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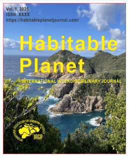

Coralline algae as integral components of shallow-marine ecosystems: Anecdotes of past resilience and future outlook

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ABSTRACT

Coralline red algae are among the major groups of calcified benthic biota thriving in the marine photic zone globally as crustose and erect forms, attached to the substrate or forming free-living nodules (rhodoliths). From the deep-time geological past to the modern era, coralline algae have been highly valuable carbonate producers and ecosystem engineers but received lesser attention compared to the visually dominant corals and kelps. Coralline algal beds denoting extremely productive habitats cover wide-ranging coastal shelf and upper slope horizons of the Earth but several gaps persist in our understanding of their systematics, productivity, net carbon flux dynamics and inputs to the oceanic carbon cycle. The current review emphasizes on the taxonomy, ecology and distribution of coralline algae in the shallow-marine ecosystems deciphered both in the context of Recent environments and fossil archives. Numerous discrepancies exist particularly in the taxonomy of fossil coralline algae, strongly dependent on morpho-anatomical study approaches. The communities of biologists and palaeontologists worldwide need to manifest a shared knowledge platform and present a viable nomenclature scheme to facilitate summarizing the critical functional traits associated with coralline algae. Persistent occurrence of several coralline genera from the Cretaceous period to the Holocene epoch reflect high-end resilience across multiple extreme events including Cretaceous-Palaeogene (K–Pg) mass extinction, Palaeocene-Eocene Thermal Maximum (PETM), Early Eocene Climatic Optimum (EECO) and Middle Eocene Climatic Optimum (MECO). In view of the ongoing global change phenomena like ocean warming, acidification and adverse sea-level fluctuations, future outlook pertaining to the studies of coralline algae should essentially seek both quantitative and qualitative datasets from diverse domains of the Earth. This should be supplemented with special focus on the response of corallines to past hyperthermals and climate change, when corals perished at large scales compared to the relatively tenacious corallines.

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Research Highlights

- Key habitat modifiers, coralline red algae contribute enormously to the global carbonate budget.
- Determination of coralline palaeodiversity is jeopardized by challenges in sampling and morpho-anatomical approaches.
- Despite a debatable origin, these are well-defined, imperative components of Cenozoic shallow-marine environments.
- Persistent evolution of several coralline genera spanning >140 Myr reflect extreme ecological resilience.
- Rapid decline of coral reefs can increase the roles of coralline algae in reef-building worldwide.

1 Introduction

Coralline red algae (Subclass: Corallinophycidae) are heavily calcifying benthic macroalgae thriving commonly as crustose forms and free-living rhodoliths in widespread euphotic to mesophotic ecosystems from polar to tropical horizons (Nelson, 2009; Teichert, 2024). Crustose coralline carpets and rhodolith beds are both representatives of large-scale globally distributed coralline algal-dominated marine habitats with the latter forming under conditions of low hydrodynamic energy as intense water movement could scatter or bury slow-growing rhodoliths (Nelson, 2009; McCoy and Kamenos, 2015). Plethora of factors like biogeography, evolution, climate, plate tectonics, sedimentary regime and oceanography acting in tandem determine their abundance and taxonomic composition (Halfar and Mutti, 2005; Sarkar, 2017). The coralline thalli are characterized by calcified (high-Mg calcite) cell walls, that has subsequently ensured an excellent fossil record (Aguirre et al., 2000). They are highly prevalent across the Cenozoic with robust archives but their origin is still disputed with some workers stating it to be in the Early Cretaceous/Mesozoic while some argue in favor of their earliest records in the Palaeozoic (Teichert, 2024).

Owing to their extensive and incessant growth across hundreds of years, coralline algae serve as valuable palaeoenvironmental indicators. This application is attributed to the presence of annual and subannual growth bands composed of high-Mg calcite in several species of both the non-geniculate crustose corallines and rhodoliths (Fig. 1). These are highly significant in palaeoenvironmental reconstructions as critical data pertaining to past climate can be ascertained by evaluation of the seasonal banding patterns reflecting alterations in the degree of cellular calcification. Lighter bands linked to faster, low-density growth in summers and darker bands indicating the winters allow the researchers to study past growth patterns and environmental conditions of the corallines. These studies are included under the discipline of algochronology which uses the analysis of structural metrics obtained from the growth bands of coralline algae to determine environments and climate regimes of the past (McCoy and Kamenos, 2015, and references therein). However, several corallines with encrusting growth-forms do not show the growth bands due to (1) action of grazing herbivores, and (2) fixed level of vertical thickness. Geniculate corallines also do not form growth bands since their growth features formation of new apical segments.

Coralline algae are highly significant proxies in shallow-marine settings worldwide as critical carbonate producers and ecosystem engineers. They are among the most prolific carbonate producers contributing to the oceanic carbon cycle (Basso, 2012; Cornwall et al., 2023). Prevailing data shows four orders of magnitude pertinent to carbonate production by coralline algae, with the highest rates in tropical reefs, in the Mediterranean infralittoral communities and the maerl beds of the French Atlantic, whereas the lowest values being from temperate seagrass epiphyte and deep soft-bottom assemblages indicating a wide latitudinal belt (Basso, 2012). However, research assignments to assess the magnitude and direction of associated carbon fluxes (linked to net organic carbon metabolism and carbonate dynamics) with regard to coralline algal beds have been very limited in comparison to coral reefs and kelps.

The equilibrium of marine biodiversity dynamics culminates from continuous biotic interactions and environmental change. Behavior of ecosystem engineers with potential for modifying resource availability have established considerable effects on modern community ecology and diversity, although their precise roles in ancient ecosystems over geological time remain understudied. Acting as ecosystem engineers with strong controls on benthic communities, rhodoliths provide three-dimensional habitats whereas crustose corallines commonly act as the cement that holds coral reefs together (Littler and Littler, 2013; Cornwall et al., 2023). The coralligenous habitat pertinent to intertidal-subtidal environments and rocky shores is an excellent

