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Diverse geniculate coralline algae in Cenozoic fossil records: knowledge gaps and applications in palaeoecology

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ABSTRACT

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Coralline red algae (Corallinophycideae) are marine calcifying primary producers documented in euphotic habitats globally. Cenozoic carbonate sediments of India put forward an excellent opportunity for the analysis of coralline algae, their contribution to the reconstruction of benthic palaeoenvironments and response to climate change. Compared to the common integrated analysis of non–geniculate coralline morphotypes with benthic groups like corals and larger benthic foraminifera, the application of geniculate coralline algae is relatively very poor in palaeoecological studies. In order to understand their diversity and status in the Cenozoic fossil records, analysis of limestones and benthic assemblages from the Lakadong Limestone, Prang Formation (Meghalaya, NE India), Fulra Limestone Formation (Kutch Basin, W India), Long Formation (Little Andaman Island) and Guitar Formation (Car Nicobar Island) is carried out in addition to a concise review of existing literature. Critical gaps in our understanding of fossil geniculate coralline algae are discussed emphasizing on the usually overlooked methodological constraints.

Key–words—Coralline red algae, Geniculates, Palaeoenvironment, Benthic, India.

INTRODUCTION

CORALLINE red algae are receiving significant attention across the earth and ecological sciences in the context of climate change research. This biotic group is characterised by two major morphotypes: (i) geniculate forms (i.e. articulated thalli with non–calcified flexible genicula alternating with rigid calcified intergenicula), and (ii) non–geniculate forms that include crustose coralline algae forming bio–encrustations (associated with soft–bottom and more commonly hard–bottom substrates like rocks, pebbles and boulders) and the unattached nodular aggregations termed as rhodoliths (only in case of coralline algae making up >50% volume of the biogenic nodule, otherwise referred to as coatings). The morphology of geniculate or articulated coralline algae comprises an algal frond growing from a basal crust. Geniculate corallines show strong patterns of zonation across intertidal (Fig. 1) and subtidal zones globally depending upon their tolerance to light, desiccation, and grazing pressure (Martone, 2010; Guenther & Martone, 2014). Owing to their vast geographic distribution across diverse habitat types and latitudes, they play a key role in the ecology of benthic communities worldwide. Considerable information on coralline algal (living) ecology has been documented till date from several natural and laboratory experimental case studies, despite high diversity in their growth–forms and significant cryptic diversity emerging from the contemporary molecular studies (McCoy & Kamenos, 2015).

Corallines are also finding increased application in palaeoecological case studies (Cabioch *et al*., 1999; Aguirre *et al*., 2007; Ghosh & Sarkar, 2013; McCoy & Kamenos, 2015; Sarkar, 2016, 2018; Sarkar & Narasimha Rao, 2018; Coletti & Basso, 2020). Trends of diversification shown by coralline algae over the geological time endorse the ability of this group to colonize a wide range of environments and thrive as important components of benthic marine communities with disparate ranges of light, temperature, nutrient regime and hydrodynamic conditions (Aguirre *et al*., 2000). Non–geniculate coralline algae are widely used as palaeoecological proxies in shallow–marine settings where

Fig. 1—Temperate geniculate *Corallina officinalis* (pink coloured arborescent growth–form) in a shallow intertidal pool of Portsmouth, UK.

they usually co–occur with corals, green algae, larger benthic foraminifera, molluscs, etc. However, the applicability of geniculate corallines has been highly limited in spite of their common occurrences in most of these assemblages. Commonly occurring geniculate coralline algae in various Cenozoic carbonate sediments of India offers an excellent opportunity to analyse their ecology in these fossil records. Sedimentary successions representing various stages of the geological timescale allow to study the diversity of geniculate forms and their response to change in deep time ecological parameters. In this paper, geniculate coralline algae from the late Palaeocene–earliest Eocene Lakadong Limestone and middle Eocene Prang Formation (Meghalaya, NE India), middle Eocene Fulra Limestone Formation (Gujarat, W India), middle Miocene Long Formation (Little Andaman Island) and late Pliocene Guitar Formation (Car Nicobar Island) are analysed. These are compared to the major biotic components, especially the non–geniculate coralline algae in terms of their potential and role in determining the palaeoecological interpretations of the skeletal assemblages. Based on this study and literature analysis, the main ecological drivers regulating the particular skeletal assemblages are summarised. This paper aims to provide new insights regarding the evaluation of fossil geniculate corallines with the methodological constraints pertaining to these benthic biota and have definite implications for future research on their palaeoecology.

