

Ecology of Coralline Red Algae and Their Fossil Evidences from India

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Abstract Coralline red algae are important components of numerous tropical and temperate carbonate systems throughout the world. The environmental factors such as light, water depth, temperature and ocean chemistry have been acknowledged by researchers worldwide to have an impact on the recruitment and diversity of shallow-water coralline algae in marine benthic environments. The potential of coralline red algae as marine climate archives has also been highlighted in many recent studies. A brief overview of the fossil coralline red algae from various sedimentary basins of India is presented herein as well as their palaeoecological applications. The shortcomings and future prospects of coralline algal studies in India pertinent to significant aspects such as palaeoecology, palaeoenvironmental reconstructions, climate dynamics and extinction episodes are also discussed succinctly.

Keywords Coralline algae · Palaeoecology · Environment · Sedimentary basins · India

Introduction

The discipline of ecology is associated with numerous laws in the form of widespread, repeatable patterns existing in nature. However, to identify and understand such patterns in relic ecosystems, a plethora of biotic proxies and environmental variables need to be considered for polished palaeoecological evaluations. Temperature, light intensity, salinity, nutrient

regime, hydrodynamic energy, water transparency, oxygen and CO₂ concentrations, Mg/Ca ratio and water pH have all been acknowledged as important limiting factors regulating populations of marine communities (Hallock and Schlager 1986; Carannante et al. 1988; Hallock et al. 1988; Stanley and Hardie 1998). In addition, bathymetry of the sea floor and substrate requirements are equally important in determining the spatial distribution of benthic marine communities (Pomar and Ward 1999; Pomar et al. 2004).

Coralline red algae (Orders Corallinales and Sporolithales; Division Rhodophyta) are among the most common and ecologically important organisms occurring in a wide range of marine habitats, from the intertidal to the lower photic zone, and from the polar to the tropical regions (Nebelsick et al. 2013; McCoy and Kamenos 2015). Contrary to other groups of calcareous red algae (Peyssonneliales and Nematiales), they are major carbonate contributors and framework builders in the tropical systems as well as temperate/cool-water settings (Bosence 1983; Carannante et al. 1988; Freiwald and Henrich 1994; Iryu et al. 1995; Basso 1998, 2012; Foster 2001; Pomar et al. 2004; Savini et al. 2012).

Corallines first appeared in the Early Cretaceous (Ghosh and Sarkar 2013a; Table 1) and displayed progressive diversification peaking in diversity in the Early Miocene. This was followed by a phase of stabilization during the Neogene (Aguirre et al. 2000a). Corallines are presumed to have played an important role in the carbon and carbonate cycles of shallow-water ecosystems since the Late Mesozoic and have shown to be important contributors to Cretaceous and Tertiary platform deposits (Carannante et al. 1995; Aguirre et al. 2000a, b, 2007; Bassi 2005; Halfar and Mutti 2005; Quaranta et al. 2012; Nebelsick et al. 2013). During the Burdigalian to Tortonian periods in particular, global coralline algal deposits reached their acme (Halfar and Mutti 2005). Coralline algae have the ability to colonize a wide range of

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Table 1 A summary of families, subfamilies and common genera of coralline red algae with their stratigraphic ranges (References: Bassi et al. 2000; Harvey and Woelkerling 2007; Aguirre et al. 2010; Kundal 2011)

Family & subfamily	Genus	Stratigraphic range
Corallinaceae		
Metagoniolithoideae	Metagoniolithon	Late Palaeocene to Recent
Corallinoideae	Arthrocardia	Early Cretaceous to Recent
	Jania	Late Cretaceous to Recent
	Corallina	Late Cretaceous to Recent
	Calliarthron	Middle Eocene to Recent
	<i>Alatocladia, Bossiella, Cheilosporum, Chiharaea, Haliptilion, Marginosporum, Masakiella, Serraticardia, Yamadaea</i>	Modern
Mastophoroideae	Lithoporella	Late Cretaceous to Recent
	Spongites	Early Palaeocene to Recent
	Neogoniolithon	Early Palaeocene to Recent
	Karpathia	Palaeocene to Miocene?
	Porolithon	Late Miocene to Recent
	<i>Hydrolithon, Lesueuria, Mastophora, Metamastophora, Pneophyllum</i>	Modern
Lithophylloideae	Lithophyllum/Titanoderma	Early Cretaceous to Recent
	Amphiroa	Early Cretaceous to Recent
	<i>Ezo, Lithothrix, Paulsivella, Tenarea</i>	Modern
Hapalidiaceae		
Austrolithoideae	<i>Austrolithon, Boreolithon</i>	Modern
Choreonematoideae	<i>Choreonema</i>	Modern
Melobesioideae	Lithothamnion	Early Cretaceous to Recent
	Mesophyllum	Early Cretaceous to Recent
	Phymatolithon	Early Eocene to Recent
	Aethesolithon	Early Miocene to Recent?
	Clathromorphum	Holocene to Recent
	<i>Exilicrusta, Kvaleya, Mastophoropsis, Melobesia, Synarthrophyton</i>	Modern
Sporolithaceae	Sporolithon	Early Cretaceous to Recent
	<i>Heydrichia</i>	Modern
Uncertain Affinity ^a	Distichoplax	Late Cretaceous? to Late Eocene
	Subterraniophyllum	Middle Eocene to Early Miocene

Genera like *Palaeophyllum*, *Bicorium* and *Solenophyllum* have not been included in this list due to their uncertain taxonomic affinity and also their negligible records from the sedimentary basins of India

The genera with confirmed fossil records are marked in bold letters

^a *Distichoplax* and *Subterraniophyllum* are considered under subfamilies Lithophylloideae and Corallinoideae respectively by some workers but there are certain question marks on their exact classification

habitats due to their variable adaptations to a number of environmental (for e.g. light, temperature, hydrodynamic exposure) conditions from Cretaceous to Recent (Aguirre et al. 2000a, 2010).

