

Upper Pliocene heterozoan assemblage from the Guitar Formation of Car Nicobar Island, India: palaeoecological implications and taphonomic signatures

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Abstract The upper Pliocene Guitar Formation outcrops in Car Nicobar Island, a near-pristine locality of the Andaman-Nicobar Group of Islands, India. Tropical-subtropical photozoan and cool-water heterozoan assemblages have been broadly studied up to now, but little is known about the tropical heterozoans that require deeper analysis. The major objectives of the current assessment pertaining to the Guitar Formation are evaluation of biotic diversity, palaeoecological processes governing the depositional environment and general taphonomic signatures. The carbonate sediments rich in algal and benthic foraminiferal assemblages are dominated by lithophylloids and nummulitids, respectively. Secondary biotic constituents are corals, barnacles, bryozoans, echinoderms, molluscs and gastropods. In particular, a reefal environment is indicated after a thorough examination of the heterozoan assemblages including relative abundance of the algal-foraminiferal taxa. The results indicate that carbonate sedimentation occurred in warm, tropical waters under meso-oligotrophic conditions and shallow to mildly deeper bathymetric levels ranging close to or below the fair-weather wave base.

Keywords Coralline algae · Benthic foraminifera · Heterozoans · Guitar Formation · Car Nicobar · Upper Pliocene

Introduction

Since the early Miocene, the Indo-Pacific region (30°S–30°N, 90°–160°E), that includes the Andaman-Nicobar Group of Islands, features as a global marine biodiversity hotspot (Renema et al. 2008; Mihaljević et al. 2014). This coincides with a significant enhancement in carbonate area in the region and is characterised by a shift in the major carbonate producers from larger benthic foraminifera (LBF) to corals (Wilson 2008). In addition to corals and benthic foraminifera, coralline red algae are common to abundant biogenic components of Neogene shallow-water carbonate and mixed carbonate-siliciclastic sediments (Brachert et al. 2001; Checconi et al. 2007; Ghosh and Sarkar 2013). The Pliocene Epoch (5.33–2.58 Ma) spans a critical period in the earth's history, characterised by the considerable environmental transition from relatively warm to the substantially cooler Pleistocene climate (Knowles et al. 2009; Schepper et al. 2014). As the late Pliocene represents the most recent interval of elevated global temperatures, insights into various palaeoecological parameters should provide beneficial data that are supposed to aid in understanding the benthic scenario during this critical time slice. This study deals primarily with coralline algae and benthic foraminifera, which are the most abundant benthic components of the upper Pliocene carbonate sediments outcropping in the Car Nicobar Island, India.

Numerous classes of biota produce carbonate sediments that reveal the environmental conditions during their genesis period. Therefore, carbonate sediments and rocks are multiproxy archives (e.g. temperature, light intensity, salinity, trophic resources, bathymetry, oxygen levels and hydrodynamic energy) for evaluation of palaeoecological perspectives and reconstruction of depositional palaeoenvironments (Tucker and Wright 1990; Flügel 2004; Zoeram et al. 2015). Lees and Buller (1972) and Lees (1975) described tropical

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carbonates, also known as the foramol associations, in which typical tropical biogenic components (e.g. hermatypic corals, calcareous green algae and ooids) are absent. Foraminifers and molluscs are mostly present as dominant constituents in the foramol associations. Other common components are coralline red algae, echinoderms, bryozoans, barnacles, ostracods, sponges (calcareous spicules), worms (tubes), and ahermatypic corals. The foramol associations dependent on factors like geographical latitudes, water temperature and light dependence have also been described as non-tropical (Nelson et al. 1988), cool-water (Schlager 2000) and heterozoan (James 1997) carbonates, respectively. In addition to the frequently observed foramol components, chlorozoan and chloralgal associations always contain hermatypic corals and calcareous green algae, respectively. These two associations constitute the tropical (Nelson et al. 1988; Rao 1996; Schlager 2000) or photozoan (James 1997) carbonates. Lees and Buller (1972) and Lees (1975) demonstrated that, while chlorozoan and chloralgal associations were prominent and limited only to the tropics, foramol associations were found both in the higher latitude domains as well as inside the tropical belt (i.e. between 30°N and 30°S). Heterozoan assemblages are reported from a wide array of locations influenced by different climatic regimes (Samankassou 2002; Pomar et al. 2004; Braga et al. 2006; Brandano et al. 2009; Westphal et al. 2010; Klicpera et al. 2015). The tropical photozoan and non-tropical heterozoan carbonates have been subject to a wide range of studies to define a useful framework to interpret the sedimentary record on the basis of grain associations (Lees and Buller 1972; Lees 1975; James 1997). However, the tropical heterozoan carbonates have received less attention, thereby resulting in many constraints in the analysis of ancient deposits (Pomar et al. 2004; Wilson and Vecsei 2005; Westphal et al. 2010). Here, a late Pliocene tropical shallow-water heterozoan assemblage from the Car Nicobar Island, India, is presented.

The Andaman-Nicobar Group of Islands has been studied by several workers since the early twentieth century because of its importance in understanding the geology of India and northern Indian Ocean. This is primarily due to the presence of abundant fossil material, including foraminifera, radiolaria, diatoms, nannoplankton, ostracods, silicoflagellates and calcareous algae, etc., present in the relic sediments that bear high potential to analyse critical factors like their bathymetric zonation, hydrocarbon prospects and the regional tectonic history (Gee 1927; Van Bemmelen 1949; Rodolfo 1969; Srinivasan 1969, 1975, 1988; Badve and Kundal 1998; Chandra et al. 1999; Sharma and Srinivasan 2007; Ghosh and Sarkar 2013; Sarkar and Ghosh 2015). However, the Neogene sediments of the Andaman-Nicobar Islands have not received substantial impetus in terms of understanding the carbonate fossil assemblages, their diversity, ecological and taphonomical characteristics. The last few decades have

witnessed substantial progress and modifications in the field of taphonomy as a valuable discipline of earth sciences. It has shifted the perception of understanding fossilisation as a process of losing geological information to considering it as a source of supplementary knowledge regarding the origin of materials (Brett and Baird 1986; Zabini et al. 2012; Serrano-Brañas and García 2014). Here, the diversity analysis, palaeoecological implications and brief taphonomic overview of the heterozoan assemblages from this relatively pristine locality of the tropical realm is discussed. The integrated study of the Car Nicobar benthic fossils serve as a valuable tool for the interpretation of the carbonate sedimentary environment.