MATERIAL AND METHODS

Data pertaining to the fossil geniculate coralline algae have been evaluated from numerous carbonate successions outcropping in diverse geographic localities of India to attain a general idea of their ecology. In Meghalaya (NE India), rich fossiliferous limestone samples from a succession in Mawmluh, East Khasi Hills attributed to the Lakadong Limestone (Sarkar *et al*., 2022), and a limestone quarry near Lumshnong in the West Jaintia Hills belonging to the Prang Formation (Sarkar, 2017) were examined. The middle Miocene limestones from the Little Andaman Island were studied from a succession in the Hut Bay region along the south–eastern coastline of the island (Sarkar *et al*., 2016). The late Pliocene samples were analysed from a section located ~1 km north–east of the Kakana Village located at south–eastern part of the Car Nicobar Island (Ghosh & Sarkar, 2013; Sarkar, 2016). The lithology and site details of these study sections are documented in the respective case study publications as referenced above and will not be duplicated here. The same set of materials used for these publications have been examined in the present study with special emphasis on the geniculate corallines. For Fulra Limestone Formation in the Kutch Basin, samples were collected from two sections exposed around the Jhadwa Village (23º30'35"N; 68º36'32"E) but only one of them with approximately 2 m thickness and monotonous limestone lithology yielded productive samples. Materials from the other section were highly weathered and no microfossils could be identified. In total, 8 samples were collected from the productive study section and 16 randomly oriented petrographic thin–sections were analysed for evaluating the skeletal components. Thin–sections obtained from 5 samples yielded geniculate corallines (Fig. 2). As the overall record of geniculate forms in the succession is not abundant but common, therefore lack of articulated forms in some samples with only two thin–sections per sample is not unexpected.

Several publications pertaining to the records of fossil geniculate coralline algae from Cenozoic sediments of India have been referred in the current study (for e.g. Kundal & Wanjarwadkar, 2000; Kundal & Dharashivkar, 2003; Kundal

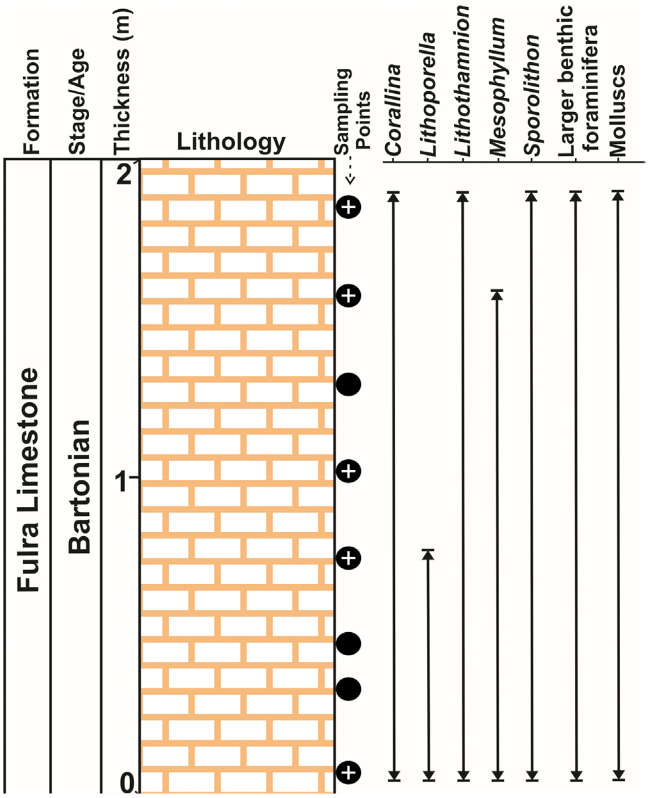

Fig. 2—Lithocolumn of the study section showing the sample positions by black circles and distribution of coralline algal genera and major biotic groups in the studied section. Samples yielding geniculate genus *Corallina* are indicated by plus sign.