Coralline red algae are important in tropical ecosystems because they contribute significantly to the carbonate reef structure, provide nursery habitats for juvenile invertebrates, act as settlement cues for coral larvae and a host of molluscan invertebrates, and assist in the stabilization/development of reef structures (Kamenos et al. 2004; Tierney and Johnson 2012; McCoy and

Kamenos 2015). In addition, coralline algae are among the highest sediment producers in photic carbonate factories. Case studies with a special emphasis on coralline red algae are gaining large-scale attention in the context of global environmental changes like ocean acidification (Martin and Gattuso 2009; Kamenos et al. 2013), and their indispensable roles in maintaining marine ecosystems across a wide spectrum of latitudes and habitat types (Burdett et al. 2011; McCoy and Kamenos 2015). Owing to their abundance in Cenozoic shallow, marine carbonates, coralline algae are finding increased application in

palaeoecological studies and reconstruction of palaeoenvironments (Braga and Martín 1988; Perrin et al. 1995; Bassi 1998, 2005; Cabioch et al. 1999; Halfar et al. 2000; Braga and Aguirre 2001; Aguirre et al. 2007; Burdett et al. 2011; Williams et al. 2011; Ghosh and Sarkar 2013b, c; Sarkar 2015a, b).

The purpose of this paper is to highlight the ecology of coralline red algae dwelling in shallow, marine benthic ecosystems with precise information pertaining to the environmental factors that influence their recruitment and diversity. The potential of coralline red algae in analyzing the anticipated consequences of climate change, especially global warming and ocean acidification, has been briefly discussed. A concise overview of the fossil coralline red algae recorded from different sedimentary basins of India is presented herein. The present drawbacks and future prospects of palaeoecological studies in India emphasizing on coralline red algae are also highlighted.

Environmental Factors Influencing Coralline Red Algae

The principal environmental factors affecting coralline red algae are light, temperature, ocean chemistry and bathymetry. Bathymetry comprises the fluctuations in water depths that are associated with variations in hydrodynamic energy. These factors influence the growth and development of corallines in a multitude of benthic environments worldwide. Palaeoenvironmental evaluations of the ancient ecosystems depend on the examination of fossil species with documented ecological functions (Adey and Steneck 2001; Perry and Hepburn 2008; McCoy and Kamenos 2015). Since majority of fossil coralline red algae have living representatives with recognized environmental tolerances and roles in the marine ecosystems, these are typically used in the reconstruction of carbonate environments. Important aspects such as reef development (Payri and Cabioch 2004; Tierney and Johnson 2012) and community recovery dynamics related to various local/global disturbance events (Aguirre et al. 2007; Toth et al. 2012) can also be analyzed over time using coralline red algae in tandem with sedimentological inputs. Such reconstructions can provide valuable palaeoclimatic data regarding the depositional environment (Braga and Aguirre 2001). For example, species-specific bathymetric zonations can be used to reconstruct the sea-level changes or reef accretion at a given locality during different geological time slices (Cabioch et al. 1999; Yamano et al. 2001). Coralline algal ridges (also known as bioherms or mounds) provide very accurate estimates of sea-level, as they are restricted to the wave crest zone, and can

assist in reconstruction of mm-cm scale sea-level changes (Adey 1986; Gherardi and Bosence 2005).

Water Depth and Light

Water depth (bathymetry) plays a key role in determining the composition of coralline red algal assemblages in different sub-environments within a given locality. The amount of incident light directly associated to the bathymetric levels is a very important ecological factor controlling the diversity and abundance of coralline algal assemblages. Water transparency is another important factor linked to water depth that is involved in the growth and development of coralline communities. Shading by other organisms (like macrophytes) and reflectivity of the sea-floor are other significant aspects regulating the algal assemblages (Kroeger et al. 2006).

Coralline red algae display strong patterns of zonation throughout the intertidal and subtidal zones of the marine benthic ecosystems depending upon their light, temperature, pH, desiccation, and grazing tolerances (Martone 2010; Guenther and Martone 2014; McCoy and Kamenos 2015). Phases of moderate disturbance in the surrounding environment frequently facilitate the development of coralline algal communities. Coralline red algae are often dominant in areas of high stress and disturbance potential where several other macrophytes are very limited or totally absent (Steneck 1986; Dethier 1994). This includes the habitats characterized by the preponderance of herbivores, sand scour, and low productivity potential such as the low photic zone, shaded understories of large macrophyte beds, and the intertidal zone vulnerable to action of storms/cyclones (Dethier 1994; Steneck and Dethier 1994; Dethier and Steneck 2001; McCoy and Kamenos 2015).

Bathymetric Affinities of Non-geniculate Coralline Algae

Mastophoroid Algal Assemblages

Mastophoroid corallines are commonly dominant in very shallow-water, tropical environments (Adey 1979; Iryu et al. 1995; Braga and Aguirre 2004). Mastophoroid-rich algal assemblages are usually characterized by crustose habit, and comprise superimposed encrusting and fruticose thalli overgrowing a variety of bioclasts (Braga and Aguirre 2004). They commonly grow in close vicinity of corals, foraminifera, gastropods and bryozoans (Braga and Aguirre 2004). In recent reef environments in the Indo-Pacific region, coralline algal assemblages dominated by mastophoroids characterizes reef crests and uppermost reef slopes exposed to intense wave action in water depths <10 m (Adey et al. 1982; Cabioch et al. 1999; Camoin et al. 2006), or even <3 m below spring low tides where