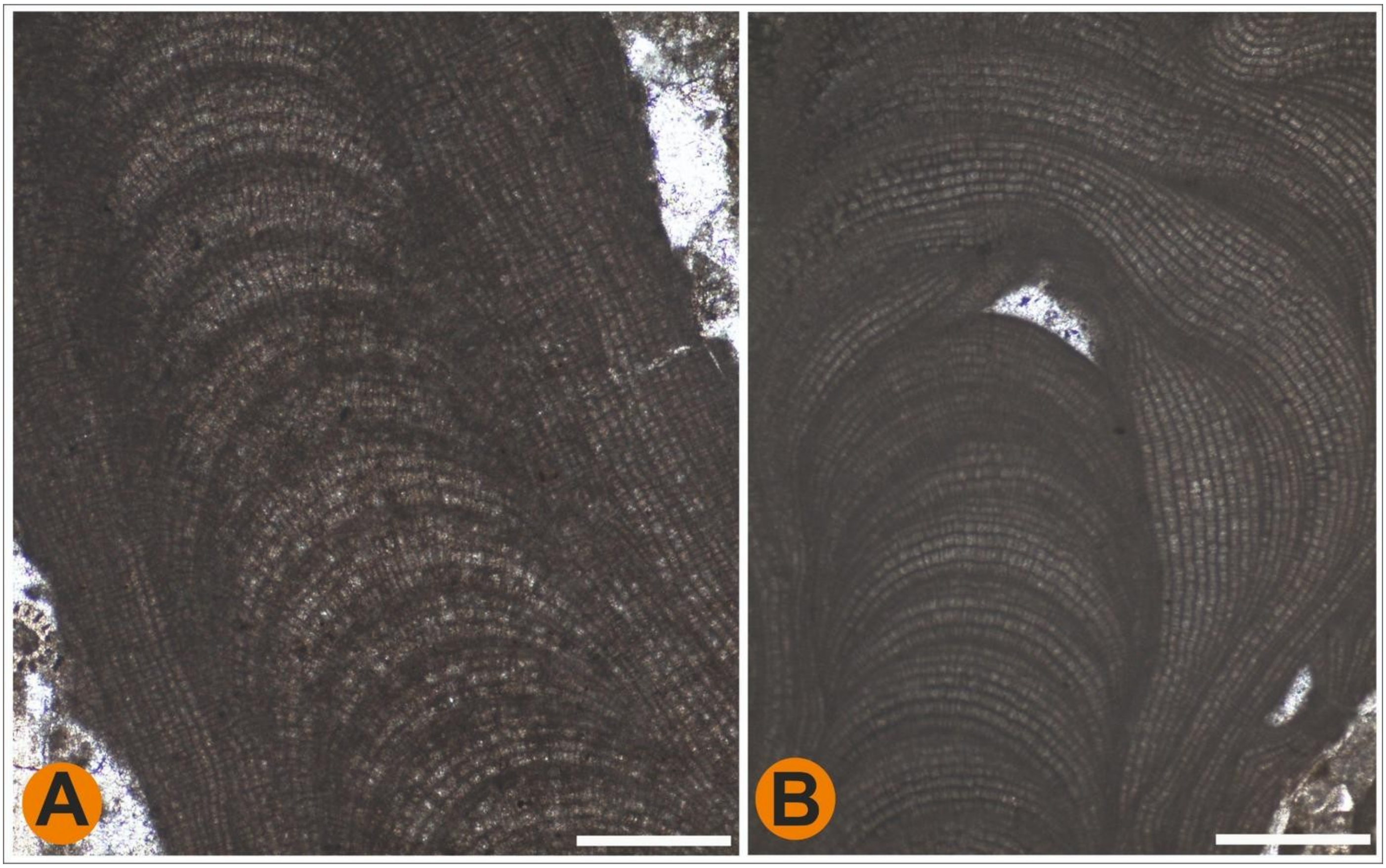

Fig. 1. Petrographic thin-sections of fossil non-geniculate coralline red algae (from late Palaeocene of NE India) showing seasonal growth bands in (A) Rhodolith, and (B) Crustose specimens. Scale Bars: 0.3 mm.

example of carbonate bioconstruction involving the corallines (Basso et al., 2022).

This review discusses the underrated status of coralline red algae as important benthic components of shallow-marine ecosystems distributed globally with a brief overview of the taxonomic constraints hampering their fundamental identification and analysis, especially in the geological record. Their widespread distribution and ecological resilience along a long stratigraphic column continuing till date presents an interesting example of a biotic group displaying persistent survival despite high level of sensitivity to global changes like ocean acidification. Both improved taxonomic and ecological assessments are crucial in better understanding of their roles at higher levels—productivity of coralline algal beds and contribution of corallines to the carbon flux dynamics and overall oceanic carbon cycle.

2 Challenges in taxonomy

The taxonomic orders within the subclass Corallinophycidae representing coralline red algae are Corallinales, Hapalidiales, Corallinapetrales, Sporolithales and Rhodogorgonales (Fig. 2) in addition to the indeterminate forms and outgroups (*incertae sedis*). Based on morphology, coralline red algae can be broadly classified into two major groups—geniculate (articulated) and non-geniculate (non-articulated or encrusting). The former is considered to have evolved from the latter although few instances of reversals in this trend have also been reported (Peña et al., 2020). Non-geniculates are characterized by completely calcified thalli contrary to the presence of non-calcified genicula (with calcified intergenicula) in the geniculate corallines presenting very rare cases of preservation. This is reflected in numerous case studies on fossil non-geniculate corallines with species-level identifications, while study of fossil geniculates have been relatively limited (Sarkar, 2024). Fossil specimens of intergenicula fragments have even been suggested to be placed under the informal group "Geniculate *sensu lato*" (Bassi et al., 2000), although some workers continue to attempt species-level identifications for the geniculates purely based on morpho-anatomy. This involves the identification of preserved intergenicula assignable to genera like *Amphiroa*, *Arthrocardia*, *Corallina*

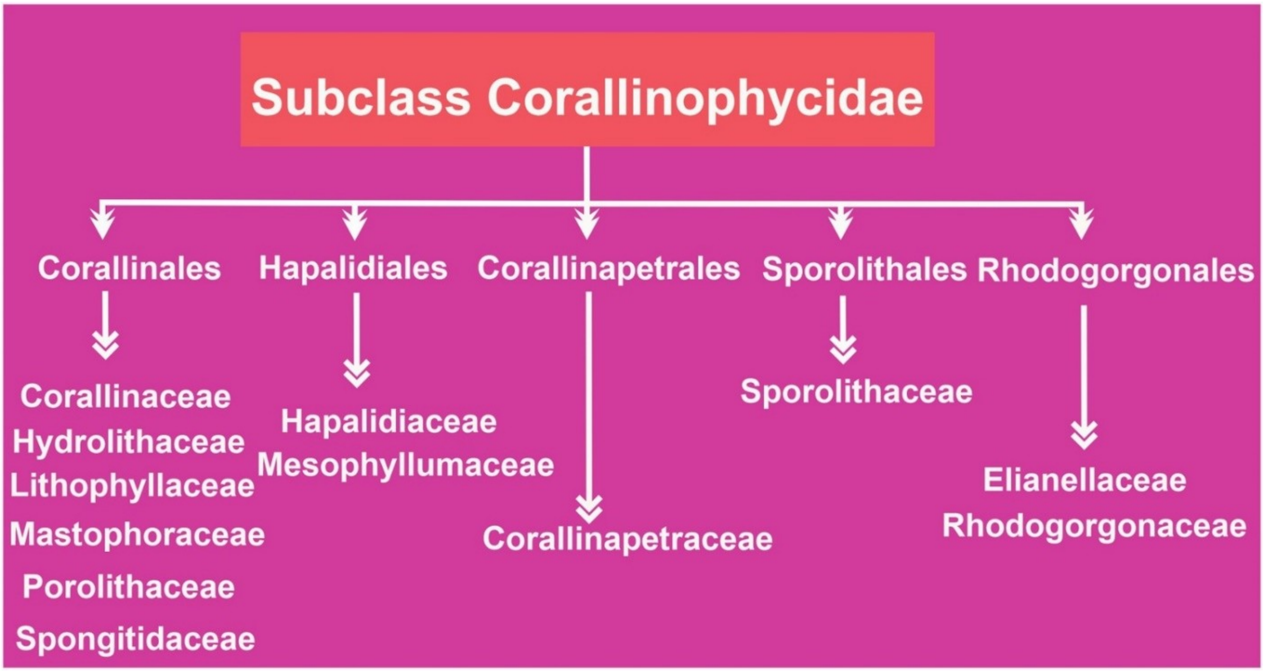

Fig. 2. Taxonomic orders and families within the subclass Corallinophycidae comprising all species of coralline red algae. From AlgaeBase (Guiry and Guiry, 2023). Note: Outgroups are not indicated here.

and *Jania* to the species rank that possibly appears implausible or requires an extremely cautious approach (Sarkar, 2024). Nomenclature of both fossil and living non-geniculate coralline algae also suffers from several inconsistencies with the free-living forms described as coatings, gravels, maerls, rhodolites apart from most commonly known rhodoliths. Numerous non-geniculate coralline algal species have also been observed within coated pebbles or individual rhodoliths, thereby leading to confusion over the perfectly applicable terminology (McCoy and Kamenos, 2015). Therefore, referring all coralline thalli unattached to any hard-bottom substrates or other macroalgae and biota as rhodoliths seems the most well suited approach. Crustose coralline algae could be described as those forms that grow radially on hard to soft substrates and demonstrate mm- to cm-scale thickness.

