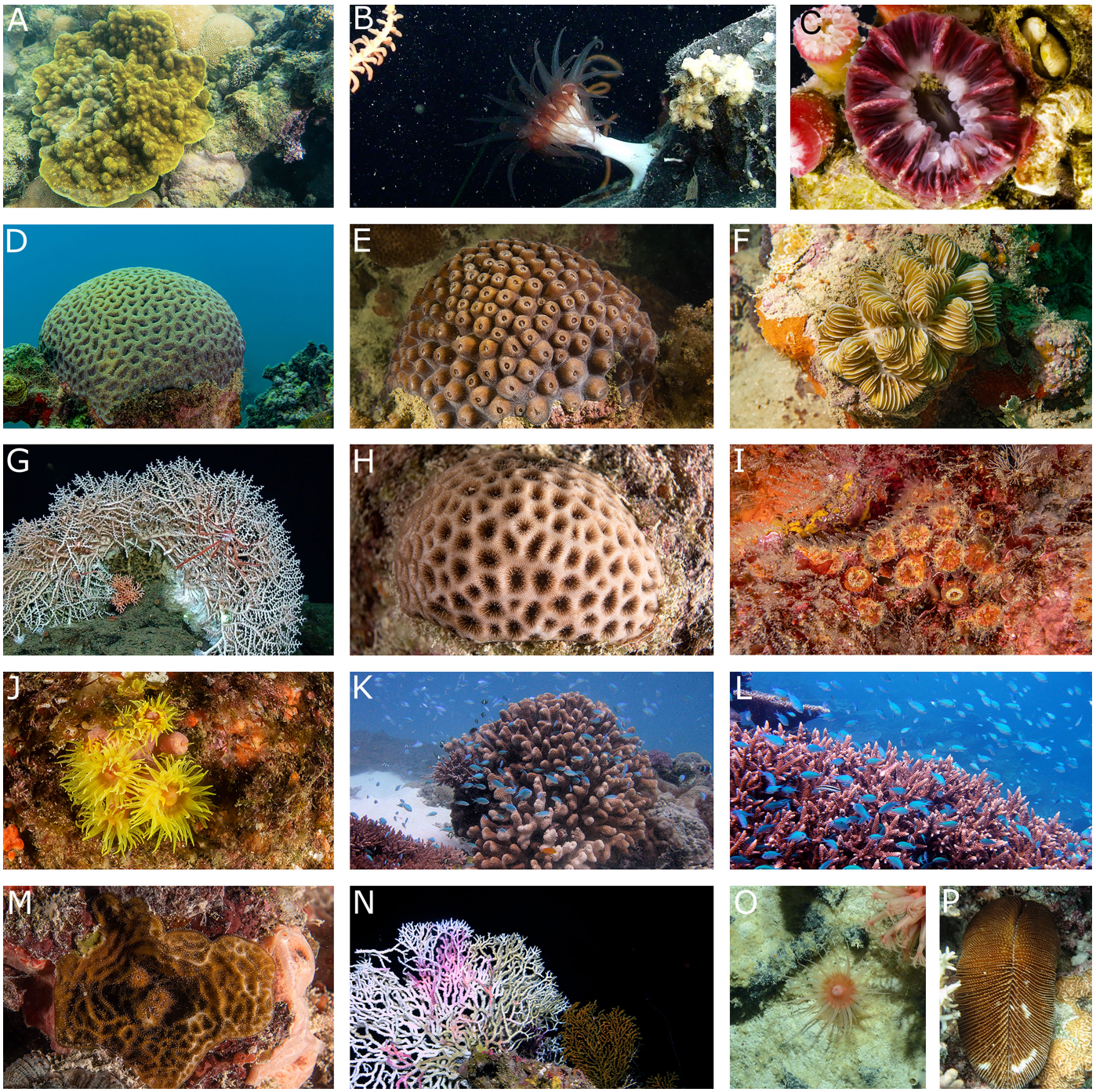
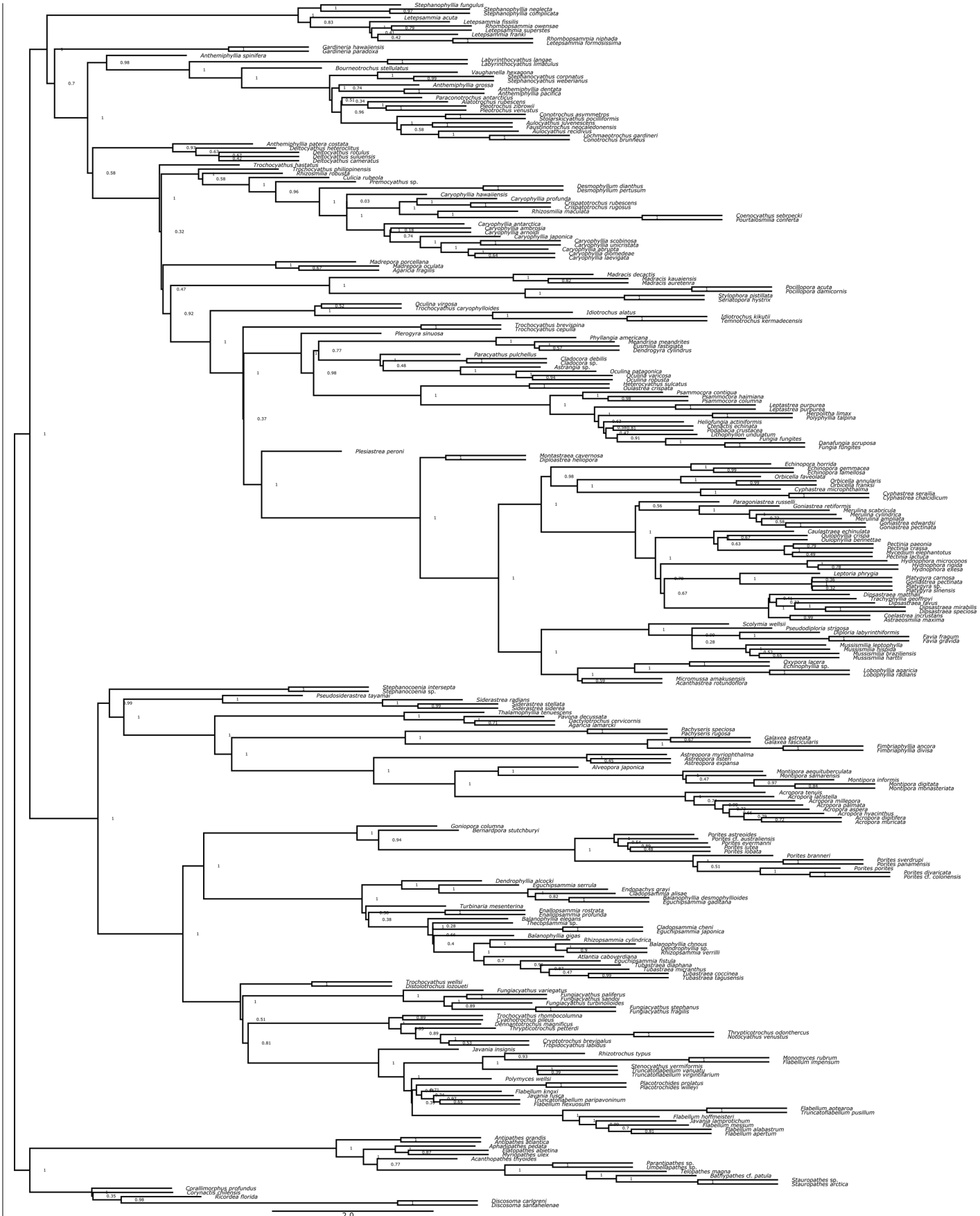