vermetid gastropods are also associated with the coralline algae (Laborel 1986). *Neogoniolithon brassica-florida* and *Spongites fruticosus* dominate the shallow-water assemblages in the western and central Mediterranean Messinian reefs (Braga et al. 2009). Species of *Hydrolithon* (*H. craspedium*, *H. onkodes* and *H. reinboldii*) have been reported from the very shallow-water reefal environments of the Andaman Islands with average depth 3–5 m (Sarkar and Sarkar 2015). The upper 15 m bathymetric zone in the Safarga Bay, northern Red Sea features coralline crusts dominated by thick encrusting *H. onkodes* and *N. brassica-florida* (Cabiocch et al. 1999; Braga and Aguirre 2004). As per another study, *N. brassica-florida* is particularly restricted to the upper 10 m zone (Rasser and Piller 1997; Braga and Aguirre 2004). Mastophoroid assemblages dominated by *H. onkodes* encrusting *Acropora* (coral) colonies have been recorded from very shallow-water reef settings (<6 m) in Tahiti, French Polynesia (Montaggioni and Camoin 1993; Montaggioni et al. 1997).

Lithophylloid Algal Assemblages

Lithophylloid coralline algae are indicative of low to moderate energy environments and depths >10 m (Ringeltaube and Harvey 2000; Camoin et al. 2006). Coralline assemblages dominated by lithophylloid taxa with subordinate proportions of mastophoroids mostly occur in shallow-water environments of the temperate marine systems (Braga and Aguirre 2004). In numerous localities of the Mediterranean realm, coralline assemblages dominated by *Lithophyllum* are epilithic and compose the algal nodules in the upper 10–12 m bathymetric zone (Adey 1986; Di Geronimo et al. 1993; Braga and Aguirre 2004). *Lithophyllum* is common in ~20 m depth (Bosence 1991; Braga et al. 2009), but can also be found at deeper levels (Canals and Ballesteros 1997; Braga and Aguirre 2004). *L. pustulatum* has been reported from 10-m depth pertinent to the Heron Reef in the Great Barrier Reef (Ringeltaube and Harvey 2000; Braga and Aguirre 2004) and up to 45 m in the British Isles (Adey and Adey 1973; Braga and Aguirre 2004). This species also occurs as a very minor component (<1 %) of the rhodolith assemblages at 60-m depth on the eastern Australian shelf (Lund et al. 2000; Braga and Aguirre 2004). *Lithophyllum tessellatum* is commonly restricted to depths <10 m but has also been reported from deeper bathymetric levels in the Indo-Pacific region (Cabiocch et al. 1999; Braga and Aguirre 2004). *Lithophyllum incrassatum* ranges from shallow littoral zone in South Africa (Chamberlain 1996) up to 60-m depth on the eastern Australian shelf (Lund et al. 2000; Braga and Aguirre 2004). Algal assemblages dominated by *Lithophyllum kotschyianum* occur in

the intertidal and shallow subtidal back-reef settings in the northern Red Sea where the species thrive as coralline frameworks or rhodoliths (Piller and Rasser 1996; Rasser and Piller 1997; Braga and Aguirre 2004). *L. kotschyianum* has also been reported from similar bathymetric zones and sub-environments of One Tree Reef in the Great Barrier Reef (Braga and Davies 1993; Braga and Aguirre 2004). Thick encrusting *Lithophyllum congestum* are preponderant in the reef crests at St. Croix, Virgin Islands in the Caribbean (Steneck and Adey 1976; Bosence 1984) where they have been reported to show intergrowths with thick *Hydrolithon* thalli (Braga and Aguirre 2004). They are also found in the exposed algal-ridge and fore-reef habitats in Holandés Cays, Panama (Macintyre et al. 2001).

Melobesioid and Sporolithoid Algal Assemblages

Melobesioid and sporolithacean coralline algae commonly dominate the coralline assemblages in deep tropical and shallow to deep temperate settings ranging >20 m and reaching up to depths of 110–120 m depending on the local environmental parameters (Adey 1979, 1986; Iryu et al. 1995; Lund et al. 2000; Braga and Aguirre 2004; Camoin et al. 2006). *Sporolithon* (Family Sporolithaceae) commonly shows association with melobesioids in deep-water bathymetric levels corresponding to the low-latitude regions (Braga and Aguirre 2004). In modern-day settings, melobesioids and *Sporolithon* are significant biotic components below 10–15 m zone in One Tree Reef at the southern end of the Great Barrier Reef region (Braga and Davies 1993; Braga and Aguirre 2004) and in the Safarga Bay reefs in the Red Sea (Rasser and Piller 1997; Braga and Aguirre 2004). This assemblage is also recorded from the reef bases <15 m in the Sulawesi Archipelago in Indonesia (Verheij and Erftemeijer 1993; Braga and Aguirre 2004). *Lithothamnion superpositum* is a melobesioid coralline species common in the subtidal zone of South Africa (Keats et al. 2000). Melobesioid taxa *Mesophyllum* and *Lithothamnion*, together with *Sporolithon*, are the main rhodolith components on the outer platform off Fraser Island, Queensland (Lund et al. 2000; Braga and Aguirre 2004).