Literature review has clearly revealed that coralline red algae as crustose forms or free-living rhodoliths are important components of the Cenozoic benthic communities in several modern and fossil settings worldwide (Aguirre et al., 2000; Halfar and Mutti, 2005; Sarkar et al., 2022; Aguirre and Braga, 2024; Teichert, 2024) but not given as much detailed attention compared to the very widely recognized coral, kelp and even larger benthic foraminifera (LBF) assemblages. This discrepancy could be attributed to poor knowledge and awareness within the scientific fraternity regarding coralline algae, connected to the taxonomic uncertainties associated with the group especially related to fossil forms. There have been long standing issues with coralline algal identification (Hind et al., 2014). DNA sequence analyses applied in multiple case studies over the last few decades have exposed numerous gaps in our understanding of coralline systematics at all taxonomic ranks (Twist et al., 2020). Genetic datasets have led to revision of coralline diversity (both generic and species), novel understanding of the geographic and ecological distribution pertinent to numerous species, and a reassessment of criteria for allocation of generic and species' names to coralline specimens. These revisions appear never ending with the modern, sophisticated DNA sequencing approaches raising questions on the credibility of applying holistic morpho-anatomical methods for fossil coralline studies. Acknowledgment of cryptic diversity among coralline algae is attaining rapid impetus as a consequence of DNA sequencing analyses. However, in comparison to modern materials it is a highly complicated process and mostly impossible to extract coralline DNA from carbonate or mixed carbonate-siliciclastic sediments/rocks. Factors like diagenesis, micritization and encrustation (by other forms) strongly affect the possibilities of reliable experimental results in addition to the fundamental yet critical constraints of cost and time.

Presently the taxonomy of fossil coralline red algae aims to get synchronized with modern biological nomenclature as closely as possible. Irrespective of the opinion of several workers emphasizing on DNA records, morpho-anatomical taxonomy remains a strong tool in the analysis of fossil algae when diagnostic characteristics are available for the identification process. These primarily include size, shape and organization of the vegetative cells and the nature of conceptacles or the asexuate compartments (Rasser and Piller, 1999; Hrabovský et al., 2015). Clear observations of these diagnostic features indicate consistent generic designations to the fossil corallines. Although the morphotaxonomy of modern coralline algae involves several diagnostic structures poorly preserved or not recorded in fossil specimens (for e.g., epithallial cells and the stages of formation of gametangial conceptacles), most of the criteria applied by the biologists are useful for fossil coralline studies.

3 Environments of coralline algae: past and present

Coralline algae in the modern environments occur from shallow intertidal zones (Fig. 3A–B) up to relatively deeper (∼300 m) water depth depending on the turbidity of the water column (Littler et al., 1991). Despite being an important component of shallow-marine ecosystems, modern crustose coralline algae are understudied from India with few exceptions like the scientifically monitored reefal environments in the Gulf of Mannar marine national park. Here, abundant *Mesophyllum* rhodoliths are thriving on dead stony Acroporidae coral reefs (hard substrates), *Sporolithon* occurs as lumpy nodular forms while species of *Lithothamnion* and *Hydrolithon* are observed to overgrow on black hammer oyster *Malleus malleus* (Ramesh et al., 2021). Similarly, shallow-water reef systems of numerous sites in the Andaman Islands are also characterized by multiple coralline algae like *Hydrolithon* (crustose habit) and articulated genera like *Amphiroa*, *Corallina* and *Jania* growing intimately with the highly dominant scleractinian coral species (Sarkar and Sarkar, 2016). The shallow-marine habitats inhabited by the coralline red algae are also characterized by diverse organisms like corals (coral reefs limited to tropics), seaweeds (Fig. 3C), other groups of algae, benthic foraminifera, mollusks, echinoderms and barnacles (Fig. 3D). Occurrence of free-living rhodoliths in deeper environments can mostly be attributed to transport rather than being in-situ records. Light availability and hydrodynamic energy are the principal controlling factors determining their distribution and growth-forms including the morphology of rhodoliths (Aguirre et al., 2000; Coletti and Basso, 2020; Sarkar et al., 2024). Coralline algae, especially the attached crustose forms are very useful proxies for reconstruction of palaeobathymetric zonations based on the distribution patterns of their major groups like Corallinales and Hapalidiales (Coletti and Basso, 2020). Here again, the application is impeded by lack of precise datasets on their modern depth distribution in several shelves of the world, in addition to their complicated taxonomic history. External shape and inner arrangements in rhodoliths along with the specific taxa forming the rhodoliths are very useful in palaeoenvironmental analyses. Dominant discoidal rhodoliths are associated with calm waters, while mixed discoidal-spheroidal rhodoliths are linked to higher energy environments, resulting from frequent turnovers caused by water movement and benthic creatures (Aguirre et al., 2017, Teichert, 2024 and references therein).

Coralline algal taxa show varying responses to temperature and nutrient regimes both in the modern and geological context with the latter relatively difficult to quantitatively estimate due to the taxonomic problems discussed above. The patterns of rhodolith beds from Albian (Mesozoic) to later stages of the Cenozoic have been recently summarized (Aguirre and Braga, 2024 and references therein). During the Early Palaeogene, regime shifts between (1) coral-coralline algal and, (2) coralgal-LBF dominant assemblages in the Tethyan platform environments highlight diverse climatic affinities of coralline algae within the shallow-marine biome (Fig. 4). Western Jaintia and eastern Khasi Hills of Meghalaya, NE India representing ecosystems of the eastern Tethys (Fig. 5) form an interesting domain where abundant coralline algae and LBF thrived nearly through the entire late Palaeocene mainly due to very high temperatures persistent since pre-PETM that did not allow corals to develop (Sarkar et al., 2022). Rare instances of late Palaeocene solitary corals are known from Meghalaya but there are no signatures of any reefal frameworks or coralgal communities well evident in several other Tethyan sites like western Carpathians, northern Adriatic platform, Pyrenees and northern Calcareous Alps (Sarkar et al., 2022). Majority of the other Tethyan platform sites were characterized by dominant coralgal (coral-coralline algal) communities during the late Palaeocene that were subsequently replaced by LBF-dominated communities with the onset of PETM (Sarkar et al., 2022). It is notable that Tunisia and western Morocco are two other prominent sites that have recorded an exception to this large-scale trend, but do not feature coralline algae as dominant organisms (see Fig. 4). The corallines were important biotic components of numerous shallow-marine benthic communities worldwide even during the Early to Middle Eocene which were punctuated by global hyperthermals like EECO and MECO. A major phase of global expansion in rhodolith beds is recorded in the Priabonian (Aguirre and Braga, 2024). The relatively cooler environments of Miocene (Burdigalian to early Tortonian) corresponded to a large-scale shift from coral- to rhodolith-dominated carbonate assemblages (rhodolith beds) worldwide with an abundance peak in the Langhian (Halfar and Mutti, 2005; Aguirre and Braga, 2024). This phase is widely acknowledged as the acme of coralline algal diversity and abundance that implies better response to temperature, sea-level fluctuations and nutrient conditions compared to corals. Cool-water carbonates represented by coralline-dominant rhodalgal skeletal associations within

