Lethaia
AN INTERNATIONAL JOURNAL OF PALAEONTOLOGY AND STRATIGRAPHY

The Quilon Limestone, Kerala Basin, India: an archive for Miocene Indo-Pacific seagrass beds

MARKUS REUTER, WERNER E. PILLER, MATHIAS HARZHAUSER, ANDREAS KROH, FRED RÖGL AND STJEPAN ĆORIĆ

LETHAIA

Reuter, M., Piller, W.E., Harzhauser, M., Kroh, A., Rögl, F. and Ćorić, S. 2010. The Quilon Limestone, Kerala Basin, India: an archive for Miocene Indo-Pacific seagrass beds. *Lethaia*, DOI: 10.1111/j.1502-3931.2010.00226.x.

The facies of the fossiliferous Quilon Limestone in SW India is described for the first time in detail at the Padappakkara-type locality. Facies (fossiliferous, micrite-rich, bioturbated sediment with intercalated sand pockets) and faunal composition (epiphytic foraminifers, seagrass feeding *Smaragdia* gastropods, bioimmuration of celleporiform bryozoan colonies) indicate a seagrass environment. The large discoidal archaiasin foraminifer *Pseudotaberina malabarica*, in particular, is considered as a proxy for seagrass communities. Recent seagrasses have their centre of generic richness in the Indo-Pacific where they cover wide areas in the tidal and shallow sub-tidal zones. However, their geological record is only fragmentary and their palaeobiogeographic distribution has a big stratigraphical gap in the Miocene Western Indo-Pacific region. The described nannoplankton flora and planktonic foraminifers from the Quilon Formation demonstrate that the deposition of the studied seagrass bed occurred in nannoplankton biozone NN3. This timing suggests formation during the closure of the Tethyan Seaway. The Quilon Limestone is thus an early Western Indo-Pacific seagrass bed and an important step in reconstructing the history of seagrass communities. ☐ *Quilon Formation, Pseudotaberina malabarica, seagrass facies, Burdigalian, Indo-Pacific.*

Markus Reuter [markus.reuter@uni-graz.at] and Werner E. Piller [werner.piller@uni-graz.at], Institute for Earth Sciences, Graz University, Heinrichstrasse 26, 8010 Graz, Austria; Mathias Harzhauser [mathias.harzhauser@nhm-wien.ac.at], Andreas Kroh [andreas.kroh@nhm-wien.ac.at] and Fred Rögl [fred.roegl@nhm-wien.ac.at], Natural History Museum Vienna, Burgring 7, 1010 Vienna, Austria; Stjepan Ćorić [stjepan.coric@geologie.ac.at], Geological Survey of Austria, Neulinggasse 38, 1030 Vienna, Austria; *manuscript received on 13/01/2010; manuscript accepted on 20/04/2010.*

Seagrasses are the only angiosperms that managed marine life (Hemminga & Duarte 2000). At present-day, they reach their greatest diversity in the Indo-Pacific ocean, where they cover extensive areas in the intertidal and shallow sub-tidal zones (Hoeksema 2007). Together with mangroves and coral reefs, such seagrass meadows are part of the coastal marine ecosystem and carry out important ecosystem services such as sediment stabilization, filtering of coastal run-off, cycling of nutrients and global gases. Since they provide food sources and highly structured refuges for a number of algae, invertebrates and vertebrates, seagrass habitats are the sites of high benthic biodiversity of coastal areas (Dorenbusch *et al.* 2006; Orth *et al.* 2006; Unsworth *et al.* 2008).

Seagrasses originated during the Late Cretaceous in the Tethys Seaway (Ivany *et al.* 1990) and present-day seagrass ecosystems include the coastal areas of all continents except Antarctica (Den Hartog 1970; Brasier 1975a; Eva 1980). Because the calcareous skeletons of many seagrass dwellers contribute significantly to the sediment, seagrass meadows became substantial places of carbonate production in the Cenozoic. Even though the preservation of fossil seagrass bodies is exceptional, these skeletal associations are used for the identification of seagrass beds in the geological past (e.g. Brasier 1975a; Eva 1980; Ivany *et al.* 1990; Beavington-Penney *et al.* 2004; Moisette *et al.* 2007). However, considering these skeletal associations as indicators of fossil seagrass beds is problematic because most organisms that benefit from the seagrass occur also in a wide range of other shallow marine environments (e.g. Haunold *et al.* 1997).