Temperature

Temperature is one of the most important factors controlling carbonate sedimentation and species composition of coralline algal assemblages in different geographic realms. The distribution of coralline algal species in the North Atlantic has been correlated with temperature/habitat boundaries (Adey and Adey 1973; Wilson et al. 2004). Melobesioid species *Lithothamnion corallioides*

presents an interesting example pertaining to the impact of temperature on coralline algae. Absence of this species from Scotland is either because winter temperatures occasionally drop below the minimum survival temperature of this species (2–5 °C) or because threshold temperatures do not sustain long enough to support their endurance (Adey and McKibbin 1970; Wilson et al. 2004). Laboratory experimental studies have shown that *Phymatolithon calcareum* survived up to 2 °C, died at 0.4 °C, and the optimum temperature for growth was 15 °C (Adey and McKibbin 1970; Wilson et al. 2004). According to a recent study, elevated temperature has a stronger negative impact on coralline algae by means of photodamage in comparison to reduced ocean water Ph (Vásquez-Elizondo and Enriquez 2016). It also implies that out of the two critical worldwide phenomena - global warming and ocean acidification, the former has a greater influence on the physiology of coralline algae. It is however difficult to relate changes in sedimentary environments and skeletal association to absolute temperature values. This is mainly because the temperature values usually refer to the sea surface temperatures (SSTs) whereas several biogenic components of a marine ecosystem including coralline red algae thrive at various bathymetric levels/zones. The exact position of thermocline and relative decrease of temperature with increasing depths in the ancient environments may be difficult to reconstruct only from study of fossil material. The minimum winter temperature and maximum summer temperature should both be carefully analyzed to understand the impact of temperature on coralline taxa (Kroeger et al. 2006). In addition to water depth, other control factors operating in the seascape should also be considered in order to evaluate the minimum threshold temperatures for various coralline algal genera and species.

Non-geniculate coralline red algae feature a high-Mg calcite skeleton with distinct annual (for e.g., *Lithothamnion glaciale*, *L. muelleri*, *Clathromorphum compactum*) and sub-annual (for e.g., *P. calcareum*) growth bands (Blake and Maggs 2003; Halfar et al. 2008; Kamenos and Law 2010; Burdett et al. 2011). The frequency of these bands has been reviewed in detail by Foster (2001). Several encrusting coralline species do not show rhythmic growth bands, possibly due to high incidence of herbivory (McCoy and Kamenos 2015). Since the geniculate species grow primarily by forming new apical segments, they do not form growth bands. In rhodoliths, factors like reduced light availability and lower temperature during winter, reduced water movement, burial, monthly/lunar growth cycles driven by tidal patterns and possible large-scale climate patterns (for e.g., El Niño) induce the formation of growth bands (Foster 2001; McCoy and Kamenos 2015). In *L. glaciale* a negative

correlation exists between calcite density of calcified cells and temperature (Kamenos 2010), and also temperature and light availability (Burdett et al. 2011). Positive relationships with instrumental SSTs were generated by averaging the growth bands of multiple *C. compactum* or *C. nereostratum* thalli, enabling reconstruction of SSTs (Halfar et al. 2010, 2011). Smaller, better calcified cells are deposited within each annual growth band during the winter period and larger, less calcified cells are deposited during summer (Freiwald and Henrich 1994; Foster 2001; Burdett et al. 2011). The application of densitometric alveochronology based on the study of the coralline band widths has proven to be useful in understanding the cloud cover histories and their linkage to the irradiance-temperature relationships (Burdett et al. 2011).

Some coralline species have been reported to continue their growth cycle during dark winters by means of physiological adaptations like utilization of starch grains stored in the perithallial cells (Freiwald and Henrich 1994) and CO₂ dark assimilation (Kremer 1981). Calcite chemistry and growth band architecture reveals important information pertaining to the responses of coralline algae to the ambient environmental conditions. This enables them to act as palaeoenvironmental proxies, with the longest temperature reconstruction extending over 650 years (Kamenos 2010; Burdett et al. 2011; McCoy and Kamenos 2015).

Response to Ocean Acidification

During the last few decades scientific investigations pertaining to the appalling impacts of ocean acidification on calcifying marine biota have witnessed a significant rise. This is mainly aimed towards understanding the sensitivity of organisms and biomes to this large-scale global phenomenon. Increasing levels of *p*CO₂ in the surface ocean causes major shifts in the seawater acid–base gradient and is likely to decrease the overall pH by 0.2–0.4 units over the course of the 21st century (Caldeira and Wickett 2005; Martin and Gattuso 2009). Coralline red algae are one of the calcifying organisms that are highly sensitive to ocean acidification and absent in naturally acidified seawater where several other calcifying organisms can survive and proliferate (Hall-Spencer et al. 2008). Their susceptibility is related to the solubility of their Mg-calcite thalli which is the most soluble form of CaCO₃ (Milliman 1974; Hall-Spencer et al. 2008; Kuffner et al. 2008; Martin and Gattuso 2009). Several facets of coralline algal ecology like recruitment (Kuffner et al. 2008), thallus growth (Jokiel et al. 2008) and calcification (Anthony et al. 2008) are all negatively affected under high *p*CO₂ conditions. Occurrence of surface lesions (Martin and Gattuso 2009), epithelial cell damage (Burdett et al. 2012) and modeled structural stress

(Ragazzola et al. 2012) are some other negative impacts of high $p\text{CO}_2$ levels on coralline algae. Conversely, some studies have also shown non-negative responses. For example, intracellular concentrations of the algal antioxidant dimethylsulphoniopropionate (DMSP) did not increase under conditions of gradual change to lower pH (Burdett et al. 2012). A recent study by Kamenos et al. (2013) has demonstrated that the coralline algal structure is more sensitive to the rate of ocean acidification rather than its magnitude. Changes in the balance between coralline carbonate production and active dissolution induced by elevated $p\text{CO}_2$ and temperature may have severe harmful impact by affecting the carbonate chemistry of the water column and the capacity of the marine bodies to take up atmospheric CO_2 (Andersson et al. 2005; Martin and Gattuso 2009). Considering the wide spectrum of ecological services coralline algae are associated with, any change in their structural integrity may have long-term detrimental consequences for the ecosystem as a whole. Although some evidences of increased calcification under ocean acidification have been demonstrated (Martin et al. 2013; Kamenos et al. 2013) this does not necessarily result in repair of the already damaged coralline skeletons or imply that the newly calcified skeleton possess similar functionality as that deposited under higher pH conditions (Kamenos et al. 2013).