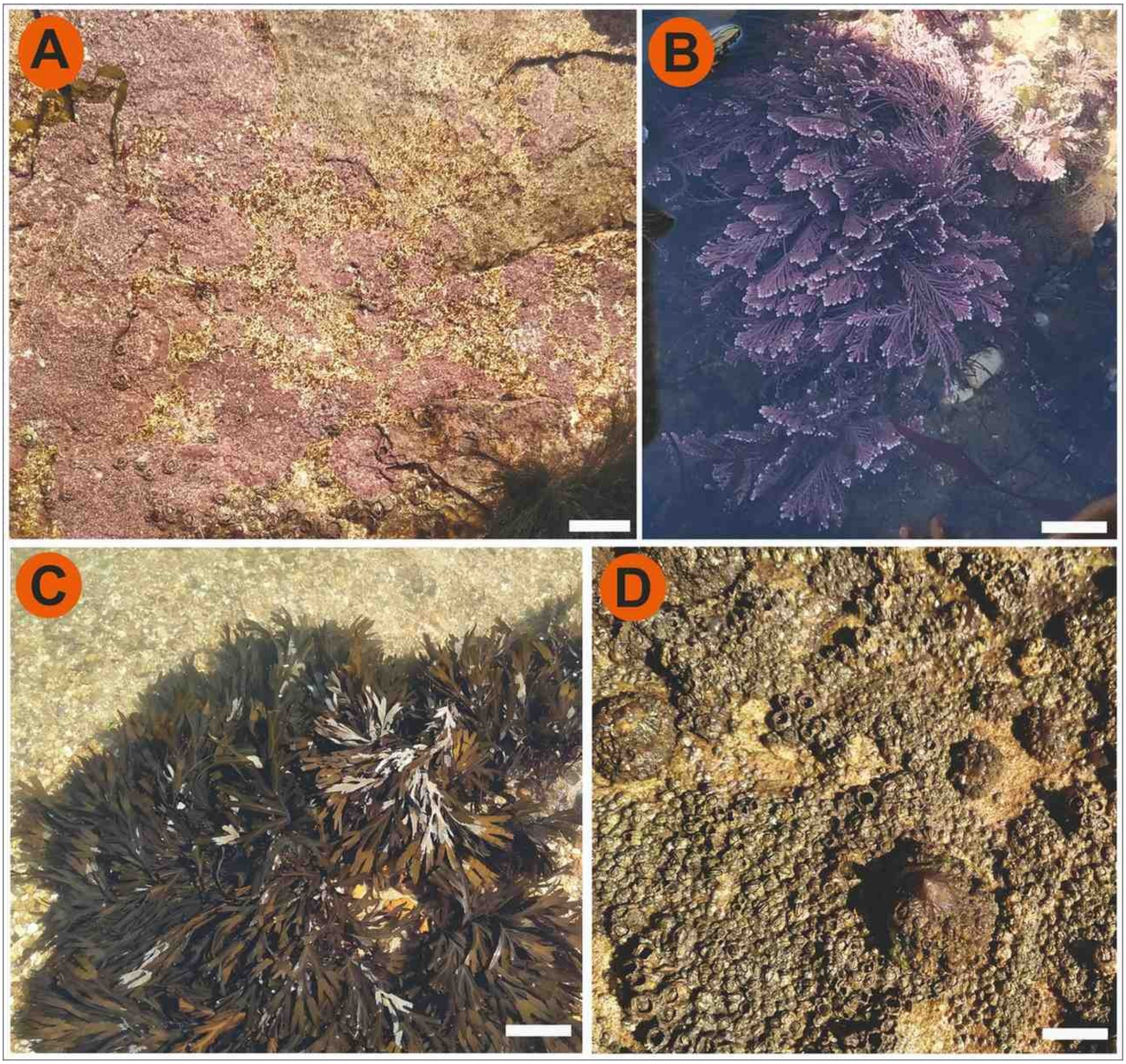

Fig. 3. Examples of major biota from a shallow-marine tidal pool in Portsmouth, UK with thriving coralline red algae and other components. (A) Crustose coralline alga *Lithothamnion* with pink-coloured encrusting thalli. (B) Arborescent (growth-form resembling a tree) pink-coloured geniculate coralline alga *Corallina.* (C) Seaweeds and (D) Barnacles. Scale Bars: (A, C–D) 10 cm; (B) 5 cm.

a warm-water profile (coral framestone-boundstone dominant), have even been reported from oligo-mesotrophic Early Miocene Qom Formation in central Iran (Sarkar et al., 2025) that is a rare site in the subtropical domain except strongly eutrophic settings. This paradox is largely attributed to high levels of terrigenous input besides rapid variations in carbonate saturation levels and water temperature (Sarkar et al., 2025). It is to be noted that coralline algae are not suitable for salinity reconstructions owing to their resilience to salinity alterations as long as the environment is marine, with even a freshwater coralline alga *Pneophyllum cetinaensis* having been recorded from the Cetina River in Adriatic Sea watershed (Ragazzola et al., 2020).

Coralline red algae are significant components of reefal environments pertaining to the tropical regions but have also been recorded from non-tropical shallow-marine deposits of North Island, New Zealand (Basso et al., 2009) and Svalbard (Teichert, 2014). The truly cosmopolitan biogeography of the corallines have been further evidenced by a recent study archiving the first record of late Cretaceous coralline algae (three morphotypes of *Sporolithon*