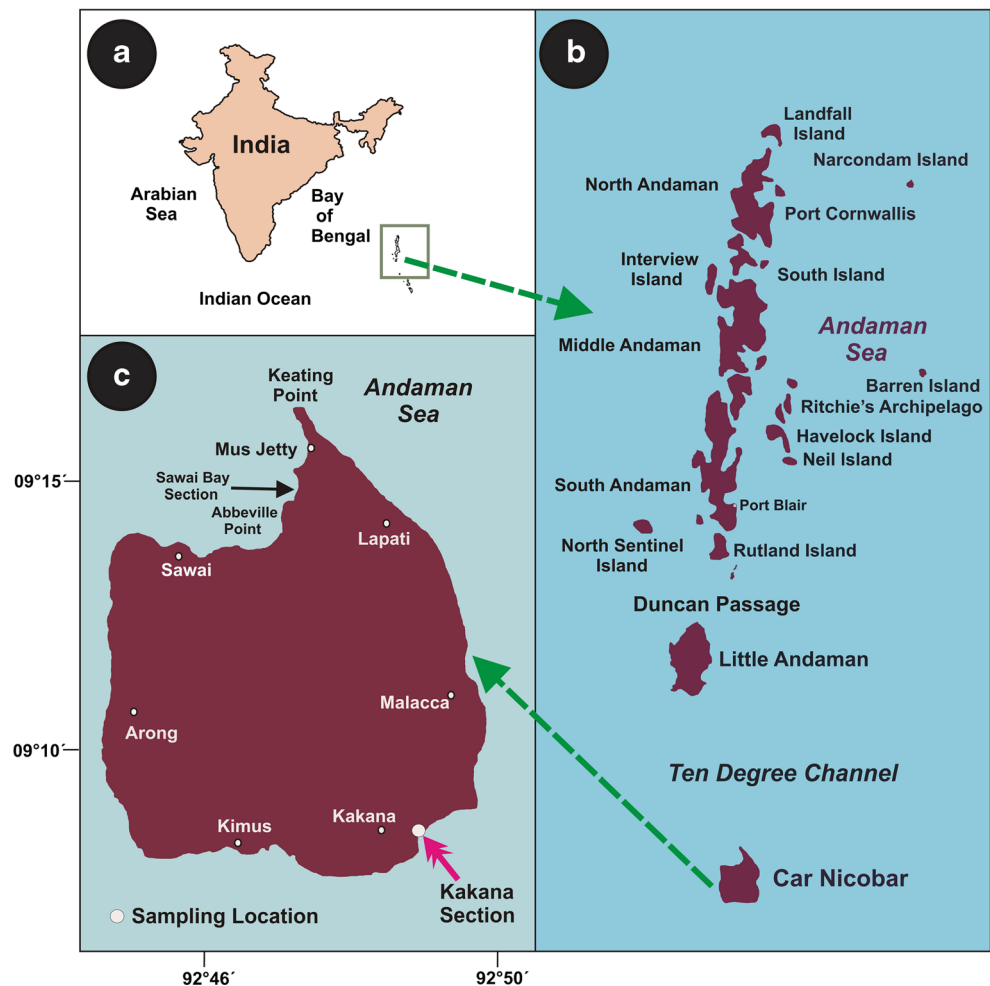
Geological setting

The Andaman and Nicobar Islands are the sub-aerial expression of a continuous ridge which connects the Arakan-Yoma Range of Western Burma to the drape of islands, south and west of Sumatra. They are divided into two groups: the Andamans in the north and the Nicobars in the south, with the Ten Degree Channel separating the two (Fig. 1). These islands can be separated into two concentric arcs, i.e. the western (outer) sedimentary arc comprising major islands of the Andamans and the Nicobars, extending southeastwards to form the Indonesian orogenic belt, and the eastern (inner) volcanic arc including the conical volcanoes of Narcondam and Barren Islands. A third island arc to the west of the Andaman-Nicobar Islands is in the process of emergence (Eremenko and Sastri 1977; Sharma and Srinivasan 2007).

The Andaman and Nicobar Group of Islands are characterised by a thick marine sedimentary succession ranging from late Mesozoic to Quaternary, divided in five lithostratigraphic groups: Porlob (Upper Cretaceous), Serpentine (Upper Cretaceous to Eocene), Baratang (Upper Cretaceous to upper Eocene), Port Blair (upper Eocene to Oligocene) and Archipelago (lower Miocene to Pleistocene) (Srinivasan 1988; Sharma and Srinivasan 2007; Sarkar and Ghosh 2015). The Archipelago Group encompassing the Neogene sediments unconformably overlies the Palaeogene Port Blair Group. The Neogene sediments are mainly composed of mudstones, chalks and limestones. Abundance of microfossils like foraminifera, barnacles and coralline algae mark the principal characteristic feature of the Neogene sediments pertinent to the Archipelago Group.

Car Nicobar is the northernmost island of the Nicobars, situated between 09°07'–09°13'45"N and 92°43'–92°50'E (Fig. 1). It is characterised by flat topography and low relief. Principal rock types lack much diversity, including mainly limestones and mudstones. Three lithostratigraphic units, Sawai Bay Formation (Srinivasan and Azmi 1976), Guitar Formation (Srinivasan and Azmi 1976) and Malacca Limestone Formation (Srinivasan and Sharma 1973), outcrop in the

Fig. 1 **a** The location of Andaman-Nicobar Islands; **b** enlarged view of the Andaman Group of Islands and the Car Nicobar Island; **c** Car Nicobar Island highlighting the location of the studied section (denoted by pink arrow)



Car Nicobar Island. The Sawai Bay Formation is characterised by light grey to bluish grey, moderately hard, calcareous mudstones. The Guitar Formation conformably overlies the Sawai Bay Formation and is mainly composed of well-bedded, pale yellow to grey, moderately sorted chalky carbonates rich in coralline algae (Ghosh et al. 2004; Sharma and Srinivasan 2007; Ghosh and Sarkar 2013). The carbonates, at some places, are affected by recrystallisation and range from sandy to coarse-grained varieties. The Malacca Limestone Formation unconformably overlies the Guitar Formation and encompasses white, compact, semicrystalline foraminiferal carbonates. The Guitar Formation deposits in the Car Nicobar Island are assigned to the late Pliocene (Piacenzian) time slice by virtue of characteristic age-marker planktic foraminifera recorded from these sediments (Sharma and Srinivasan 2007; Ghosh and Sarkar 2013). The nomenclature of various lithostratigraphic units of the Andaman-Nicobar Islands has been subject to numerous modifications in the last few decades (Sharma and Srinivasan 2007). Previously described as “arenaceous limestone” (Jacob and Sastri 1951), Sawai Bay limestone Member (Srinivasan and Sharma 1973) and the Kakana Formation (Chandra and Saxena 1998; Chandra

et al. 1999; Ghosh et al. 2004) at the Car Nicobar Island, all correspond to the Guitar Formation. The Guitar Formation shows wide distribution in the Andaman-Nicobar Islands. In Guitar Island, the type area, the formation overlies the silty mudstone component of the Long Formation (Sharma and Srinivasan 2007).

Materials and methods

A complete stratigraphic column representing the type section of the Guitar Formation was analysed from a single outcrop located at about 1 km NE of the Kakana village (09°07'N, 92°48'E) on the southeastern coast of the Car Nicobar Island. This section is also exposed on both sides of the Malacca-Kakana Road (in a hill slope on the right side and in a cliff on the left side), and near the Mus Jetty, Car Nicobar (Chandra et al. 1999; Ghosh et al. 2004). The studied succession is continuous and represents the stratigraphic log of the deposits outcropping in a single locality.

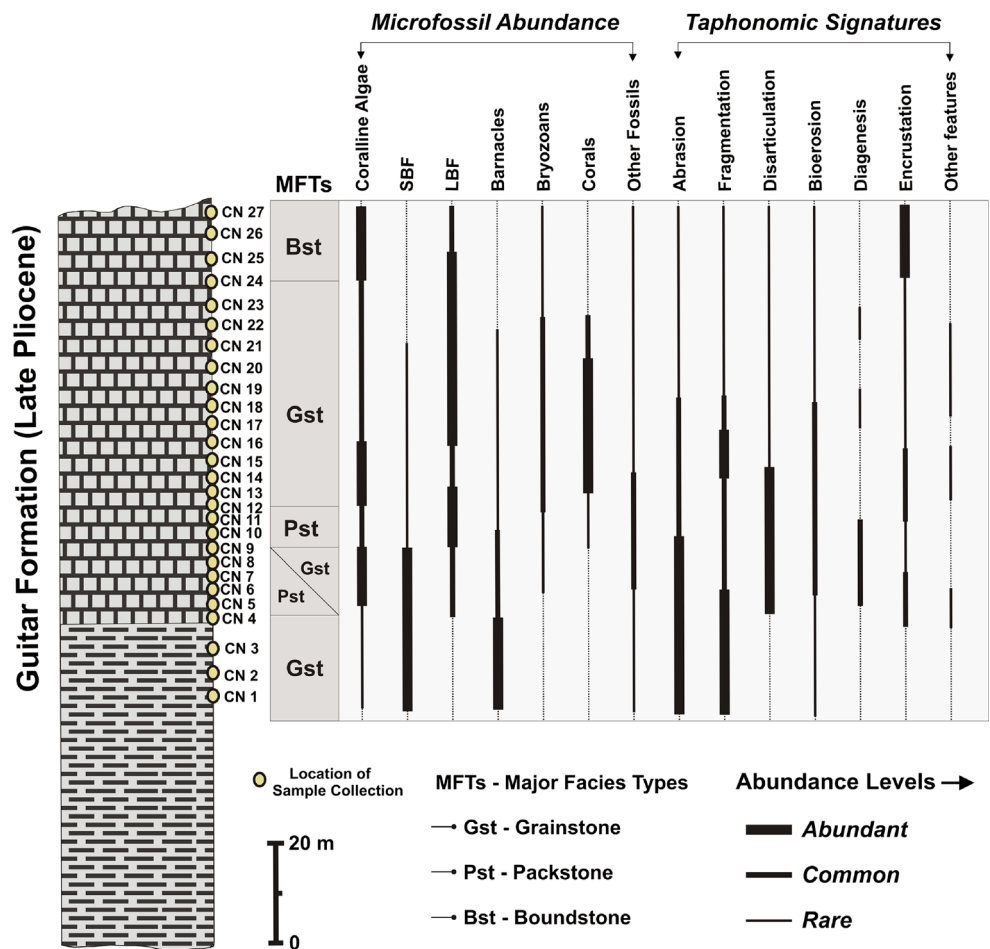
The present case study and sampling was confined just to the Kakana village section. A total of 27 random-sized, pale