Other Factors

Despite being an important ecological factor, detailed information pertaining to the trophic tolerances of coralline red algae is lacking. Non-geniculate coralline algae are generally susceptible to nutrient input (Kroeger et al. 2006). Any nutrient equilibrium shift towards eutrophy normally triggers bloom in the populations of rapidly growing organisms and favors them in competition for space. It is therefore very unlikely that slow growing coralline red algae with average growth of 0.015–2.5 mm/year (Freiwald and Henrich 1994; Blake and Maggs 2003; Burdett et al. 2011) will proliferate in high nutrient conditions. Non-geniculate coralline red algae tolerate short periods of annual eutrophication as a consequence of nutrient upwelling (Halfar et al. 2004; Kroeger et al. 2006). It is noteworthy that in contrast to the non-geniculate algae, geniculate coralline taxa are more tolerant of eutrophic conditions as well as variable salinities (Johansen 1981; Kroeger et al. 2006). A recent experimental study concluded that herbivore reduction when coupled with nutrient enrichment triggers a rise in the non-calcifying, filamentous algae which surpass the calcifying, encrusting coralline red algae in the reefal environment of Central Red Sea (Jessen et al. 2013).

In case of salinity, the growth of *P. calcareum* is impaired at salinities <24 units (King and Schramm 1982; Wilson et al. 2004) whereas *L. glaciale* has shown robust resilience to reduced levels of salinity in comparison to several other red macroalgae (Burdett et al. 2015). However, due to an increase in the overall absorbance of *L. glaciale* thalli in the low- and very low-salinity treatments, possibility of dynamic photoinhibition cannot be ruled out (Burdett et al. 2015).

Till date coralline red algae have been considered as exclusive marine organisms. However, a recent report of coralline alga *Pneophyllum cetinaensis* from the Cetina River (Adriatic Sea watershed; Žuljević et al. 2016) defies this long-term paradigm and presents the possibility of discovering more coralline species from freshwater ecosystems. Particular characteristics such as hard water enriched with dissolved calcium carbonate and pH similar to the marine environments favors colonization of the Cetina River by coralline species. To generalize the incidence of coralline algae from such freshwater systems, greater number of experimental studies and long-term monitoring are required.

Fossil Coralline Red Algae from India

India is a country of diverse environments and fossil reserves including numerous carbonate successions spread all across its vast landscape. Several taxa of calcareous algae including coralline red algae have been reported from various sedimentary basins of India (Fig. 1). Among these the Andaman-Nicobar, Assam Shelf, Kachchh and Saurashtra Basins have received substantial attention from the phycologists for evaluating the coralline assemblages, especially for taxonomic and basic palaeoenvironmental studies.

Andaman-Nicobar Basin

The Andaman and Nicobar Islands represent a junction of the Indian and Pacific lithostratigraphic plates in the Bay of Bengal. The Andaman and Nicobar Islands are divided into the northern Andaman and the southern Nicobar with the Ten Degree Channel separating the two groups. The main ridge of the Andaman-Nicobar is dominated by the lithological units dating Palaeogene whereas the islands situated on either side of the main ridge and those constituting the Ritchie's Archipelago are characterized by a multitude of Neogene successions (Sharma and Srinivasan 2007).

The first record of fossil coralline algae from the Andaman and Nicobar Islands is by Gee (1927). This includes the report of *Lithothamnion nummuliticum* and *L. suganum* (Middle Andaman) and fragments of *Lithothamnion* (Hut Bay, Little Andaman and Wilson Island) from post-Eocene sediments. In

Fig. 1 Map of India showing the location of fossil coralline red algae deposits from various sedimentary basins and islands of India: (A) Kachchh (B) Saurashtra (C) Narmada Valley (Bagh Beds) (D) Bombay Offshore (E) Lakshadweep (F) Kerala (G) Cauvery Basin (H) Assam Shelf (I) Andaman & Nicobar