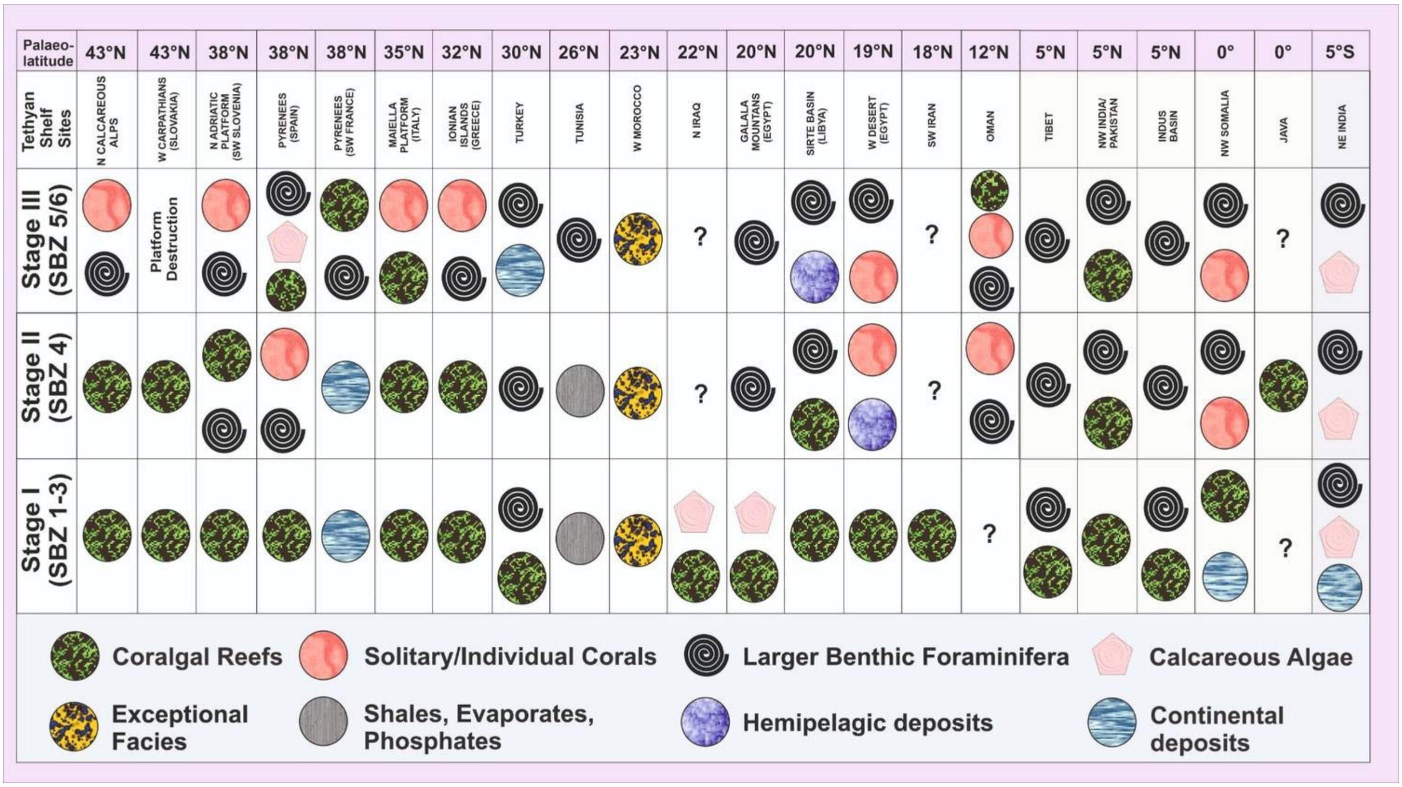

Fig. 4. Schematic representation of dominant organisms in benthic ecosystems of the ancient Tethyan Ocean during Palaeocene-earliest Eocene. Calcareous algae and larger benthic foraminifera were abundant in NE India, in sharp contrast to various other regions of the Tethys where coralgal communities transformed into LBF-dominant communities during late Palaeocene to earliest Eocene (modified from Sarkar et al., 2022).

sp. mainly as branch filaments) from the northeast Pacific region in Vancouver Island, British Columbia, Canada (Haggart et al., 2024). This study also corresponds to a high energy shallow-marine environment with coralline red algae recorded with oysters and various kinds of mollusk fossils. Rhodolith beds can expand up to several square kilometers in both tropical and temperate environmental settings, thereby playing a significant role in calcium carbonate production pertinent to the continental shelves (McCoy and Kamenos, 2015). These are highly significant bioengineering ecosystems in the modern marine systems, ranging from coastal settings to deeper depths ranging >100 m (Nelson, 2009; Aguirre and Braga, 2024). Highest abundance of rhodolith beds have been recorded from the Tethan-Paratethyan-Mediterranean domain (Aguirre and Braga, 2024) with significant phases of expansion during Priabonian (Late Eocene) and Aquitanian-Langhian (Early to Middle Miocene). After attaining maximum levels in the Langhian, rhodolith beds sharply declined to a minimum in the Zanclean (Early Pliocene). Again, they resumed their expansion during the Pleistocene to get close to the Langhian levels. A recent evaluation of modern biogeography has marked the central Indo-Pacific and temperate Australasia as the most diverse domains with coralline algal beds, emerging from a study of 62 distinct provinces across 11 realms (Rebelo et al., 2021).

4 Enduring ecological resilience by corallines

The origin of coralline algae is subject to considerable debate as has been stated above and also recently summarized in detail (Teichert, 2024). Irrespective of their origin, a number of coralline genera pertaining to Orders Sporolithales, Corallinales and Hapalidiales have shown continuous records worldwide since the Early Cretaceous to Recent summing up the existence of these genera on the Earth to >140 million years (Fig. 6). Despite few exceptions of extinct coralline genera like *Distichoplax* (Sarkar, 2018) and *Subterraniphyllum* (Bassi et al., 2000), the overall ecological resilience of the coralline algae cannot be negated. Silurian taxa *Graticula gotlandica* (possibly belonging to order Sporolithales) and *Aguirrea fluegelii* (supposed affinity to order Corallinales) are characterized by pretty short stratigraphic ranges. They even failed to extend deeper into the later stages of Palaeozoic and, their abundance also does not come close to that of coralline

Fig. 5. Field photographs of late Palaeocene-early Eocene carbonate successions characterized by dominant calcareous algae (with larger benthic foraminifera) from (A) Early Eocene of western Jaintia Hills, and (B) Late Palaeocene-earliest Eocene of eastern Khasi Hills in Meghalaya, NE India. These succession outcrops are remnants of the eastern Tethys.

genera known from the Mesozoic and Cenozoic stages. Therefore, even if the Palaeozoic forms are believed to be true ancestors of the modern corallines those individual taxa could not show the true resilience and plasticity characters pertinent to the Mesozoic-Cenozoic coralline genera.

Past responses of biota to environmental shifts present important baseline data for estimating the potential resilience of extant species to future climate change. Expansion and decline in biodiversity unveil from the complex interplay between biotic and abiotic controls, functioning across temporal and spatial scales. The widely recognized environmental perturbations like ocean acidification and hypoxia affecting the modern marine ecosystems, have the most severe impact on the shallow benthos. Signatures of ocean acidification recorded at the K–Pg boundary and during various Palaeogene hyperthermals are associated with severe extinctions. Coralline algae are highly susceptible to global ocean change, mainly due to the sensitivity of their high Mg-calcite skeletons to ocean acidification (Hofmann and Bischof, 2014).

However, given the persistent geological record of maximum coralline genera across the Cenozoic stages ranging up to the modern settings, it can be inferred that they showed enough resilience to potential ecological risks that could trigger rapid generic extinctions. The ecological crisis events included K–Pg extinction and severe hyperthermals like PETM, EECO and MECO. The PETM for example, featured an increase of ∼5 °C in the global oceans and a massive change in the carbon cycle culminating with a large amount of CO_2 being absorbed by the marine bodies (Frieling et al., 2017). The alterations with respect to temperature and pH can be monitored in the modern environments but hard to envisage in the fossil records (especially the rapidity of these changes), therefore presenting a complicated issue to tackle while understanding the impact of global changes on marine organisms including coralline red algae. A reasonable explanation for the survival and continued diversification of the coralline algae could be that their biomineralogical control is only limited to polymorph specification and was actually ineffectual in the regulation of skeletal Mg incorporation (Ries, 2006). Therefore, possibly during Cretaceous and Palaeogene hothouse climate regimes, the Mg/Ca ratio of the ocean favoured the precipitation of low Mg calcite that is more stable to dissolution (Ragazzola et al., 2020).

Biotic interactions such as mutualism and commensalism are prevalent in ecosystems established by foundation taxa like coralline red algae, and pivotal in ensuring their ecological functions and longevity. A recent study from a Mexican Caribbean bay highlighted the impact of seagrass-coralline algae (rhodoliths) mutualism in protecting the