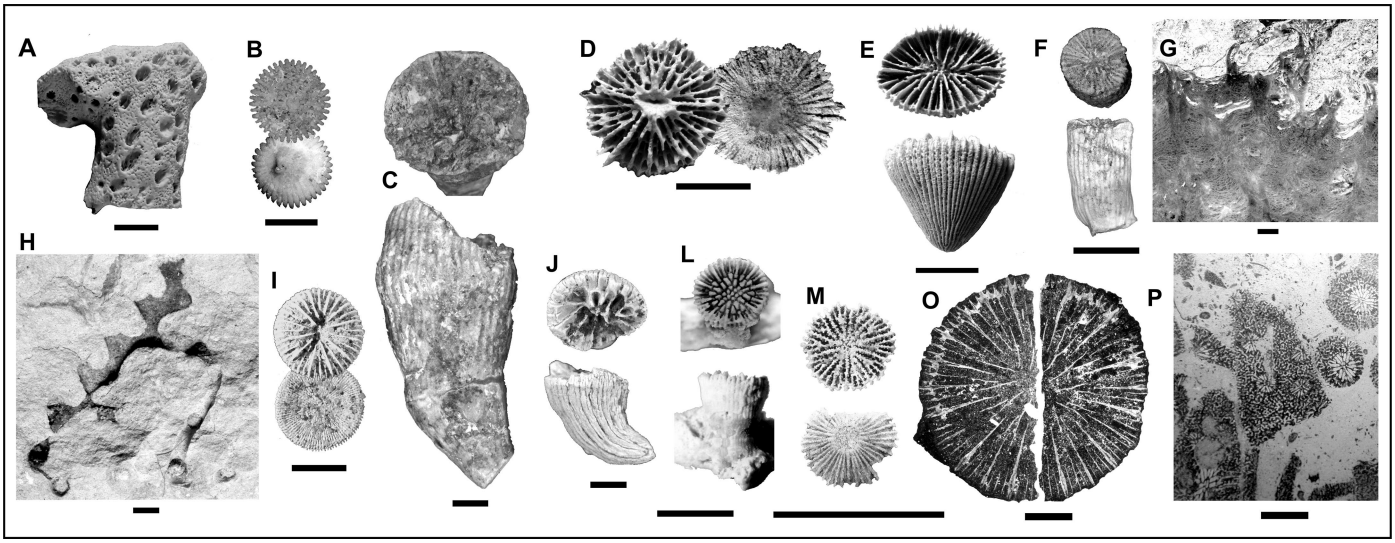