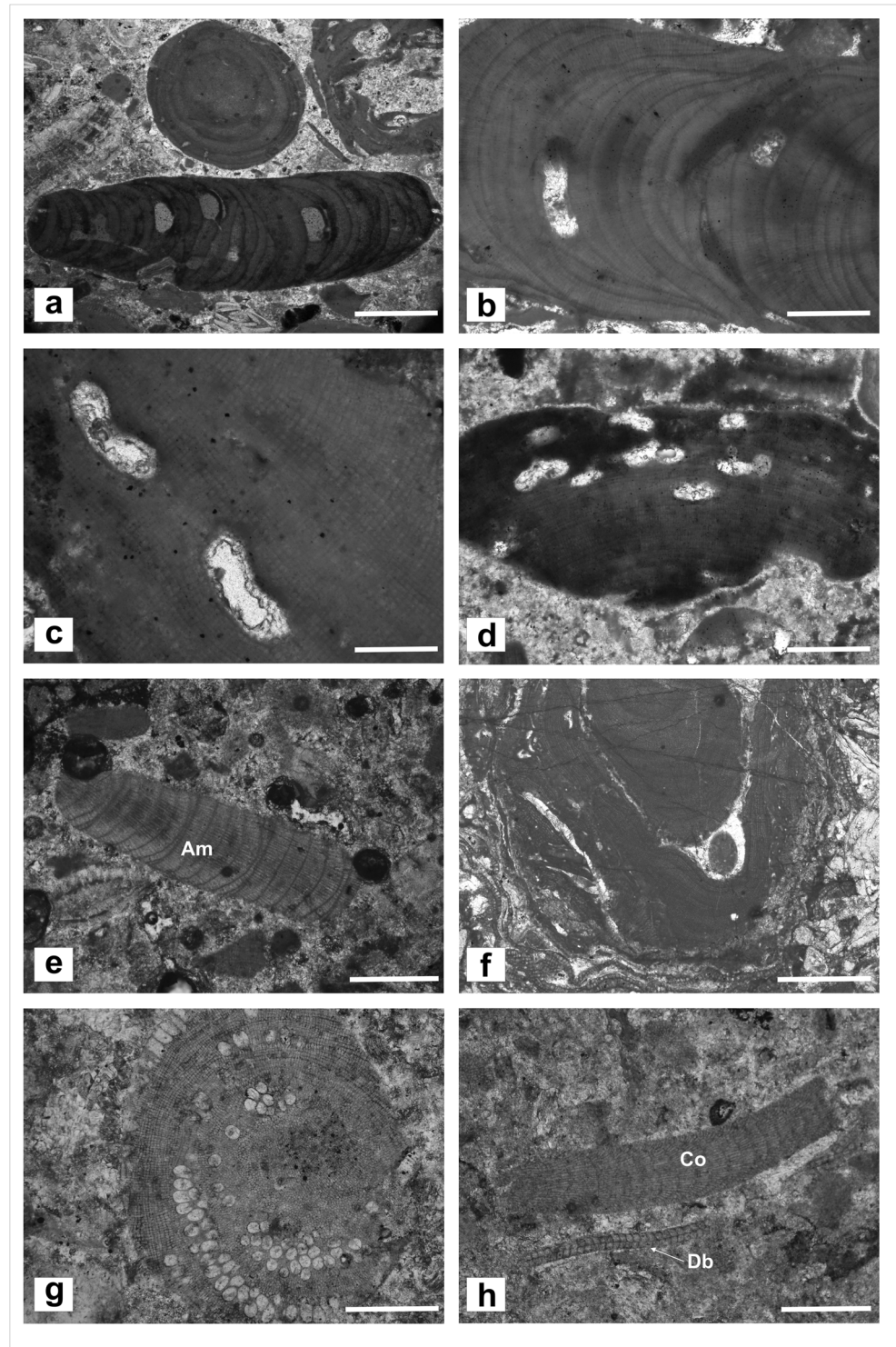
the late 20th century several studies pertaining to coralline red algae have been carried out from the Cretaceous-Palaeogene (Badve and Kundal 1986, 1988; Kundal and Wanjarwadkar 2000) and Neogene (Chatterji and Gururaja 1972; Venkatachalapathy and Gururaja 1984; Chandra et al. 1999) sediments of the Andaman-Nicobar basin. Rich assemblages of coralline red algae have been recovered from the Neogene successions of the Little Andaman (Saxena et al. 2005; Sarkar and Ghosh 2015; Sarkar et al. 2016) and Car Nicobar (Chandra et al. 1999; Ghosh et al. 2004; Ghosh and Sarkar 2013c; Sarkar 2015c). A new record of coralline algae has recently been reported from the Pleistocene sediments of the Neill West Coast Formation, Neil Island in South Andaman (Kishore et al. 2015). Lithophylloid corallines represented by species of *Lithophyllum* and *Amphiroa* show the maximum abundance in the Neogene sediments of the Andaman-Nicobar Group of Islands, followed by melobesioids (*Lithothamnion*, *Mesophyllum*) and mastophoroids (*Spongites*, *Lithoporella*, *Neogoniolithon*). Benthic foraminifera, corals, bryozoans, echinoderms, gastropods and barnacles are the other major biotic components reported from these sediments in association with coralline algae. Based on the coralline red algal assemblages reported, intertidal to mildly deeper water depths featuring moderate to high hydrodynamic energy conditions in tropical

depositional environments have been envisaged for the Andaman-Nicobar carbonates. Some examples of coralline red algae from the Neogene sediments of Hut Bay, Little Andaman have been illustrated in Fig. 2 (microphotographs a–e).

Assam Shelf

Assam Shelf in north-east India is one of the best studied sedimentary basins of India with respect to fossil calcareous algae. It is the north-eastern extension of the Indian Craton and includes Jaintia, Khasi, Garo, Mikir Hills, Shillong Plateau and the upper Assam Valley. The Sylhet Limestone Group in the Assam Shelf encompasses three carbonate units – Lakadong Limestone, Umlatdoh Limestone and Prang Formation in the ascending order intercalated with Lakadong Sandstone and Narpuh Sandstone (Jauhri and Agarwal 2001; Misra et al. 2011). Based on biostratigraphy pertinent to larger benthic foraminiferal studies, the carbonate lithounits of the Sylhet Limestone Group are assigned to various time slices of Palaeogene ranging from Late Palaeocene to Middle Eocene (Jauhri and Agarwal 2001; Jauhri et al. 2006; Matsumaru and Sarma 2010; Sarkar 2015a). The Sylhet Limestone Group is a carbonate ramp/tidal flat setting (Tewari et al. 2010a, b). It is underlain by the late Early to Middle Palaeocene Therria Sandstone and overlain by shale/

Fig. 2 Examples of coralline red algae from India: (a–e) Neogene (Middle Miocene) of Hut Bay, Little Andaman Island: **a** Non-geniculate coralline protuberances, BSIP Slide No. 14860; **b** Melobesioideae gen. et spec. indet., BSIP Slide No. 14798; **c** *Lithothamnion libanum*, BSIP Slide No. 14801; **d** *Spongites* sp., BSIP Slide No. 14811; **e** Geniculate coralline red alga *Amphiroa* sp. (Am), BSIP Slide No. 14860; (f–h) Palaeogene (Late Palaeocene–Early Eocene) of Meghalaya, Assam Shelf, N-E India: **f** Encrusting coralline algae from Early Eocene, BSIP Slide No. 14661; **g** *Sporolithon* sp. from Late Palaeocene, BSIP Slide No. 15956; **h** *Corallina* sp. (Co) and *Distichoplax biserialis* (Db) from Late Palaeocene, BSIP Slide No. 15847. Scale bars: (a) 1 mm, (b–e) 150 μ m, (d–h) 300 μ m