& Humane, 2003, 2005, 2006a, b, 2012; Chaurpagar *et al*., 2009; Kishore *et al*., 2009; Kundal & Mude, 2009, 2010; Singh *et al*., 2010; Kundal, 2011; Kundal *et al*., 2011; Misra *et al*., 2016; Mude *et al*., 2021). The analysis of the geniculate corallines is based completely on morpho–taxonomic criteria and identifications are limited to the generic level owing to issues with nomenclature mentioned in the subsequent discussion below. Fundamental keys to the identification of the geniculate coralline genera are described in the review by Kundal (2011). In the present study, three noteworthy geniculate coralline genera recorded are *Amphiroa*, *Corallina* and *Jania*. Genus *Amphiroa* in fossil material is distinguished by varying alternations of well–marked rows of long and short cells. Cell rows of the core region are longer and join regularly in the genus *Corallina* and irregularly in the genus *Jania*. Cells in the core filaments are wedge–shaped in *Jania*, and regular squared to rectangular in *Corallina*. Other genera like *Arthrocardia*, *Calliarthron*, *Metagoniolithon* and *Subterraniphyllum* are not observed in the present study materials or rare in occurrence, thereby having no notable applicability to the palaeoecological interpretations of the skeletal assemblages.

The relative abundance of the major biotic groups was determined by the quantitative methodology of Perrin *et al*. (1995). Geniculate corallines were specifically quantified in the study materials by point–counting and a semi–quantitative approach was followed for descriptions using classes of relative abundance (abundant, >20; common, 5–20; rare, <5). Description of carbonate textures follows the classification schemes by Dunham (1962), Embry & Klovan (1971) and Flügel (2010).

RESULTS

The study sections are all characterised by varying proportions of red and green calcareous algae and small to larger benthic foraminifera which compose the major microfacies. Carbonate textures include grainstones, packstones, rudstones and bindstones in all the sections with wackestones and boundstones prominent in parts of the Long and Guitar formations. Diverse biota like gastropods, bivalves, bryozoans, echinoids and sponge remains are observed in all the study materials but rare in quantities. Corals and barnacles are rare to abundant in the Neogene Andaman–Nicobar sediments but absent in the Palaeogene sediments of Meghalaya. Macroscopic fragments of corals were observed in the Jhadwa section during the field analysis but no signatures could be recorded in the thin–sections.

Geniculate coralline algae are represented by abundant intergenicula segments of *Corallina* and *Jania* in the Mawmluh section, while the Lumshnong section comprises abundant *Corallina* with rare *Jania*. Rare occurrences of genus *Arthrocardia* are also recorded from the Meghalaya materials. The Neogene sections are characterised by highly abundant *Amphiroa* and *Corallina*, with rare occurrences of *Jania* in both the study sections. Representative images of the noteworthy geniculate genera from the study sections are illustrated in Fig. 3. The relative abundance of geniculates in the coralline–dominant microfacies reaches up to 25% in the Neogene sediments while they are slightly less abundant in the Palaeogene records (~18%). The distribution of geniculate coralline genera in various sedimentary basins of India is summarised in Table 1. Information with regard to the stratigraphic range, principal associated skeletal components and the interpreted palaeoenvironment of the major geniculate coralline algae recorded in the current study is presented in Table 2.

The Jhadwa section comprises non–geniculate *Lithothamnion*, *Mesophyllum, Lithoporella* and *Sporolithon* with few indeterminate forms assignable to the Order Hapalidiales. Geniculate corallines are represented by common occurrences of *Corallina*, while few small fragments appeared articulated but could not be identified to the generic rank. Larger benthic foraminifera are also prominent in the section featuring *Alveolina elliptica*, *Assilina exponens*, *Discocyclina dispansa, Nummulites acutus*, *N. beaumonti,* *N. maculatus* and, *N. stamineus* identified by means of field observations and thin–section study thereby assigning the section to the Bartonian Fulra Limestone Formation. Several other nummulitids, alveolinids and orthophragmines are present but could not be identified up to the generic rank in the thin–sections.