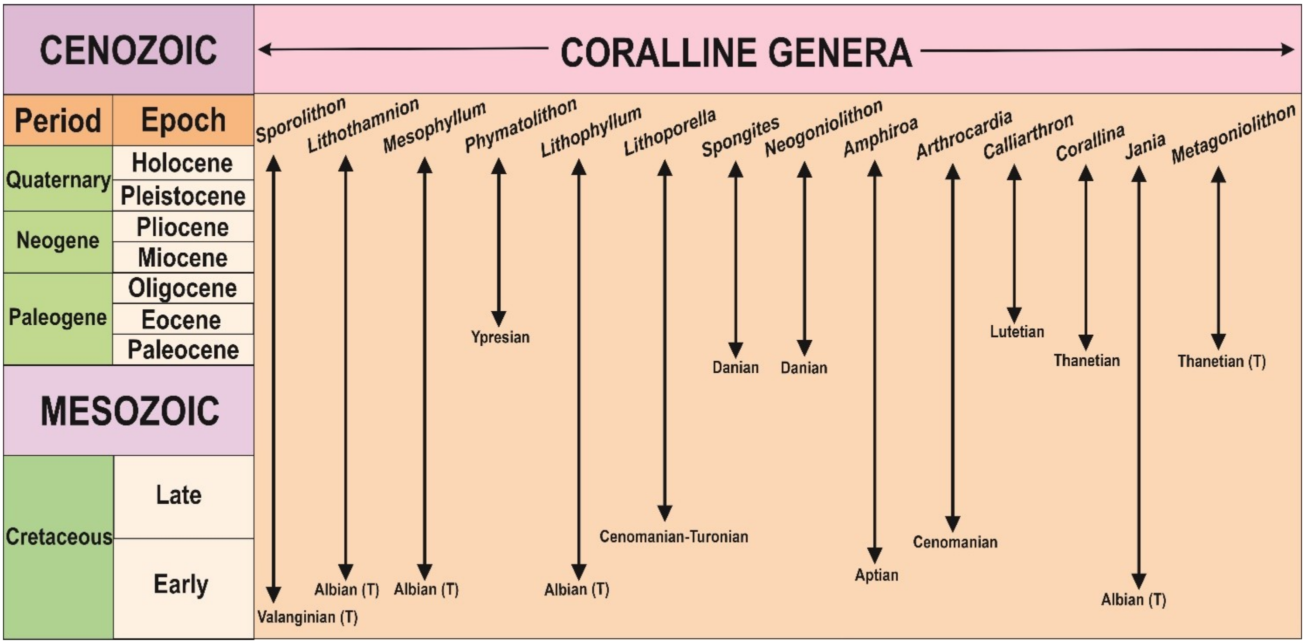

Fig. 6. Depiction of stratigraphic ranges of various coralline algal genera across Mesozoic and Cenozoic stages. All these genera are found in the modern environments globally. Zonations based only on published literature sources from fossil records are shown (unpublished observations excluded) with data compiled from multiple literature sources (e.g., Bassi et al., 2000; Sarkar, 2017). T—Generic identifications claimed and published but not supported by comprehensive taxonomic descriptions, therefore arguable records.

seagrass *Thalassia testudinum* from detrimental overgrazing by green turtles (Martínez López et al., 2024). Here the quality of one of the major global underwater ecosystems pertaining to shallow coastal waters—seagrass meadows, depended on the interactions between seagrasses, coralline algae and green turtles. Spatio-temporal variations in the benthic setting of the bay showed prolific development of rhodolith beds (negligible in 2009) gaining a vast area of 6934 m^2 in 2016. Such rapid expansion of rhodolith beds is not common in seagrass meadows but positive feedback mechanism brought about by grazing of seagrass canopy by the turtles triggered increased growth of coralline algae. Increase in coralline algal populations provided conditional grazing-protection to the seagrasses and dense aggregations of rhodoliths also reduced sediment re-suspension increasing the extent of coralline survival.

At the geological scale, mutualism between corals and crustose coralline algae has been highly beneficial, contributing immensely to the ecological perseverance and success of both the groups (Teichert et al., 2020). This long association of around 150 million years has not been uninterrupted due to the evolution of novel herbivore groups like echinoids during Selandian-Thanetian (Hopkins and Smith, 2015), and parrot fish during Serravallian (origin) and Zanclean-Piacenzian boundary (lineage diversification) (Choat et al., 2012). However, these intermittent crises have been controlled well by coralline red algae using several morphological adaptive strategies (Teichert, 2024 and references therein). Short ecological timescales corresponding to interspecific competition are inferred as one of the principal mechanisms governing the structure of the coralline algal communities. Despite high prospects of cryptic diversity existing in the coralline algal group (problem is worse for crustose forms that are almost impossible to numerically discern in fossil records). Hence, their quantitative biodiversity is really hard to evaluate, with the possibility of underestimations very high. Still, several coralline genera (Fig. 7) have survived numerous critical crisis episodes in the geological history and continue to thrive in the marine ecosystems globally. Species-level extinctions are not rejected but these organisms supposedly succeeded in long-term competitive exclusion against phases of rapid climate change and also their associate benthic groups across numerous marine niches.

5 Future outlook and concluding remarks

The last few decades have witnessed ongoing global change developing as one of the leading challenges for the scientific fraternity, demanding better quantitative datasets pertaining to the carbon pathways between lithosphere, hydrosphere, atmosphere, and biosphere. To apprehend the response of each component of these dynamic systems to the variations in surrounding abiotic and biotic