sandstone alternations of the Late Eocene Kopili Formation (Jauhri and Agarwal 2001; Jauhri et al. 2006; Sarma et al. 2014). Coralline red algae are among the principal biotic components of the Palaeogene carbonate sediments outcropping in Meghalaya, Assam Shelf (Jauhri et al. 2006; Tewari et al. 2010a; Misra et al. 2011; Ghosh and Sarkar 2013b; Kalita

and Gogoi 2015; Sarkar 2015a, b). Some examples of coralline red algae from the Late Palaeocene–Early Eocene sediments of Meghalaya, Assam Shelf have been demonstrated in Fig. 2 (microphotographs f–h). *Lithothamnion*, *Mesophyllum*, *Lithophyllum*, *Distichoplax*, *Lithoporella*, *Spongites*, *Sporolithon*, *Corallina* and *Jania* are the common coralline

taxa reported from various carbonate lithounits of the Sylhet Limestone Group. They show various growth-forms from encrusting to free-living (rhodoliths/maerls) in lagoonal to proximal outer shelf facies (Sarkar 2015a, b). The relative abundance of corallines increase gradually from Late Palaeocene to Middle Eocene and is correlated to the evolution of a reefal environment (Sarkar 2015b). High dominance of calcareous green algae, especially genera like *Halimeda* and *Ovulites* in the Umlatdoh Limestone is an interesting observation which can be attributed to changes in substrate lithology and competition dynamics in the benthic environment during the course of evolution. Fossil green algae have been reported from all the carbonate lithounits of the Sylhet Limestone but do not show considerable richness in the Lakadong and Prang units, where coralline red algae are the principal algal components. The $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotope data has recently been obtained from the Lakadong Limestone sediments and indicate a shallow marine depositional environment (Tewari et al. 2010a). These isotope data suggest palaeotemperatures in the range of 27–30 °C which indicate optimal conditions for the coralline algae and associated benthic foraminifera during the deposition of the Lakadong Limestone. The abundance, diversity and frequency of coralline red algae and other calcareous algal taxa indicates the overall depositional environment for the Sylhet Limestone at shallow depths within the fair-weather wave base.

Kachchh Basin

The Kachchh Basin is a pericratonic rift basin situated in the western margin of India with rich fossiliferous sequences. It is situated at the northwestern fringe of the Indian Peninsula and bounded by the Arabian Sea on the west, Rajasthan on the east, the Great Rann of Kachchh on the north, and the Gulf of Kachchh and the Little Rann of Kachchh on the south. The rock units present in this basin date Middle Jurassic to the Recent. It is one of the most well documented sedimentary basins of India in terms of palaeontological records including coralline red algae and other fossil algal taxa. The Fulra Limestone Formation (middle Eocene), Maniyara Fort Formation (Oligocene), Khari Nadi Formation (early Miocene) and Chhasra Formation (early middle Miocene) are the four lithounits in the onshore sequence of the Kachchh Basin that have yielded rich assemblages of coralline algae (Kundal and Humane 2012; Kundal 2014). Likewise, the Godhra Formation (early Miocene) represents a unit with coralline algal record from the offshore sequence of the Kachchh Basin (Kundal and Humane 2012). The non-geniculate coralline algae include species of *Lithophyllum*, *Lithoporella*, *Spongites*, *Neogoniolithon*, *Lithothamnion*, *Phymatolithon*, *Aethesolithon*, *Mesophyllum* and *Sporolithon*. The geniculate coralline algae show high abundance and diversity from the Kachchh Basin sequences.

Geniculate coralline assemblages include species of *Corallina*, *Jania*, *Arthrocardia*, *Calliarthron*, *Amphiroa*, *Subterraneanphyllum* and *Metagoniolithon* (Misra et al. 2006a; Singh et al. 2009, 2011; Humane and Kundal 2010; Kundal and Humane 2006, 2012; Kundal 2014). In addition to the coralline algae, Kachchh Basin carbonates feature diverse and abundant quantities of dasyclads, halimeds and udoteacean fossil algae (Kundal and Humane 2012; Kundal 2014).

Bathymetric analyses of the coralline algal species indicate a moderate-energy shallow marine depositional environment for the carbonate sequences of the Kachchh Basin yielding coralline algae. Most of the coralline species recorded from these sequences have thin crusts with delicate framework (Kundal and Humane 2012). Therefore high-energy conditions denoted by thick crust corallines with robust framework (Bosence 1991) seem a bleak interpretation. Since the geniculate corallines have been recorded in high abundance with dasycladalean, halimedacean and udoteacean algae, greater proportion of the depositional process within the inner shelf seems a strong possibility. In all probabilities, the algal forms thrived in a moderate-energy inner-middle shelf environment.

Saurashtra Basin

The Saurashtra Basin is a pericratonic shelf basin located in the northern part of the western continental margin of India. The basin lies north of the Bombay Offshore Basin and south of the Kachchh Basin. A detailed lithostratigraphic classification of the Cenozoic-Quaternary sediments of the Saurashtra basin has been provided by Pandey et al. (2007). The Saurashtra Basin is geologically significant due to numerous signatures of sea level fluctuations, depositional environments and hydrocarbon reservoirs (Kundal et al. 2014). Abundant coralline algae have been recorded from three horizons of the Saurashtra Basin: Dwarka-Okha (Kundal and Dharashivkar 2005; Kishore et al. 2012), Porbandar (Kundal and Mude 2009a, b; Mude and Kundal 2012) and Diu (Kundal et al. 2011, 2014). Early Miocene to Late Holocene sediments are exposed in Dwarka-Okha area, while the Porbandar sediments date Middle Miocene to Late Holocene. The Diu area has sediments ranging Middle Pleistocene to Late Holocene. The coralline algae include both non-geniculate forms - species of *Lithophyllum*, *Titanoderma*, *Lithothamnion*, *Lithoporella*, *Mesophyllum*, *Phymatolithon*, *Porolithon*, *Spongites*, *Sporolithon* and *Neogoniolithon*, and geniculate forms - species of *Amphiroa*, *Corallina*, *Jania*, *Arthrocardia*, *Metagoniolithon* and *Subterraneanphyllum*. Calcareous green algae like *Dissocladella* and *Halimeda* spp. have also been recorded from the Diu sediments (Kundal et al. 2014).