DISCUSSION

The three major geniculate coralline genera recorded in the current study are *Amphiroa*, *Corallina* and *Jania* that are interpreted to have thrived in the upper photic zone of the inner to middle shelf platform environments. *Amphiroa* shows extensive records in the Neogene sediments of the Andaman–Nicobar sediments but is completely absent in the Palaeogene carbonates of both the Lakadong Limestone and Prang Formation in Meghalaya, NE India. Very high temperature regime has been interpreted as the major cause for the lack of any prominent coral reefs in NE India (exception to majority of the Tethyan domains) during the late Palaeocene to earliest Eocene (Sarkar *et al*., 2022). Since the Prang Formation also does not indicate any coral reef records, it can be deduced that corals could never thrive and develop reefal structures in NE India during the Palaeogene. *Amphiroa* in the Long and Guitar formations show frequent co–occurrence with corals in a well–developed reefal environment (Ghosh & Sarkar, 2013; Sarkar *et al*., 2016). Several species of *Amphiroa* are also known from the Dwarka–Okha area of Gujarat, W India (Kundal & Dharashivkar, 2003; Kishore *et al*., 2012) with a reefal affinity although the other benthic components in the sediments are not listed and discussed in the paper leaving a major gap in the palaeoecological understanding of the study genus in the particular environment. *Corallina* and *Jania* show moderate to good records in both the Lakadong Limestone and Prang Formation which indicates better resilience to higher temperatures. *Amphiroa*, just like corals is interpreted to show lesser adaptability to abrupt increase in temperatures although it is common in the warm, shallow tropical to subtropical regions of the world.

The analysis of the Lakadong Limestone shows a severe decrease in geniculate corallines along with depth–sensitive dasycladalean taxa coinciding with a rise in depth (Sarkar *et al*., 2022). This population collapse could be attributed to a combination of several factors including the hyperthermal (PETM) core and increase in bathymetry (also indicated by a rise in the thinner encrusting corallines and flattened orthophragminids). Geniculate *Corallina* in the Jhadwa section (Fulra Limestone) co–occurs with larger benthic foraminifera and non–geniculate coralline genera *Lithoporella*, *Sporolithon*, *Lithothamnion* and *Mesophyllum* with the latter three showing nearly equal abundance. Bathymetric interpretation of *Sporolithon* is problematic since it is recorded from very shallow to deeper habitats within the euphotic zone (Rasser & Piller, 1997; Basso *et al*., 2009; Braga *et al*., 2009; Chelaru *et al*., 2019). *Mesophyllum* is the genus with the highest affinity towards light among the genera of Hapalidales (Cabioch *et al*., 1999; Coletti & Basso, 2020). Since genus *Lithothamnion* with proximity to deeper water habitats and larger benthic foraminifers, like endosymbiotic *Alveolina* are abundant across the section with *Sporolithon* and *Mesophyllum*, an overall depth <40 m is interpreted for the depositional environment. A well–lit oligotrophic environment is interpreted for the assemblage and intergenicula fragments of the genus *Corallina* with evidences of abrasion indicate transportation from shallower depth habitats where they appeared to have originally dwelled. However, the present study is limited to primary observations from a single section and further work is needed to ascertain

Table 1—Distribution of geniculate coralline genera in various sedimentary basins of India (Data compiled from various references listed in the paper).