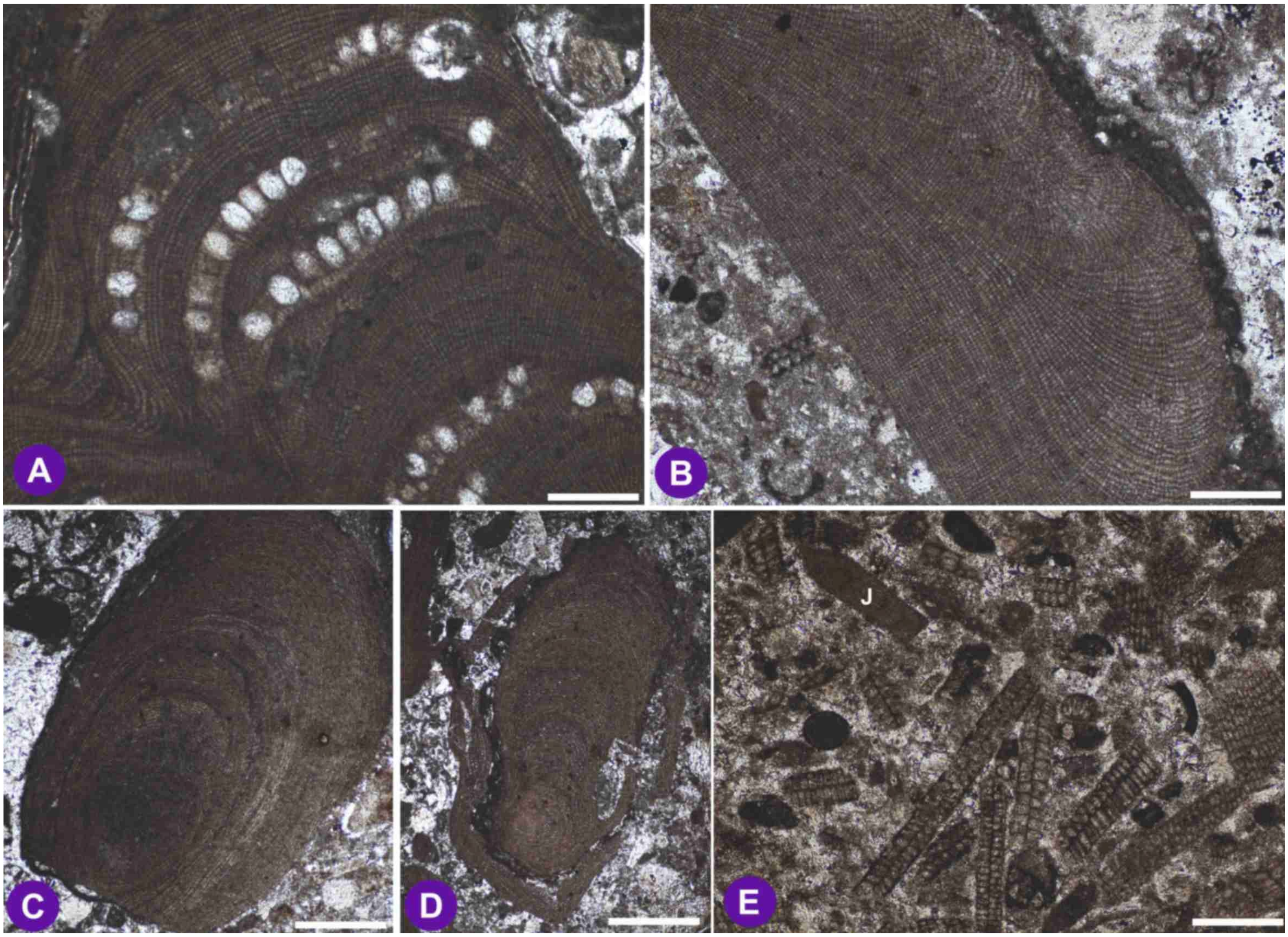

Fig. 7. Examples of some coralline red algal genera (fossil archives) that have shown ecological resilience and persisted from the Early Cretaceous to Recent environments. (A) *Sporolithon*. (B) *Lithophyllum*. (C–D) *Lithothamnion*. (E) Geniculate *Jania* (J) with several isobilateral thalli fragments of extinct coralline alga *Distichoplax*. Scale bars: (A–C, E) 0.15 mm, (D) 0.1 mm.

parameters is also very important. Calcifying marine biota, their sensitivity to global change and contributions to the global carbonate budget are attracting the attention of scientists worldwide with increasing number of field and laboratory case studies getting published. Despite immense potential in carbonate production and accumulation with a worldwide distribution, coralline red algae have not received substantial global focus to date. Corallines could possibly contribute even more than corals to reef carbonate production in particular shallow-marine domains (Cornwall et al., 2023). Coralline algae and corals both produce reefs, and provide habitats by building three-dimensional structures. Main difference is the production of bioherms (true buildups) by corals, and biostromes (lateral extension of rhodolith beds) by coralline algae as the latter are not attached to any fixed substratum. However, owing to the significant photosystems of coralline algae, they can survive even up to depths of ∼300 m. Coral reefs are limited to tropical domains, whereas coralline algal beds are characterized by a much wider geographic extent up to the temperate regions and poles. This shows coralline algae can build habitats in lot more diverse localities of the world although the patterns of habitat-building over geological timescales need further taxa-specific analysis. Tracing and describing the extent and production of coralline algal carbonate factories with regular monitoring is truly mandatory for future research to manifest a reliable carbonate budget for the shelf ecosystems globally.

Research focus on coralline red algae is developing gradually with an increased necessity to emphasize on both quantitative as well as qualitative analyses to understand their evolution and ecological affinities since deep time. A viable nomenclature scheme for the coralline red algae acceptable to both the biologists and palaeontologists is the primary prerequisite to produce polished, globally usable datasets pertinent to the analysis of their functional traits, which in turn are fundamental to their ecological roles in the marine ecosystems. Understanding the impact of past hyperthermals and global change on coralline algae by making accurate identifications at generic and specific ranks is key to making projections on how the coralline-dominated ecosystems will respond to the ongoing climate change in the short to long run. Coralline algae have appeared to show greater resilience than corals to global change in the geological past but with increasing global warming and ocean acidification threats looming over the marine ecosystems worldwide, it is important to carry out global-scale studies to test the cumulative response of coralline communities. With rapid increase in detrimental phenomena like coral bleaching and phase-shifts (invasion of coral reefs by macroalgae) severely hampering corals, the role of reef-building by coralline algae may find better recognition worldwide. It is to be noted, however, that the algal reefs can never completely substitute the ecological roles of the coral reefs. Still coralline algae as foundation species in several ecosystems with multiple ecological functions in diverse habitats worldwide, valuable photosynthesizers, calcifiers, and palaeoclimate archives hold critical benefits in diverse disciplines such as conservation biology, ecology, geology, phycology and physiology. Studies at the morpho-anatomical to molecular levels are needed with an interdisciplinary and multiproxy approach in the future to promote their applications in the right direction and gain the maximum benefits for mankind from these undervalued organisms at the global level.

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Declaration of competing interest

The author declares that he has no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Credit Author statement

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References

Aguirre, J., Braga, J.C., 2024. Rhodolith beds in a shifting world: a palaeontological perspective. Aquat. Conserv.: Mar. Freshw. Ecosyst. 34, e70015. doi:10.1002/aqc.70015.

Aguirre, J., Braga, J.C., Bassi, D., 2017. Rhodoliths and rhodolith beds in the rock record, in: Riosmena-Rodriguez, R., Nelson, W., Aguirre, J. (Eds.), Rhodolith/Maerl Beds: A Global Perspective. Springer International Publishing, Cham, p. 105–138.

Aguirre, J., Riding, R., Braga, J.C., 2000. Diversity of coralline red algae: origination and extinction patterns from the Early Cretaceous to the Pleistocene. Paleobiology 26, 651–667. doi:10.1666/0094-8373.

Bassi, D., Woelkerling, W.J., Nebelsick, J.H., 2000. Taxonomic and biostratigraphical re-assessments of Subterraniphyllum Elliott (Corallinales, Rhodophyta). Palaeontology 43, 405–425. doi:10.1111/j.0031-0239.2000.00133.x.

Basso, D., 2012. Carbonate production by calcareous red algae and global change, in: Basso, D., Granier, B. (Eds.), Calcareous algae and global change: from identification to quantification. Geodiversitas 34, 13–33. doi:10.5252/g2012n1a2.

Basso, D., Bracchi, V.A., Bazzicalupo, P., Martini, M., Maspero, F., Bavestrello, G., 2022. Living coralligenous as geo-historical structure built by coralline algae. Front. Earth Sci. 10, 961632. doi:10.3389/feart.2022.961632.

Basso, D., Nalin, R., Nelson, C.S., 2009. Shallow-water *Sporolithon* rhodoliths from North Island (New Zealand). Palaios 24, 92–103. doi:10.2110/palo.2008.p08-048r.

Choat, J.H., Klanten, O.S., Van Herwerden, L., Robertson, D.R., Clements, K.D., 2012. Patterns and processes in the evolutionary history of parrotfishes (Family Labridae). Biol. J. Linn. Soc. 107, 529–557. doi:10.1111/j.1095-8312.2012.01959.x.

Coletti, G., Basso, D., 2020. Coralline algae as depth indicators in the Miocene carbonates of the Eratosthenes Seamount (ODP Leg 160, Hole 966F). Geobios 60, 29–46. doi:10.1016/j.geobios.2020.03.005.

Cornwall, C.E., Carlot, J., Branson, O., Courtney, T.A., Harvey, B.P., Perry, C.T., Andersson, A.J., Diaz-Pulido, G., Johnson, M.D., Kennedy, E., Krieger, E.C., Mallela, J., McCoy, S.J., Nugues, M.M., Quinter, E., Ross, C.L., Ryan, E., Saderne, V., Comeau, S., 2023. Crustose coralline algae can contribute more than corals to coral reef carbonate production. Commun. Earth Environ. 4, 105. doi:10.1038/s43247-023-00766-w.

Frieling, J., Gebhardt, H., Huber, M., Adekeye, O.A., Akande, S.O., Reichart, G..J., Middelburg, J.J., Schouten, S., Sluijs, A., 2017. Extreme warmth and heat-stressed plankton in the tropics during the Paleocene-Eocene Thermal Maximum. Sci. Adv. 3, e1600891. doi:10.1126/sciadv.1600891.

Guiry, M.D., Guiry, G.M., 2023. AlgaeBase. National University of Ireland, Galway.