Based on the coralline algal associations, 25–60 m water depth with a moderate hydrodynamic energy regime has been

interpreted for the deposition of the Dwarka-Okha sediments including the Kalyanpur Limestone Member (Early Pliocene) of the Dwarka Formation and the Okha Shell Limestone Member (Middle to Late Pleistocene) of the Chaya Formation (Kundal et al. 2014). Based on a detailed study of ichnofossils from this area, the depositional environment for these sediments has been stated to be littoral to sandy shoreline (Kundal and Dharashivkar 2006). The Aramda Reef Member (Middle Pleistocene) of the Chaya Formation is characterized by thick branched and encrusting coralline algal species including abundant *Amphiroa* (Kundal and Dharashivkar 2005; Kishore et al. 2012; Kundal et al. 2014). A depositional depth of 0–20 m has been interpreted for the Aramda Reef Member. Kishore et al. (2012) have divided the Aramda Reef Member into two parts: the lower part dominated by warty to layered *Mesophyllum*, *Lithothamnion* and *Sporolithon* is interpreted to have deposited under warm, low-moderate energy environment, while the upper part is dominated by fruticose *Lithophyllum* and *Titanoderma* which indicate high-energy conditions.

The Dwarka Formation sediments dating Middle Miocene outcropping in Porbandar area encompasses plentiful coralline algae with robust framework and thick branches (Kundal and Mude 2009a, b; Kundal et al. 2014). Water depth of 0–20 m has been interpreted for the deposition of the Dwarka Formation and the Porbandar Calcarenite Member of the Late Pleistocene to Late Holocene Chaya Formation (Kundal et al. 2014). The Adatiana Member of the Miliolite Formation (Middle Pleistocene) in both Porbandar and Diu areas has been envisaged to have deposited at bathymetry of 25–30 m below the low tide level (Kundal and Mude 2009a, b; Kundal et al. 2014).

Other Basins

Apart from the aforementioned sedimentary basins, varying proportions of coralline red algae have also been reported from the Cauvery Basin (Misra and Kumar 1988; Misra et al. 2006b, 2009; Ghosh and Sarkar 2013a), Narmada Valley Basin (Durge 1965; Kundal and Sanganwar 1998), Bombay Offshore Basin (Kundal et al. 2007, 2013; Kundal 2014) and Kerala-Konkan-Lakshadweep Basin (Reuter et al. 2011; Misra et al. 2016).

Future Prospects

Despite several studies on coralline red algae from the sedimentary basins of India, the work has largely been limited to pure taxonomic descriptions of the taxa with very elementary palaeoenvironmental interpretations. This does not sufficiently justify the high palaeoecological potential of the corallines, as evident from the broad spectrum of multi-dimensional

research continuing in several laboratories of Europe, Australia and America. A large proportion of the Indian marine systems are shallower than 100 m, so further large-scale studies on coralline red algae become a necessity.

- 1) Major emphasis till date has been given to taxonomy but detailed ecological evaluations of the fossil coralline red algae are lacking. Response of the corallines to fluctuations in sea-levels, SSTs and nutrient inputs are important in understanding their evolutionary significance in the Indian subcontinent and make future projections both for climate as well as the marine benthic environment. Discerning the specific effect of individual ecological factors, and distinguishing them from the regional and global impacts is however challenging.
- 2) The distribution of ecologically important benthic facies such as those dominated by corallines on both hard and soft bottoms, is largely unknown from the Indian subcontinent, thus introducing a bias in predicting the response of the shelves to short- and long-term global changes.
- 3) Bathymetric data based on the assessment of coralline red algae is very limited. Based on the dominance and abundance of the corallines, depositional water-depths during different Cenozoic time slices need better analyses that will aid in palaeoenvironmental reconstructions.
- 4) For precise assessment of the ecological status of the coralline red algae, extensive quantitative data pertaining to the assemblage/community composition are essential. Comprehensive quantitative datasets are still relatively unknown for the Indian coralline assemblages.
- 5) In addition to the general geological setting, description of the coralline red algae both individually and at the community levels should be supplemented with the sedimentological characteristics of the lithounits and mean percentage of the algal assemblages with respect to the characterized bio/microfacies.
- 6) Regional mapping should include identification and labeling of the regions with algal-dominated lithounits by application of advanced scales and detailed monitoring.
- 7) Response of the coralline red algae to the extinction episodes are poorly understood and need better case studies to develop improved qualitative and quantitative datasets. Recovery dynamics of the coralline algae have huge potential in deciphering the past ecosystems.
- 8) Discipline of algeochronology is severely underdeveloped in India and needs attention of phycologists and palaeoclimate workers to enable reconstruction of marine cloud cover, temperature gradients, ocean productivities and ecosystem models.
- 9) Role of coralline red algae in the carbonate budget and ocean dynamics of the tropical Indian sedimentary basins are very poorly understood and demands polished evaluations to better utilize their ecosystem functions. Locating

and describing the algal carbonate factories, and the evaluation of their extent and production are a priority for future research as a tool for the environmental management of the tropical biodiversity hot-spots and to contribute well to a reliable carbonate budget for the world shelves.

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