yellow to light grey fossiliferous carbonate samples (CN 1–CN 27) were collected. The sampling distance, distribution of major facies types, abundance of various microfossils and incidence of different taphonomic signatures are presented in the schematic lithocolumn (Fig. 2). A total of 108 palaeontological thin sections (~3.5×5.0 cm) were studied for textural characterisation and identification of the skeletal components. Analysis of thin sections with uniform microscopic field area standardised the diversity analysis during point counting of specimens by measuring the relative abundance (Perrin et al. 1995). The uncertainties associated with fossil coralline algae taxonomy (Braga and Aguirre 1995; Aguirre and Braga 1998; Rasser and Piller 1999; Bassi and Nebelsick 2000) have been avoided by conducting identifications only at the generic and subfamily level. Family, subfamily and generic circumscriptions follow standard literature sources (Woelkerling 1988; Braga et al. 1993; Aguirre and Braga 1998; Harvey et al. 2003; Iryu et al. 2009). Due to the inconspicuous nature of epithallial cells (flared or not) in several melobesiod specimens, they have been tentatively termed

as *Lithothamnion/Phymatolithon* spp. Coralline algal growth-form terminology follows Woelkerling et al. (1993). Growth-form determination in thin-section analysis is influenced by orientation and sectioning effects. As the growth-form analysis for minute algal fragments (<200 µm) was difficult to state with complete precision, they were considered for diversity determination but omitted during the overall evaluation of the algal growth-forms. The taxonomic identification of the foraminifera was based on observation of random sections of the foraminiferal tests in thin section. The description and characterisation of the taphonomic features observed in the material were established according to Nebelsick and Bassi (2000) and Basso et al. (2009). Ecological characteristics such as water depth and nutrient input were determined by evaluating the coralline red algal and benthic foraminiferal assemblages. Thin sections were analysed with an Olympus BX-50 plane light microscope and the microphotographs were taken with an Olympus PM-20 Exposure Control Unit.

The material (samples, slides) is housed in the Birbal Sahni Institute of Palaeobotany, Lucknow.

Fig. 2 Lithocolumn showing the abundance of various microfossil groups and taphonomic signatures with respect to the samples, and the major facies types



Results

Diversity of biogenic components

The major biotic components of the succession are coralline algae (Fig. 3; protuberances, encrusting, nodular, arborescent and small rhodoliths) and benthic foraminifera (Fig. 4), including smaller benthic foraminifera (SBF) and LBF. The subordinate facies components are barnacles (Figs. 4b, 5a, b), bryozoans (Fig. 5c, d), coral blocks and fragments (Figs. 3e, 4e, 5e), echinoderms, molluscs and gastropods. Rare serpulids and ostracods are also observed. The matrix of the carbonate sediments is generally dominated by coralline algal detritus, abraded and fragmented foraminifera followed by poorly cemented peloids, and echinoid plates and spines. Melobesioid coralline algae include *Lithothamnion* spp. (Fig. 3a, h), *Mesophyllum* spp., *Phymatolithon* spp., *Lithothamnion/Phymatolithon* spp. (Fig. 3b) and several indeterminate forms. Mastophoroids are represented by *Lithoporella* and *Spongites* (Fig. 3g), whereas *Amphiroa* (geniculate alga; Fig. 3f, i) and *Lithophyllum* (Fig. 3c, d) are the lithophylloid genera. *Amphiroa* is the most abundant coralline form as found throughout the course of the study. Coralline geniculate algae *Corallina* and *Jania* are also observed in the thin-sections. The relative abundance of various coralline growth-forms recorded from the evaluated samples CN 1–CN 27 is presented in Fig. 6. In each sample, relative abundance of each growth-form has been calculated based on the analysis of the thin sections. Encrusting (Figs. 3c–e, 5g), layered (Fig. 5f), warty, lumpy (Fig. 5h), fruticose, unconsolidated and arborescent are the most common algal growth-forms. *Lithophyllum* shows encrusting and lumpy growth-forms, whereas the melobesioids are represented by encrusting, warty, lumpy and unconsolidated growth-forms. Mastophoroid corallines show encrusting, lumpy, fruticose and warty growth-forms. Arborescent growth-form can be envisaged for the geniculate taxa, based on comparisons with their living counterparts (Sarkar and Ghosh 2015).

The spatial distribution of the foraminiferal assemblages is largely controlled by their skeletal structure and life style, trophic requirements and marine conditions. The LBF assemblages show moderate to high diversity (Fig. 4a–d, f), represented by *Amphistegina*, *Heterostegina*, *Operculina*, *Cycloclypeus*, *Katacycloclypeus*, *Spiroclypeus*, *Nephrolepidina*, *Eulepidina*, soritids, few miogypsinoids and several reworked specimens. The SBF assemblages consist of porcellaneous miliolids (*Austrotrillina*, *Quinqueloculina*, *Triloculina*, *Biloculina*, *Spiroloculina*, *Pyrgo*) and perforate rotaliids (*Buccella*, *Cibicides*, *Elphidium*). Several incidences of grainstone samples having SBF taxa in common assemblages with corals (Fig. 4e) have been observed. Small benthic agglutinated textulariids (*Textularia* spp.) are also common.