Haggart, J.W., Bucur, I.I., Graham, R., Beard, G., 2024. An unusual biofacies in a rocky shoreline succession of Vancouver Island, British Columbia, Canada: first record of Late Cretaceous coralline algae from the northeast Pacific region. Cret. Res. 166, 106008. doi:10.1016/j.cretres.2024.106008.

Halfar, J., Mutti, M., 2005. Global dominance of coralline red-algal facies; a response to Miocene oceanographic events. Geology 33, 481–484. doi:10.1130/G21462.1.

Hind, K.R., Gabrielson, P.W., Lindstrom, S.C., Martone, P.T., 2014. Misleading morphologies and the importance of sequencing type specimens for resolving coralline taxonomy (Corallinales, Rhodophyta): *Pachyarthron cretaceum* is *Corallina officinalis*. J. Phycol. 50, 760–764. doi:10.1111/jpy.12205.

Hofmann, L.C., Bischof, K., 2014. Ocean acidification effects on calcifying macroalgae. Aquat. Biol. 22, 261–279. doi:10.3354/ab00581.

Hopkins, M.J., Smith, A.B., 2015. Dynamic evolutionary change in post-Paleozoic echinoids and the importance of scale when interpreting changes in rates of evolution. Proc. Natl. Acad. Sci. USA 112, 3758–3763. doi:10.1073/pnas.1418153112.

Hrabovský, J., Basso, D., Doláková, N., 2015. Diagnostic characters in fossil coralline algae (Corallinophycidae: Rhodophyta) from the Miocene of southern Moravia (Carpathian Foredeep, Czech Republic). J. Syst. Palaeontol. 14, 499–525. doi:10.1080/14772019.2015.1071501.

Littler, M.M., Littler, D.S., 2013. The nature of crustose coralline algae and their interactions on reefs. Smithson. Contrib. Mar. Sci. 39, 199–212. doi:10.5479/si.1943667X.39.199.

Littler, M.M., Littler, D.S., Hanisak, M.D., 1991. Deep-water rhodolith distribution, productivity, and growth history at sites of formation and subsequent degradation. J. Exp. Mar. Biol. Ecol. 150, 163–182. doi:10.1016/0022-0981(91)90066-6.

Martínez López, I.G., Leemans, L., van Katwijk, M.M., Ávila Mosqueda, S.V., van Tussenbroek, B.I., 2024. Coralline algal population explosion in an overgrazed seagrass meadow: conditional outcomes of intraspecific and interspecific interactions. Ecosystems 27, 592–605. doi:10.1007/s10021-024-00909-w.

McCoy, S.J., Kamenos, N.A., 2015. Coralline algae (Rhodophyta) in a changing world: integrating ecological, physiological, and geochemical responses to global change. J. Phycol. 51, 6–24. doi:10.1111/jpy.12262.

Nelson, W.A., 2009. Calcified macroalgae-critical to coastal ecosystems and vulnerable to change: a review. Mar. Freshw. Res. 60, 787–801. doi:10.1071/MF08335.

Peña, V., Vieira, C., Braga, J.C., Aguirre, J., Rosler, A., Baele, G., De Clerck, O., Le Gall, L., 2020. Radiation of the coralline red algae (Corallinophycidae, Rhodophyta) crown group as inferred from a multilocus time-calibrated phylogeny. Mol. Phylogenet. Evol. 150, 106845. doi:10.1016/j.ympev.2020.106845.

Ragazzola, F., Kolzenburg, R., Zekonyte, J., Teichert, S., Jiang, C., Žuljević, A., Caragnano, A., Falace, A., 2020. Structural and elemental analysis of the freshwater, low-Mg calcite coralline alga *Pneophyllum cetinaensis*. Plants 9, 1089. doi:10.3390/plants9091089.

Ramesh, C.H., Koushik, S., Shunmugaraj, T., Ramana Murthy, M.V., 2021. Crustose coralline algae (Corallinales, Rhodophyta) diversity in the Gulf of Mannar marine national park, Southern India. Indian J. Geo-Mar. Sci. 50, 241–245. URL: https://nopr.niscpr.res.in/handle/123456789/56568.

Rasser, M.W., Piller, W.E., 1999. Application of neontological taxonomic concepts to Late Eocene coralline algae (Rhodophyta) of the Austrian Molasse Zone. J. Micropalaeontol. 18, 67–80. doi:10.1144/jm.18.1.67.

Rebelo, A., Johnson, M.E., Rasser, M.W., Silva, L., Melo, C.S., Avila, S.P., 2021. Global biodiversity and biogeography of rhodolith-forming species. Front. Biogeogr. 13, e50646. doi:10.21425/F5FBG50646.

Ries, J.B., 2006. Mg fractionation in crustose coralline algae: geochemical, biological, and sedimentological implications of secular variation in the Mg/Ca ratio of seawater. Geochim. Cosmochim. Acta 70(4), 891–900. doi:10.1016/j.gca.2005.10.025.

Sarkar, S., 2017. Ecology of coralline red algae and their fossil evidences from India. Thalassas 33, 1–14. doi:10.1007/s41208-016-0017-7.

Sarkar, S., 2018. The enigmatic Palaeocene-Eocene coralline *Distichoplax*: approaching the structural complexities, ecological affinities and extinction hypotheses. Mar. Micropaleontol. 139, 72–83. doi:10.1016/j.marmicro.2017.12.001.

Sarkar, S., 2024. Diverse geniculate coralline algae in Cenozoic fossil records: knowledge gaps and applications in palaeoecology. J. Palaeosci. 73, 157–164. doi:10.54991/jop.2024.1895.

Sarkar, S., Allameh, M., Nasiri, Y., Hadi, M., 2025. Palaeogeographical implications of an ecological paradox: cool-water carbonates in an Early Miocene mid-latitude warm realm (Qom Formation, Central Iran). Lethaia 58, 1–19. doi:10.18261/let.58.1.6.

Sarkar, S., Cotton, L.J., Valdes, P.J., Schmidt, D.N., 2022. Shallow water records of the PETM: novel insights from NE India (Eastern Tethys). Paleoceanogr. Paleoclimatol. 37, e2021PA004257. doi:10.1029/2021PA004257.

Sarkar, S., Sarkar, S., 2016. Diversity of corals and benthic algae across the shallow-water reefs of Andaman Islands: managing the valuable ecosystems. Environ. Dev. Sustain. 18, 1801–1814. doi:10.1007/s10668-015-9709-z.

Sarkar, S., Sinanoglu, D., Özgen Erdem, N., 2024. Crustose red algae in deep time environments: palaeoecological insights from northeastern India and Türkiye (Turkey). Palaeoworld 33, 1681–1696. doi:10.1016/j.palwor.2024.04.001.

Teichert, S., 2014. Hollow rhodoliths increase Svalbard's shelf biodiversity. Sci. Rep. 4, 6972. doi:10.1038/srep06972.

Teichert, S., 2024. Attached and free-living crustose coralline algae and their functional traits in the geological record and today. Facies 70, 8. doi:10.1007/s10347-024-00682-1.

Teichert, S., Steinbauer, M., Kiessling, W., 2020. A possible link between coral reef success, crustose coralline algae and the evolution of herbivory. Sci. Rep. 10, 17748. doi:10.1038/s41598-020-73900-9.

Twist, B.A., Cornwall, C.E., McCoy, S.J., Gabrielson, P.W., Martone, P.T., Nelson, W.A., 2020. The need to employ reliable and reproducible species identifications in coralline algal research. Mar. Ecol. Prog. Ser. 654, 225–231. doi:10.3354/meps.