Extended Data Fig. 1 | Photographs of different families of scleractinians. A) Poritidae, B) Flabellidae, C) Caryophylliidae, D) Faviidae, E) Montastreidae, F) Meandrinidae, G) Madreporidae, H) Siderastreidae, I) Rhizangiidae, J) Dendrophylliidae, K) Pocilloporidae, L), Acroporidae, M) Agariciidae, N) Pocilloporidae, O) Clade VI, P) Fungiidae. Photographs credits: A, C, D, E, F, H, I, J, K, L, M, P – Marcelo V. Kitahara; B, G, N – DeepCAST Expeditions from 2010-2011, co-sponsored by Schmidt Ocean Institute, Smithsonian Institution (NMNH) and National Centers for Coastal Ocean Science (NOAA); and O – Deep Towed Imaging System camera, Earth Sciences New Zealand, TAN1802 – The Ross Sea Environment and Ecosystem Voyage 2018.



Extended Data Fig. 2 | Species tree. ASTRAL III species tree with posterior probabilities calculated in ASTRAL.



Extended Data Fig. 3 | Selected fossil (Mesozoic and Cenozoic) representatives of scleractinian corals, including some examples of the possibly oldest recognized members (see Supplementary Table 2 for comparison). A. Colonial acroporiid *Acropora alvarezi* (lateral view of the branch) Paleogene, middle Eocene (47.8-38 Ma); B. Solitary anthemiphyllid (distal and basal views) *Anthemiphyllia catinata*: Paleogene, late Eocene (37.71-33.9 Ma); C. Solitary? gardineriid *Gardineria simojovelensis* (distal and lateral views) Neogene, Miocene (23.03-5.3 Ma); D. Solitary fungiacyathid *Fungiacyathus deltoidophorus* (distal and basal views) Cretaceous, Maastrichtian (72.1-66 Ma); E. Solitary turbinoliid (distal and lateral views) *Bothrophoria ornata*: Cretaceous, Maastrichtian (72.1-66 Ma); F. Solitary cladocorid (distal and lateral views) *Paracyathus cylindricus*: Paleogene, Paleocene (66-56 Ma); G. Colonial euphylliid (polished longitudinal section) *Nancygyra dissepimentata*: Paleogene, early Eocene (48.5-51 Ma); H. Colonial madreporid (lateral view) *Madrepora* sp.: Cretaceous, Maastrichtian (72.1-66 Ma); I. Solitary micrabaciid (distal and basal views) *Micrabacia coronula*: Cretaceous, Cenomanian (100.5-93.9 Ma); J. Solitary flabellid *Flabellum andersonii* (distal section and lateral view) Cretaceous, Maastrichtian (72.1-66 Ma); L. Solitary caryophyllid *Caryophyllia suevica* (distal and lateral views) Jurassic, Oxfordian (160 Ma); M. Solitary deltocyathid (distal and basal views) *Deltocyathus* sp.: Jurassic, Bajocian (168.2-170.9 Ma); O. Solitary stephanocyathid (distal thin-section) *Stephanocyathus (Stephanocyathus) antiquus*: Cretaceous, Albian (113-100.5 Ma); P. Colonial dendrophyllid (oblique and transverse sections) *Blastozopsammia guerrerolerion*: Cretaceous, upper Albian-lower Cenomanian (127 Ma). Images: C, CalPhotos, under a Creative Commons CC BY 3.0 licence; G, adapted from ref. 95, under a Creative Commons CC BY 4.0 licence; O, reproduced from ref. 96, under a Creative Commons CC BY 4.0 licence.

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Corresponding author(s): Claudia Francesca Vaga, Marcelo Visentini Kitahara

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Reporting Summary

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Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed
☒	☐ The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☒	☐ A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☒	☐ The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☒	☐ A description of all covariates tested