Geniculate Coralline Genera	**Sedimentary Basins**					
	Assam–Arakan Basin	**Kutch Basin**	**Saurashtra Basin**	**Andaman–Nicobar Basin**	**Kerala–Konkan Basin**	**Cauvery Basin** (including Cretaceous records)
Amphiroa	–	+	+	+	+	+
Arthrocardia	+	+	+	+	–	–
Calliarthron	–	+	+	–	–	–
Corallina	+	+	+	+	–	+
Jania	+	+	+	+	–	–
Metagoniolithon	–	+	–	–	–	–
Subterraniphyllum (Extinct genus)	–	+	+	–	–	–

the ecological interpretations. A deeper depth of >50 m has been interpreted in some earlier publications (Misra *et al*., 2006; Singh *et al*., 2010) but the foraminifera assemblages have not been described adequately except only the mention of genera like dominant *Nummulites* and *Discocyclina* without any illustrations or data pertaining to their morphologies and relative abundance. Ecological analysis based only on a single biotic group (in this case coralline algae) with lack of detailed information on the overall skeletal assemblage does not comply with the fundamental necessities of palaeoecological analysis and suffers from strong proxy bias.

Geniculate coralline algae show a very broad geographic distribution globally and several of these articulated genera originated during the Cretaceous diversifying for >100 million years (Aguirre *et al*., 2000; Kundal, 2011). Much of the available experimental data on coralline calcification has been obtained from geniculate coralline algae, like the genera *Amphiroa*, *Calliarthron* and *Corallina*, owing to their higher growth rates compared to non–geniculate coralline algae. Experiments on geniculate taxa have proved fruitful in presenting insights pertaining to the mechanism of calcium carbonate precipitation and nucleation in coralline algae. Calcification in geniculate corallines has been determined to be highly specified, as evidenced by partially calcified and partially uncalcified cells at the geniculum–intergeniculum interface (Johansen, 1981; Martone *et al*., 2010). Despite the very high potential in ecological studies pertaining to modern habitats and ecosystems, several factors like taphonomic disarticulation, poor degree of preservation due to several causes like weathering, micritization and other processes of diagenesis leading to ultimate complexities with identification of fossil geniculate corallines are the major problems causing hindrance in their utilisation as effective palaeoecological proxies.

Identification of coralline algae up to the ranks of genera and species is highly challenging. The complications increase manifold in fossil coralline algae which are identified by morpho–anatomical study approaches (Rasser & Piller, 1999; Maneveldt *et al*., 2016). In the case of the geniculate corallines, a major taxonomic constraint has been the lack of preserved genicula in fossil specimens with rare exceptions (Kundal, 2011). Due to the lack of complete morphological structure available for analysis and the presence of conceptacles a very rare observation, the study of geniculates suffers from imprecision compared to the better preserved non–geniculate forms. Bassi (1998) grouped all the potentially geniculate thalli and fragments under the informal group 'Geniculates' in the absence of appropriate information pertaining to these forms based on the current morpho–anatomical taxonomic concepts. In recent decades, novel molecular techniques including DNA sequencing have revealed extensive imprecision of morpho–anatomy to distinguish coralline species, and even genera (Twist *et al*., 2019, 2020). Assertion of proper appropriate identifications is very important to validate and distinguish the coralline species ensuring their proper application in ecological studies. Assertion of proper taxonomic ranks is very important in any palaeoecological studies. Kishore *et al*. (2017) criticised certain aspects of coralline taxonomy in some previous papers from the coralline algae of the Little Andaman area (Sarkar & Ghosh, 2015; Sarkar *et al*., 2016) without providing any details. Unfortunately, while making criticisms regarding taxonomic errors they incorrectly mentioned the genera *Mesophyllum*, *Lithoporella*, *Lithothamnion* and *Titanoderma* as ‘species’. They provide several palaeoecological remarks without adequate data/information on the relative abundance of all the components of the skeletal assemblages mentioned, nor do they describe the morphological features or any quantitative data with respect to the other biotic components of the study section.

Table 2—Stratigraphic range, major associated skeletal components and range of palaeoenvironments pertinent to the major geniculate coralline genera in the current study.