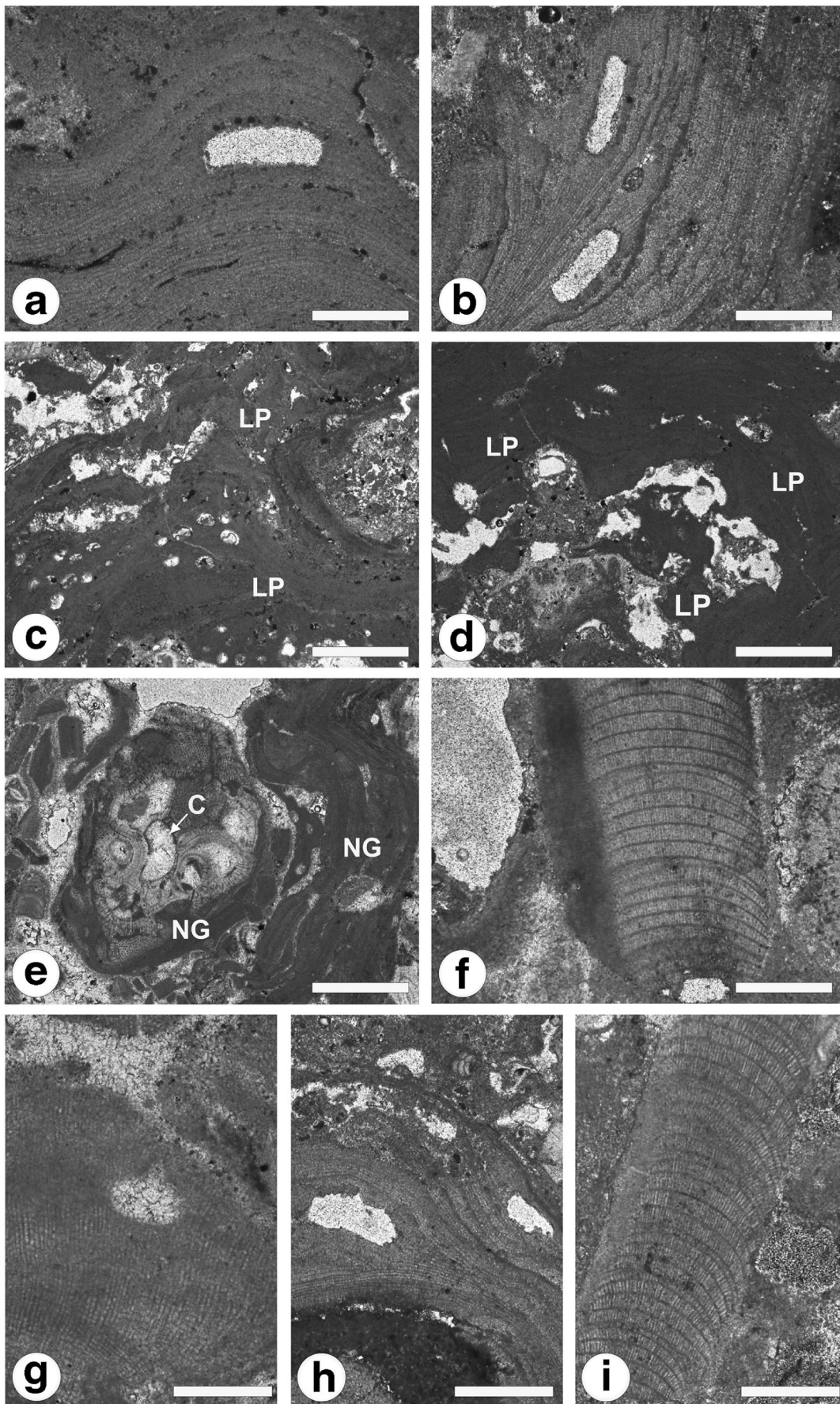
Few encrusting, perforate acervulinids (*Acervulina*) have also been observed.

Facies analysis

The Guitar Formation is characterised by grainstones, packstones and algal-dominated boundstones as the major facies types (MFTs) with secondary occurrence of wackestones. The high-energy grainstones and packstones are supposed to have been deposited across much of the Car Nicobar shelf during periods of transgression. These grainstones and packstones show cross-stratifications at few places. A total of six MFTs have been recorded in the Guitar Formation: (1) barnacle-foraminiferal grainstone, (2) coralline algal-foraminiferal grainstone-packstone, (3) foraminiferal packstone, (4) coral-coralline algal grainstone, (5) *Amphistegina* grainstone and (6) coralline algal boundstone. A reefal environment ranging from shallow intertidal to fore-reef horizon has been interpreted for the Guitar Formation (Ghosh and Sarkar 2013). Although the possibility of evolutionary changes in the composition of LBF assemblages inhabiting the platform cannot be ruled out, it is inferred that a relatively stable, normal marine environment governed the deposition of the Guitar Formation during the late Pliocene. A conceptual, schematic model showing gradients in the composition of fossil assemblages and selected ecological features of the Guitar Formation are provided in Fig. 7.

Heterozoan association

The nomenclature of grain associations have either been based on their dominant components (Lees and Buller 1972; Lees 1975), mode of life pertaining to the benthic communities (James 1997) or their geographic ranges (Betzler et al. 1997). The mode of carbonate precipitation has also been applied to classify the carbonate systems/factories (Schlager 2000, 2003). On the basis of the dominating facies components, i.e. coralline red algae and LBF, the Guitar Formation sediments of the Car Nicobar Island fit well in the foramol category which in ideal sense should have benthic foraminifera, molluscs, coralline red algae, bryozoans and barnacles as the major constituents (Lees and Buller 1972; Wilson and Vecsei 2005). It should be noted that all these biogenic entities should not necessarily be present or abundant in an assemblage to categorise it under the foramols. Coralline red algae are strongly light-dependent but may be abundant in both photozoan and heterozoan associations (James 1997; Westphal et al. 2010), since they are not dependent on warm waters and also inhabit much deeper bathymetric levels in comparison to the calcareous green algae, ranging from shallow intertidal to even >100 m (Braga and Aguirre 2004). The Guitar Formation biotic assemblages abundant in coralline algae and LBF, with subordinate occurrence of corals (Figs. 3e, 4e, 5e), barnacles (Figs. 4b, 5a, b), bryozoans



◀ **Fig. 3** Photomicrographs of the coralline algae of the Guitar Formation. **a** *Lithothamnion* sp., Sample No. CN 26 *scale bar* 300 μm . **b** *Lithothamnion/Phymatolithon* sp., Sample No. CN 16; *scale bar* 300 μm . **c, d** Encrusting lithophylloid coralline algae (*LP*, *Lithophyllum* sp.), Sample No. CN 25; *scale bars* 500 μm . **e** Non-geniculate coralline algae (*NG*) encrusting a coral block (*C*), Sample No. CN 20; *scale bar* 500 μm . **f** *Amphiroa* sp., Sample No. CN 5; *scale bar* 200 μm . **g** *Spongites* sp., Sample No. CN 18; *scale bar* 200 μm . **h** *Lithothamnion* sp., Sample No. CN 16; *scale bar* 200 μm . **i** *Amphiroa* sp., Sample No. CN 9; *scale bar* 200 μm

(Fig. 5c, d), molluscs and gastropods are assignable to heterozoan associations rather than photozoan due to complete absence of halimeds, dasyclads and other calcareous green algae. The poor to moderate frequency of corals, showing local abundance only in some grainstone samples and present mainly as scattered blocks, also present a major constraint in terming these assemblages as photozoan.

Taphonomy

The major taphonomic signatures recorded in the Guitar Formation fossil components are encrustation (Figs. 3c–e, 5f, g), fragmentation, abrasion (Fig. 5e, h), disarticulation (Figs. 3f, i, 4f, 5e), bioerosion and diagenesis. Other features such as dissolution can also be observed in some specimens. Incidences of taphonomic signatures in the material were found to be moderate to high which accounts for high water turbulence, frequent transport of sediments and herbivory. Encrustation was readily observed in the specimens involving both the non-geniculate corallines and LBF. Complex encrustation sequences can involve a variety of organisms including coralline algae, foraminifera and bryozoans (Nebelsick and Bassi 2000; Berning et al. 2009; Sarkar and Ghosh 2015). The boundstones feature abundant encrustations raising the likelihood of both strong, constructive taphonomic influence as well as the incidence of natural crustose/encrusting algal growth-forms. Disarticulation is uniformly observed in all the geniculate forms having only the calcified intergenicula preserved. No in situ preservation of robust geniculate forms with arborescent growth-forms (by virtue of encrustation) was observed in the thin-sections.

Few large melobesioid thalli showed bioerosion that can be attributed to the common agents like macroborers (e.g. bivalves, sponges), microborers (e.g. cyanobacteria, algae, fungi, micro-invertebrates) and grazers (e.g. molluscs, echinoderms). Incidences of bioerosion indicate the occurrence of herbivory in the buried sediments (Nebelsick and Bassi 2000; Basso et al. 2009; Sarkar and Ghosh 2015). Fragmentation was observed in several coralline red algal specimens and results in isolated protuberances and fruticose fragments, as well as thallial segments of crusts. Fragmentation is primarily a product of biological activity as well

as high levels of water turbulence (Basso et al. 2008; Nebelsick et al. 2011). The moderate rate of fragmentation observed in the fossils implies unfavourable physical and biological processes acting constantly with moderate to high magnitude. Degree of fragmentation was a major hindrance in the taxonomic identification and growth-form analysis (in the case of non-geniculate coralline algae) by inducing loss of diagnostic features (e.g. conceptacles) causing subsequent problems in the facies and fabric determination (Rasser and Nebelsick 2003; Nebelsick et al. 2011; Sarkar and Ghosh 2015). Abrasion is also common and evident from the production of relatively rounded components (Basso et al. 2009; Nebelsick et al. 2011; Sarkar and Ghosh 2015). A significant proportion of unidentifiable algal debris could be due to the process of abrasion caused by transport and sediment agitation that probably damaged the diagnostic features required for adequate taxonomic descriptions, especially up to the specific level. Due to the prevalence of a muddy matrix in most of the facies, the exact proportion of specimens affected by diagenesis is difficult to differentiate between the specimens covered by mud and the actually leached ones. Micritization has been observed which has resulted in masking of the anatomical characteristics, especially the cell wall and epithallium structures (Nebelsick and Bassi 2000; Sarkar and Ghosh 2015).