Herein, we describe a Burdigalian benthic assemblage representing a seagrass habitat from the Quilon Limestone (Kerala Basin, SW India). The fossiliferous limestone facies is unique for the entire SW Indian coast and its rich fauna (foraminifers, gastropods, bivalves, corals, echinoids, crabs, ostracods, bryozoans, serpulids and shark teeth) was used for palaeobiogeographic reconstructions and stratigraphic correlations (Eames 1950; Jacob & Sastri 1951; Dey 1961; Verma 1977; Sahni & Mitra 1980; Mehrotra 1982; Khosla & Nagori 1989; Padmalal & Seralathan 1991; Harzhauser *et al.* 2007, 2009). However, due to deep reaching tropical weathering, the Quilon Limestone is only

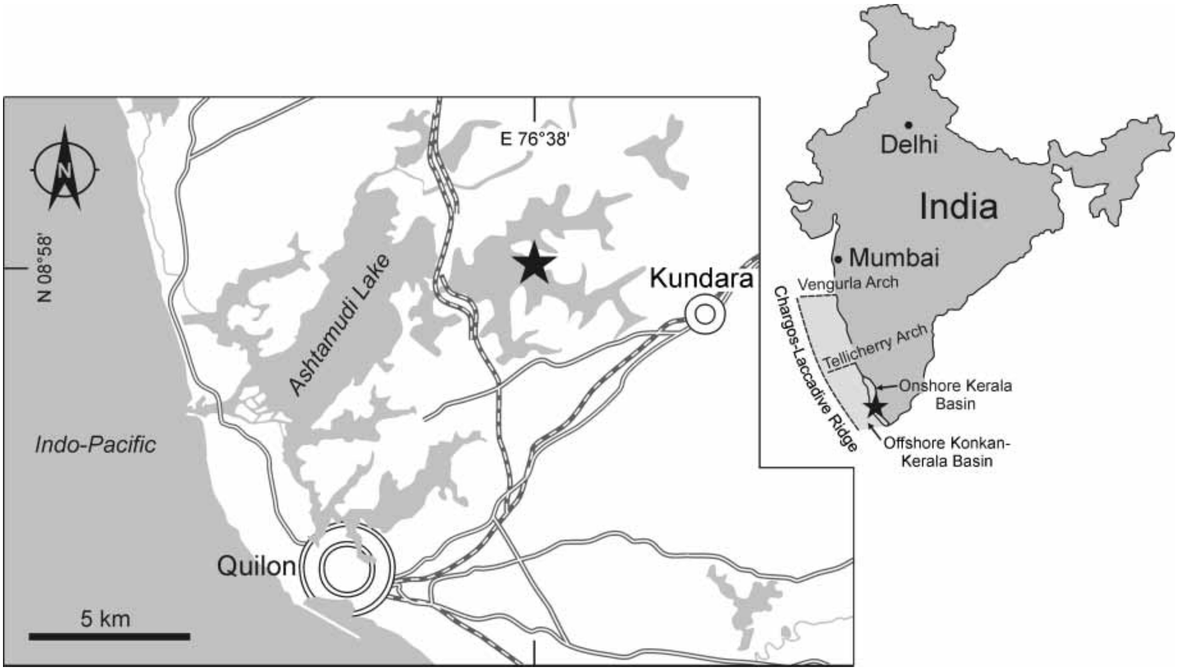

Fig. 1. Location of Channa Kodi locality (asterisk) in the Kerala–Konkan Basin.

locally exposed in small outcrops at the base of sea cliffs or currently available from material dug out of wells and building excavations (Dey 1961; Menon 1967a; Narayanan *et al.* 2007). Accordingly, stratigraphical and architectural relationships are unclear and the existing depositional model is cursory. It assumes that deposition took place on an open marine shelf with local coral reef occurrences in settings shallower than 20 m proximal to the coast (Menon 1967a; Raha & Sinha-Roy 1982; Narayanan *et al.* 2007). This study focuses on the stratigraphical and environmental interpretation of the limestone facies at the Padappakkara-type locality to improve the depositional model. Calcareous nannoplankton and planktonic foraminifers, reported for the first time from the Quilon Formation, confirm its Burdigalian age.

Geography and geological setting

The studied locality is in the southern part of the onshore Kerala Basin at the base of sea cliffs extending into Ashtamudi Lake (N 08°58′36″, E 076°38′08″; Fig. 1). This place is part of Padappakkara village, 5.4 km west–northwest of Kundara, and locally known as 'Channa Kodi'. It corresponds to the outcrop studied by Dey (1961) and Menon (1967a, b) and is the type locality of the Quilon Limestone.

Kerala Basin is the southern sub-basin of the pericratonic Konkan–Kerala Basin on the Western Indian passive continental margin (Fig. 1). The basin extends ~600 km from north to south and covers an area of about 580 000 km^2. It is separated from the northerly Konkan Basin by the Tellicherry Arch basement high and bordered by steep escarpments against the up to 2.695 m high Western Ghats in the east. To the west, the basin continues into deep-waters to the Chargos–Laccadive Ridge (Fig. 1; Shankar *et al.* 2004; Campanile *et al.* 2008).