Genus	**Stratigraphic Range**	**Associated Benthic Components**	**Palaeoenvironment**
Amphiroa	Early Cretaceous to Recent	Other geniculate and non–geniculate coralline algae, small to larger benthic foraminifera, barnacles, corals, green algae, echinoderms, molluscs, serpulids, bryozoans	Coastal, intertidal to subtidal marine domains including coral and algal reefs, mudflats, estuaries, rocky shores
Corallina	Late Palaeocene to Recent	Other corallines with mastophoroid genera and other Corallinaceae members more prominent, green algae including dasycladalean and halimedacean forms, benthic foraminifera, corals, oysters, balanids and barnacles, bivalves, echinoids, gastropods, serpulids, sponges	
Jania	Early Cretaceous to Recent	Other corallines with mastophoroid genera and other Corallinaceae members more prominent, green algae including dasycladalean and halimedacean forms, benthic foraminifera, corals, oysters, balanids and barnacles, bivalves, echinoids, gastropods, serpulids, sponges	

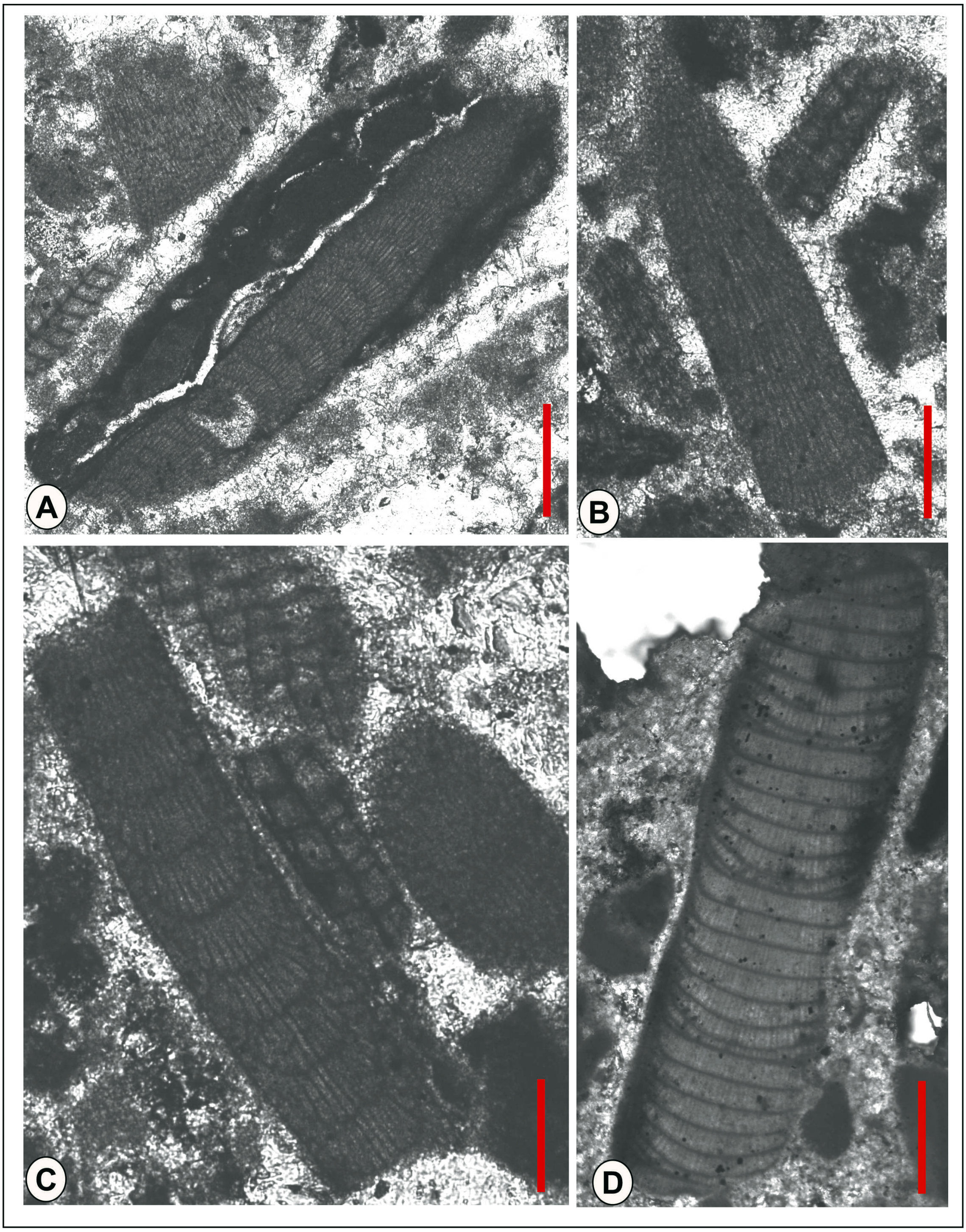

Fig. 3—Photomicrographs of the major geniculate coralline genera. (A) *Corallina*; (b) *Jania*; (C) *Arthrocardia*; (D) *Amphiroa*. Scale bars: 0.5 mm.

Certain protocols, like reporting the methodology used for the identification of study specimens should definitely be included in any report that will avoid the risk of generating ambiguous data and carrying out irreproducible science. Palaeoecological evaluation of shallow–marine benthic communities emphasise on the identification of one to several species with known environmental tolerances or ecological functions in the fossil assemblages or sediment cores for the reconstruction of the platform palaeoenvironments (Adey & Steneck, 2001; Perry & Hepburn, 2008; McCoy & Kamenos, 2015). DNA–based identifications have been recommended over the classical morpho–anatomical procedures by some workers (Twist *et al*., 2020) which is acceptable in the study of living specimens but got to be rejected in the case of fossil corallines. Application of genetic tools including DNA sequence analysis is not a feasible methodology in the extraction of specimens from rocks that are the major sources of fossil coralline algae in Neogene to Palaeogene or older sediments.

Coralline red algae have been subject to a long history of diversification and evolution that encompasses persistent records of genera, like *Sporolithon*, *Lithothamnion*, *Mesophyllum* and *Amphiroa* from various stages of the Cretaceous to the Recent. However, barring rare species, like *Lithoporella melobesioides*, there have been frequent alterations and turnovers at the rank of species in the relic coralline assemblages