The deposits suggest a low sedimentation rate due to the abundance of coralline algae in a major part of the succession. Coralline algae are very sensitive to high sedimentation rates (Adey and Macintyre 1973; Bosence 1983; Aguirre et al. 2012). Very shallow settings are usually represented by high taphonomic destruction due to a combination of high hydrodynamic energy and long-term exposure of the remains in the taphonomic active zone (Powell et al. 1989; Kidwell and Bosence 1991; Aguirre et al. 2014). In this case study, evidence of transport in several fossils by means of commonly observed signatures of abrasion and fragmentation suggests substantial taphonomic influence.

Discussion

Palaeoecological factors

Important parameters having an influence on the distribution of grain associations, and resultant platform development in space and time, are water temperature, depth, nutrient levels, salinity, oceanographic setting and water chemistry (Lees and Buller 1972; Lees 1975; Nelson et al. 1988; James 1997; Mutti and Hallock 2003; Pomar et al. 2004; Brandano et al. 2009; Westphal et al. 2010; Michel et al. 2011). LBF are

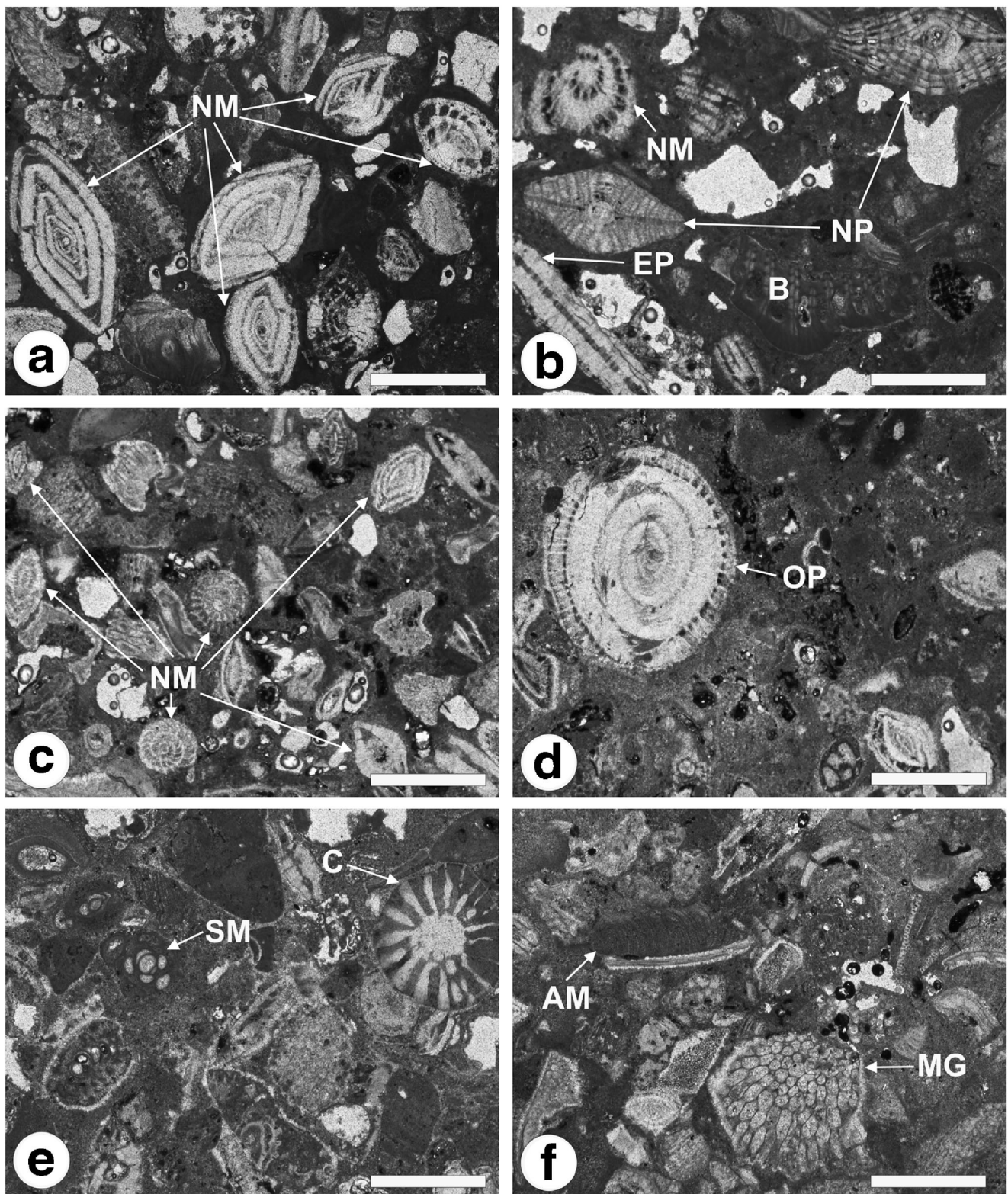


Fig. 4 Photomicrographs of the benthic foraminifera of the Guitar Formation. **a** Nummulitid (*NM*)-dominated grainstone, Sample No. CN 7; scale bar 1 mm. **b** *Nephrolepidina* (*NP*), *Eulepidina* (*EP*), nummulitids (*NM*) and barnacle shells (*B*), Sample No. CN 12; scale bar 2 mm. **c** Nummulitid (*NM*)-dominating grainstone-packstone, Sample No. CN 5;

scale bar 2 mm. **d** *Operculina* sp. (*OP*), Sample No. CN 12; scale bar 2 mm. **e** Smaller miliolid (*SM*), coral block (*C*) and algal debris, Sample No. CN 16; scale bar 1 mm. **f** *Amphiroa* sp. (*AM*), miogypsinoid (*MG*), and abraded algae-foraminifera, Sample No. CN 7; scale bar 1 mm

generally restricted to warm tropical and subtropical waters, with mean temperatures of 18–20 °C for the warmest months of the year (Adams et al. 1990), and the vast majority of occurrences are demarcated by the 25 °C summer isotherm (Wright and Murray 1972). In the case of winter isotherms, the distribution of LBF is delimited by 15–20 °C isotherms with species-dependent minimum temperatures (Langer and Hottinger 2000; Wilson and Vecsei 2005). *Amphistegina* and *Heterostegina* are typical representatives of warm water environments (Reiss and Hottinger 1984; Betzler et al. 1997; Brandano et al. 2009) and show relatively high ecological tolerances compared to other LBF (Langer and Hottinger 2000). Larger foraminifera are dependent on a tropical-subtropical range of temperatures, i.e. >18–20 °C (Betzler et al. 1997), but some forms such as *Peneroplis*, *Sorites* and *Amphistegina* are tolerant of a reduced range of temperatures, i.e. 11–14 °C (Veron 1995; Betzler et al. 1997; Langer and Hottinger 2000). Forms like *Operculina* and several orthophragminids, abundant in the sediments, have a minimum sea-surface tolerance of 20 °C (Betzler et al. 1997; Langer and Hottinger 2000; Wilson and Vecsei 2005). Although coralline red algae are reported from both warm and cold waters, some genera are dependent on temperature (Braga and Aguirre 2001). The presence of tropical genera like *Lithoporella*, *Spongites* and *Amphiroa* suggest that the carbonate sedimentation of the Guitar Formation took place in warm waters (Bosence 1983; Braga and Aguirre 2001; Brandano et al. 2009). The lithophylloids (most dominant in shallow temperate waters), mastophoroids (warmer water-dominant) and melobesioids (abundant in both temperate and warm waters at deeper levels) found in the Guitar Formation sediments along with other biogenic entities including LBF and corals indicate a tropical climate with probable temperatures of >22 °C during deposition. Detailed temperature data from the late Pliocene of Car Nicobar and other islands of the Andaman-Nicobar Group is, however, limited, and it is expected that, as more data become available, the entire course of platform development in the Andaman-Nicobar system during the Neogene time slices may be important in understanding the regional palaeoclimate. Barnacles and bryozoans are commonly related to cool-water sediments, showing rare occurrence in SE Asian case studies (Wilson and Vecsei 2005). However, these also occur in benthic zones characterised by high nutrient/eutrophic and/or low light levels due to their typical heterotrophic habit and cannot be considered as ideal cool-water indicators (Pomar 2001). The presence of these organisms in tropical Guitar Formation carbonates can also be associated with these factors.