☒	☐ A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☒	☐ A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☒	☐ For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☐	☒ For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐ For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐ Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	We used code in the phyluce package (v 1.6.8), which is available freely on line to obtain ultraconserved and exon loci from our samples.
Data analysis	List of used softwares in the analyses: Trimmomatic v 0.39; SPAdes v 3.1; Phyluce v 1.6.8 ; PhyloMad v 1.2; IQTree v 2.1; ASTRAL III (which include the programs LogCombiner and TreeAnnotator); TreeShrink v1.3.9; BEAST2 v2.5; Tracer v.1.7; RevBayes version 1.0.12; RevBayes version 1.2.2; newick utility (nw_ed). We used freely available software programs and/or code to analyze data. All programs and R packages (phytools, RevGadget) are provided in the text with relevant citations or with links to access the code.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

Nuclear UCEs and exon loci sequences were deposited as a Targeted Locus Study [TLS] at DDBJ/ENA/GenBankGenBank under the BioProject PRJNA1294964,

BioSamples #SAMN50172845-SAMN50173024, accession numbers KJBF00000000-KJIC00000000 (See also Supplementary Table 1). Scleractinia bait set and tree files: figshare https://doi.org/10.6084/m9.figshare.29242487

Research involving human participants, their data, or biological material

Policy information about studies with human participants or human data. See also policy information about sex, gender (identity/presentation), and sexual orientation and race, ethnicity and racism.

Reporting on sex and gender	n/a
Reporting on race, ethnicity, or other socially relevant groupings	n/a
Population characteristics	n/a
Recruitment	n/a
Ethics oversight	n/a

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	This is a time-calibrated molecular phylogenetic analysis, which includes hundreds of newly sequenced coral taxa, to shed new light on the deep-time evolution of scleractinian corals.
Research sample	This work is focused on the order Scleractinia (stony corals) in the phylum Cnidaria. We used 291 specimens from museum collections or using previously published data. information about each sample inlcuded in the study are included in Supplementary Table 1.
Sampling strategy	Our strategy was to use species from most families of scleractinians to ensure complete representation across the phylogeny.
Data collection	We used museum preserved specimens and already published data.
Timing and spatial scale	n/a
Data exclusions	n/a
Reproducibility	n/a
Randomization	n/a
Blinding	n/a

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☐	☒ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern
☒	☐ Plants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Animals and other research organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research, and Sex and Gender in Research

Laboratory animals	n/a
Wild animals	n/a
Reporting on sex	n/a
Field-collected samples	No field work was conducted for this present study. All specimens where deposited in collections.
Ethics oversight	n/a

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Plants

Seed stocks	n/a
Novel plant genotypes	n/a
Authentication	n/a