and the degree of resilience in the case of coralline species has not been to the level of their corresponding genera. It is virtually impossible to distinguish specific ecological characteristics of geniculate taxa in the fossil records, except in cases of possible algal blooms. Taxonomic uncertainties pertinent to fossil coralline algae have been discussed in some papers (Braga & Aguirre, 1995; Rasser & Piller, 1999; Bassi & Nebelsick, 2000) which makes it more compelling to use only generic names especially in palaeoecological studies. However, the identification of fossil geniculate coralline algal species with standard levels of preservation in taxonomic notes should not be discouraged. Palaeoecological analysis of any genus should be made with detailed data on the other benthic components of a study assemblage emphasising on their morphologies and relative abundance. Interpretation of quantitative or at least adequate semi–quantitative data is strongly recommended for attaining polished palaeoecological datasets on fossil coralline algae (both geniculate and non–geniculate taxa).

CONCLUDING REMARKS

A total of seven geniculate coralline algal genera–*Amphiroa*, *Arthrocardia*, *Calliarthron*, *Corallina*, *Jania*, *Metagoniolithon* and *Subterraniphyllum* are known from the Cenozoic records of India. In the present study, shallow–marine geniculate corallines are examined from multiple Palaeogene and Neogene successions. *Amphiroa* is highly abundant in the Neogene Andaman–Nicobar sediments whereas, it is absent in the Palaeogene sections analysed from NE and W India. Poor resilience to increase in temperature regime is interpreted as a possible reason for its absence in the late Palaeocene to middle Eocene of Meghalaya. *Corallina* is the most well–distributed genus in the current study sections evolving from the late Palaeocene to the late Pliocene, with its records extending into the modern oceans. The use of modern analytical approaches like DNA sequencing has raised questions on the morpho–anatomical methodologies for the taxonomic identifications of coralline algae but in the case of fossil specimens, the latter is the only effective and practically feasible way to examine the taxa especially in case of Palaeogene and Neogene sediments or older rocks. Due to incomplete preservation of the geniculate coralline thalli limited to the calcified intergenicula, their identifications especially at the species level should be approached with higher caution. For palaeoecological analyses, evaluation of the complete skeletal assemblages with detailed information should be a prerequisite.

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