The coralline red algae possess photosynthetic pigments chlorophyll-a and phycoerythrin that are attenuated to wavelengths of green and blue light, and are therefore common throughout the oligophotic zone. The LBF dwelling in the deeper parts of the photic zone, in comparison to corals,

commonly have a different symbiotic partner, specifically a diatom, which is more attenuated to blue and green wavelengths than the dinoflagellates in the case of corals (Lee and Anderson 1991; Wilson and Vecsei 2005). This makes the LBF adapted to low-light levels of the deeper oligophotic zone. Records of several flat LBF tests in the current case study can be attributed to their morphological adaptation of concentrating the limited available light (Hallock and Glenn 1986; Hohenegger 1999) and co-existing with deeper lithophylloids and melobesioids. Beavington-Penney and Racey (2004) distinguished the *Operculina-Amphistegina-Heterostegina* distributions which partly overlap with shallower porcellaneous larger foraminiferal areas and deeper in the lepidocyclinid area. Comparable recent LBF assemblages dominated by *Operculina ammonoides* and *Heterostegina depressa* are adapted to medium-high light intensities over wide depth ranges (Hohenegger 2004, 2005). Recent *O. ammonoides* live on fine sandy substrates from the FWB down to the storm wave base at 100 m (Hohenegger 2004; Bassi and Nebelsick 2010). Additionally, perforate hyaline foraminifera such as *Heterostegina*, *Nephrolepidina* and *Operculina* often dominate in the lower part of the upper photic zone (Bassi et al. 2007). The overall fine grain size, few sedimentary structures indicating turbulence, varying proportions of carbonate mud, and the fossil assemblages suggest the reefal sediments of the Guitar Formation to have been deposited in a low-moderate energy, shallow to mildly deeper marine environment with very limited influx of terrigenous mud from emergent basement areas. As siliciclastic sand and mud content in the outcrop is negligible, river drainage having any impact on the Guitar Formation system is not feasible. However, the dominant biogenic assemblages including coralline red algae and thin-shelled LBFs are compatible with bathymetric levels of 50–60 m for the oligophotic zone or marginally below that (Hallock and Schlager 1986; Ghosh and Sarkar 2013). Present-day melobesioid/mastophoroid assemblages thrive in mid-latitudes in shallow-water warm-temperate settings (Aguirre et al. 2000). A number of studies performed on fossil coralline assemblages have shown progressively increasing proportions of melobesioids with palaeobathymetry gradually replacing the mastophoroids as the dominating algal components (Adey et al. 1982; Braga and Martín 1988; Iryu et al. 1995; Braga and Aguirre 2004; Rasser and Piller 2004; Nalin et al. 2008; Braga et al. 2010; Ghosh and Sarkar 2013).

The larger benthic rotaliids/nummulitids, most abundant in the current analysis, are typical stenohaline organisms with tolerance limits in the range of 30–45 ‰ (Hallock and Glenn 1986). In SE Asian regions including the Andaman-Nicobar, monsoons and the subsequent rainfalls can have an impact on the salinity levels. These are expected to be slightly lower than the normal marine conditions but the overall salinity is likely to fall within the tolerance range of the LBF and corals. The

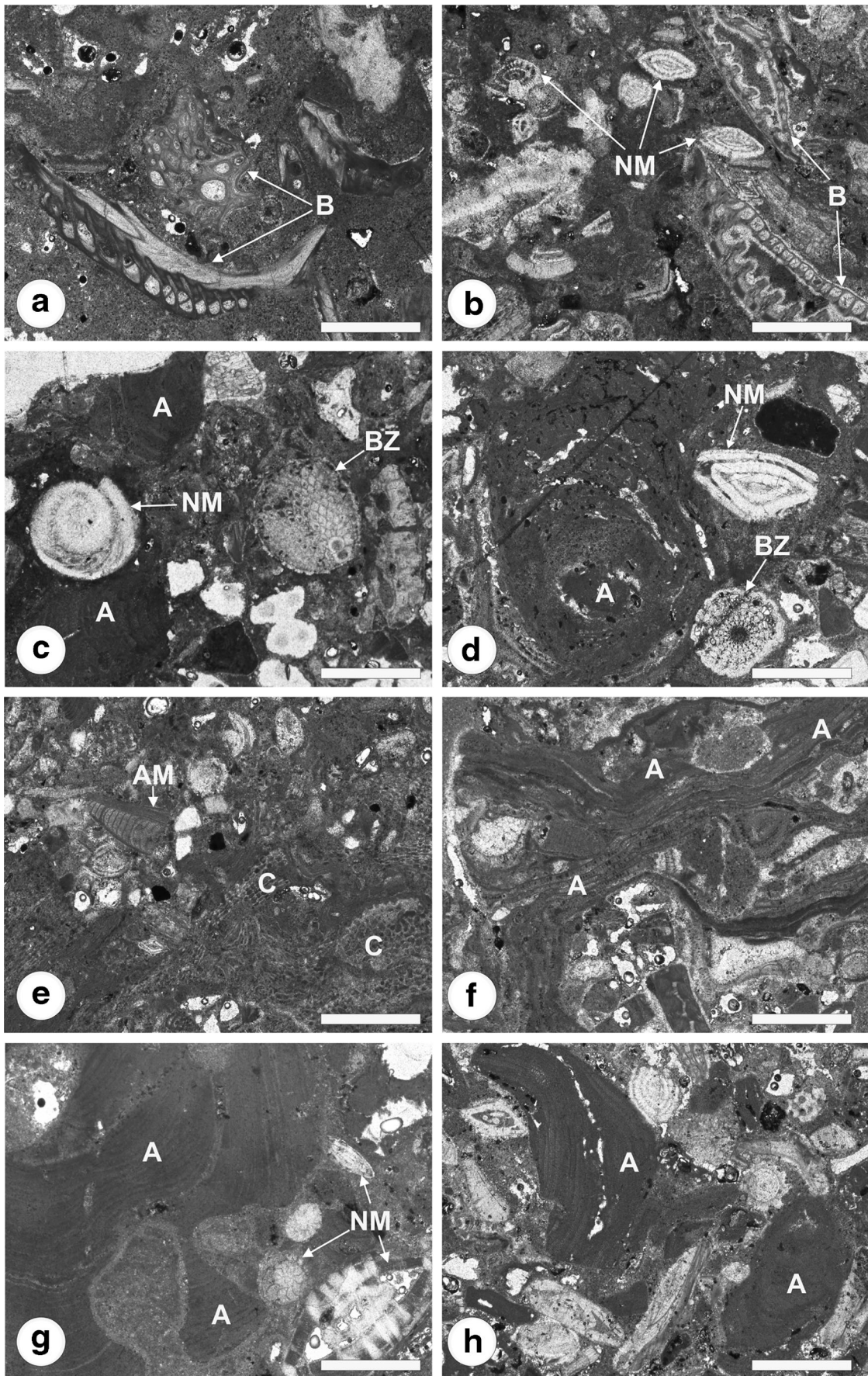


Fig. 5 Photomicrographs of various benthic components of the Guitar Formation. **a** Barnacle shells (*B*), Sample No. CN 2; *scale bar* 2 mm. **b** Barnacle shells (*B*) and smaller nummulitids (*NM*), Sample No. CN 3; *scale bar* 2 mm. **c, d** Bryozoans (*BZ*), nummulitids (*NM*) and coralline algal protuberances (*A*), Sample No. CN 21; *scale bars* 2 mm. **e** Coral blocks (*C*), *Amphiroa* sp. (*AM*) and abraded-micritized foraminifera, Sample No. CN 13; *scale bar* 1 mm. **f** Layered coralline algae (*A*), Sample No. CN 25; *scale bar* 1 mm. **g** Encrusting coralline algae (*A*) and nummulitids (*NM*), Sample No. CN 26; *scale bar* 2 mm. **h** Lumpy coralline algae (*A*) with abraded and fragmented benthic foraminifera, Sample No. CN 14; *scale bar* 1 mm

SBF assemblages indicate fluctuations in salinity levels, related to the changing connections of the inner shelf/lagoonal zone to the open ocean followed by mild influences of variations in run-offs coming from the emergent land. Greater work is required to bring out refined theories as to whether the salinity fluctuations have a real influence on the grain associations in the tropical domains. According to Lees (1975), temperature and salinity may not necessarily be the highest limiting factors in determining the grain associations, and that perhaps some linked factor plays the most important role. In the case of rain-induced reduction in salinity levels, terrigenous and nutrient inputs associated with high freshwater influx may have a deciding impact on the development of oligophotic facies (Wilson and Vecsei 2005).

The LBF abundance in the Guitar Formation sediments indicates a meso-oligotrophic nutrient regime prevailing in the Car Nicobar environment. High nutrient levels are known to hamper the development of carbonate-producing organisms (Hopley 1984). Commonly, the LBF thrive in oligotrophic (Langer and Hottinger 2000) to slightly mesotrophic (Halfar

et al. 2004) waters. Even the coralline algae are expected to be susceptible to high nutrient conditions, simultaneously affecting the levels of light availability. SE Asian waters observe high fluctuations in water clarity linked to daily or seasonal changes mostly owing to the effect of plankton blooms (Tomascik et al. 1997). Local barnacle abundance is indicative of high primary productivity, plentiful organic matter in the seascape and eutrophic nutrient levels (Sanford and Menge 2001; Leslie et al. 2005). The frequent occurrence of fine-grained sediments in the carbonates is assumed to have played a role in reducing water transparency. The presence of barnacles, with minor proportions of organisms like bryozoans and serpulids, indicates confined instances of high nutrient levels but still predominantly nutrient-deficient conditions.

Comparison of the Guitar Formation with other carbonate systems worldwide

Tropical heterozoan assemblages have been recorded from numerous modern as well as ancient carbonate systems across the globe, like the NW African shelf of Northern Mauritania (Westphal et al. 2010; Michel et al. 2011; Klicpera et al. 2015), the Yucatan shelf off Mexico (Logan et al. 1969; Westphal et al. 2010), the Nicaragua Rise (Hine et al. 1987; Hallock et al. 1988), the West Florida Shelf (Westphal et al. 2010), the Gulf of California, Mexico (Halfar et al. 2006; Hetzinger et al. 2006), the Mediterranean region (Brandano and Corda 2002; Samankassou 2002; Bouillon et al. 2004; Pomar et al. 2004; Brandano et al. 2009) and SE Asia (Wilson 2002, 2008; Wilson and Vecsei 2005). The Guitar Formation carbonates

Fig. 6 Relative abundance of coralline algal growth-forms recorded in the samples (CN 1–CN 27)

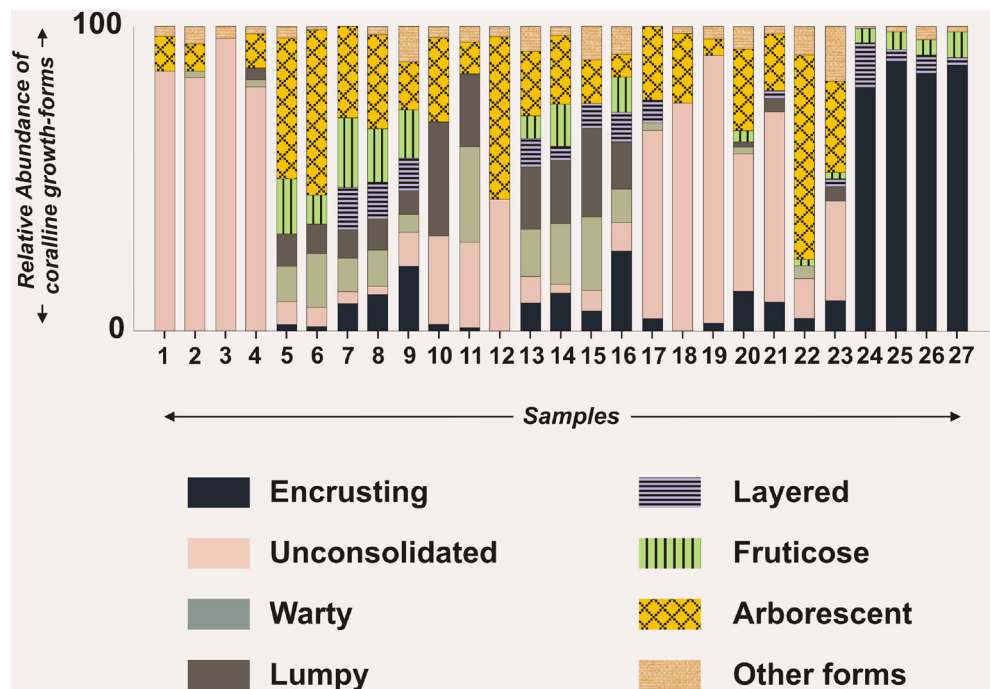
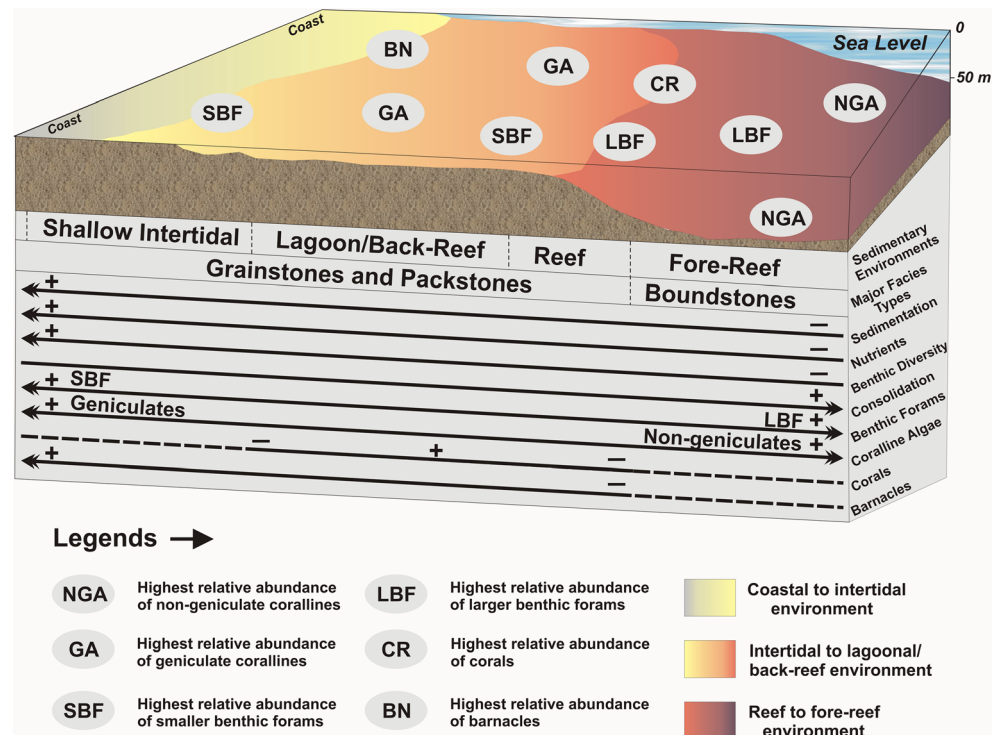


Fig. 7 Schematic palaeoenvironmental model of the Guitar Formation featuring fossil assemblage gradients and trends of selected ecological factors. (+) denotes increase in the respective gradient and (–) denotes a decrease. Highest relative abundance of the major skeletal components and various sub-environments are also presented with symbols and colour pattern signatures



are comparable to the shallow marine sediments of Golfe d'Arguin, Mauritania, in having a complete absence of green algae that are typical components of oligotrophic tropical settings (Westphal et al. 2010; Klicpera et al. 2015). However, the Mauritania sediments are characterised by the complete absence of zooxanthellate corals and sparse distribution of foraminifera, whereas the Guitar Formation shows local abundance and scattered presence of corals. Abundance of foraminifera in the Guitar Formation is also a major dissimilarity. Filter-feeding organisms like barnacles and bryozoans demonstrate a much wider distribution in the Mauritania settings owing to high productivity/nutrient levels caused by oceanic upwelling and additional fertilization by high desert input (Westphal et al. 2010). Green algae are also not found in the Gulf of California sediments, even though sparse living plants have been observed in the southern part of the gulf (Halfar et al. 2006). The Yucatan Shelf in the Gulf of Mexico is marked by photozoan carbonates with very well-developed coral reefs, in the direct vicinity of heterozoan tropical carbonates (Logan et al. 1969; Westphal et al. 2010). *Halimeda* plates are also a major skeletal component of the Yucatan sediments (Logan et al. 1969). Carbonate sediments on the western Nicaragua Rise are produced by calcareous green alga *Halimeda* (Hine et al. 1987), constituting a chloralgal system (corals absent). The eastern Nicaragua Rise along the Jamaican coast is however rich in coral reefs (Westphal et al. 2010). The West Florida Shelf is a case of an impoverished photozoan

carbonate system persisting under high trophic resources due to the high fluvial input of fine-grained terrigenous material (Doyle 1986), but tropical water temperatures (Gorsline 1963). The algal-foraminiferal assemblages of the Guitar Formation share several similarities with the heterozoan-dominated Attard Member of the Lower Coralline Limestone Formation (upper Oligocene, Malta; Brandano et al. 2009). Triloculine and quinqueloculine SBF (*Triloculina*, *Quinqueloculina*, *Austrotrillina* and *Pyrgo*), larger foraminifera (*Amphistegina*, *Heterostegina*, *Operculina* and *Nephrolepidina*) and coralline algae (*Lithothamnion*, *Spongites* and *Lithoporella*) are present in different proportions in both the Car Nicobar and the Mediterranean sediments.

A number of Cenozoic SE Asian platform systems formed partially or mostly during the Tertiary period are dominated by perforate LBF and also coralline algae (Wilson 2002; Wilson and Vecsei 2005). These include the Berai Limestone of SE Kalimantan (Saller and Vijaya 2002), and the Tonasa and Makale Platforms of South Sulawesi in Indonesia (Wilson et al. 2000), the Melinau Limestone of north Borneo (Adams 1965), the Wonosari Platform of south Java (Lokier 2000) and the Lihuhua Platform of the South China Sea (Erlich et al. 1993; Moldovanyi et al. 1995). The platform development in most of these cases began during the Palaeogene when corals were limited to remote proportions in many carbonate deposits of SE Asia (Wilson and Rosen 1998), but continued

with sediment accumulation during the Neogene. Despite the vigorous increase of corals during the Neogene, these platform deposits continue to be dominated by perforate LBF. Overall, corals are present as minor facies components, whereas they show local abundance in the platform margins or observed as patch reefs in the Berai Limestone (Wilson and Vecsei 2005). The Car Nicobar sediments are comparable to these platform deposits in terms of rich perforate LBF and coralline algal assemblages, with corals existing as one of the subordinate facies components.

The algal protuberances and occasional rhodoliths of the Guitar Formation show close affinity to the growth-forms described from the circalittoral detritic bottoms of the modern Mediterranean biocoenosis (Bressan and Nichetto 1994; Basso 1998). The circalittoral detritic bottoms are represented by different structures of coated grains and rhodoliths, which in the case of stable environmental conditions can be buried under high sedimentation rates building up the muddy detritic bottoms (Basso 1998). In an alternate scenario, these coralline algal deposits can originate a highly porous framework under low sedimentation rates (Betzler et al. 1997; Basso 1998). Substrate stability is a function of substrate composition, water turbulence and bioturbation activities. This parameter is, in fact, a critical factor involved in the development of coralline growth-forms. Coralline algae show particular preferences with respect to substrate quality and observed growth-forms (Nebelsick and Bassi 2000; Rasser and Piller 2004; Checconi et al. 2007). Due to the moderate abundance of coralline algal protuberances, the dominance of the fine matrix sediment, and the lack of evidence for submarine hard bottoms, substrate activity in all likelihood was dependent on low current activity/wave agitation. The presence of algal boundstones mainly composed of encrusting coralline algae also indicates deeper bathymetric levels, very close to or below the FWFB. Co-existence of encrusting corallines with LBF implies depths of not more than 50–60 m for the depositional environment of the Guitar Formation. The diversity of the algal assemblages may reflect a climatic expression of the coralline algal benthic community in the Car Nicobar Island lying in the Andaman Sea during late Pliocene. In particular, dominance of lithophylloids, associated with low-diversity mastophoroids and melobesioids, suggest close similarities with the present-day examples of several Mediterranean localities. Lithophylloids are the most frequent coralline algae in the infralittoral zone assemblages of the Mediterranean (Bressan and Babbini 2003; Checconi et al. 2007). A similar trend is documented in the upper Neogene temperate shallow-water coralline algal assemblages in southern Spain, where subfamily Lithophylloideae dominates the algal community (Braga and Aguirre 2001). There is a possibility of a palaeobiogeographic belt connecting the Mediterranean region with the Indo-Pacific during Pliocene times. However, further studies including a greater number of sections

from the Andaman-Nicobar region and other Indo-Pacific platforms are essential to provide conclusive evidence in this regard.

Conclusions

Although the fossil heterozoan assemblages are often related to non-tropical environments, it is well acknowledged that tropical heterozoans do exist and play a critical role in the development of platforms over a wide range of settings. The upper Pliocene Guitar Formation sediments extend widely in the limestone quarry in the SE part of Car Nicobar Island, India. In the evaluated carbonate succession, the heterozoan assemblage consists predominantly of coralline red algae and LBF. Coralline algal flora is dominated by lithophylloids whereas the LBF are mainly represented by nummulitids. Corals and barnacles show local abundance whereas the subordinate components are smaller benthic foraminifera (miliolids, rotaliids and textulariids), bryozoans, echinoderms, molluscs and gastropods. The Guitar Formation represents a reefal setting in the oligophotic zone close to or just below the FWFB. Based on biodiversity, inferred palaeoecological parameters and the taphonomic signatures, the Guitar Formation is interpreted to have developed in tropical waters, under meso-oligotrophic conditions in the study area. This is supported by the dominance of coralline algae and LBF, with local abundance of barnacles indicating a slight shift towards eutrophy but overall low nutrient levels. Affinities between coralline algal assemblages of the Guitar Formation and European lithounits suggest that a possible palaeobiogeographic belt existed from the Mediterranean to the Indo-Pacific region during the Pliocene. Further studies including a greater number of sections from the Andaman-Nicobar Islands and other localities belonging to the Indian subcontinent featuring more Pliocene outcrops might provide further detailed information in assessing the evolution of Pliocene shallow-water carbonate benthic communities.

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