The Cenozoic sedimentary succession in the onshore part of the Kerala Basin is dominated by siliciclastic sediments with interbedded lignite seams. Elevation and denudation of the Western Ghats at the rift shoulder was the source for siliciclastics (Campanile *et al.* 2008). Ostracod faunas and palynofloras from these deposits document deposition in marginal marine brackish lagoons as well as brackish and freshwater swamps (Rao & Ramanujam 1975; Rao 1995). Exceptional is the Lower–Middle Miocene mixed siliciclastic–carbonatic Quilon Formation, which extends between Edava in the south and Alappuzha in the north (Narayanan *et al.* 2007). The Quilon Formation is part of the Warkalli Group and interbedded between siliciclastics of the underlying Mayyanad Formation (Lower Miocene) and the overlying Ambalapuzha Formation (Miocene–Pliocene; Vaidyanadhan & Ramakrishnan 2008). It comprises at least two horizons of fossiliferous limestone with marine fauna (Menon 1967a). The lower limestone horizon is characterised by colonial corals, whereas the upper limestone horizon represents a *Pseudotaberina malabarica*

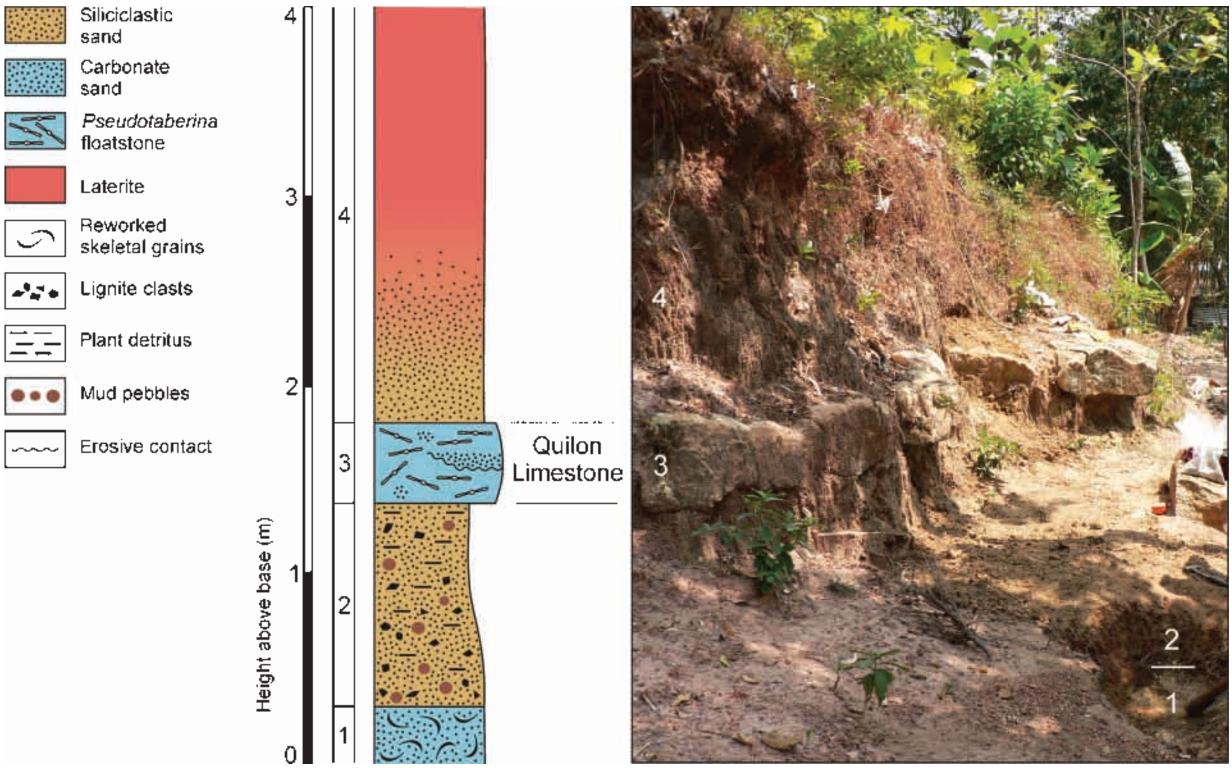

Fig. 2. Lithological log and field aspect of the Quilon Limestone at the Channa Kodi type locality.

facies, which is well-developed at the coastal cliffs of Ashtamudi Lake at Padappakkara (Fig. 1).

Channa Kodi section

The total thickness of Channa Kodi section (Fig. 2) is 12 m. At its base occurs an at least 0.3-m thick deposit of yellow, coarse-grained, poorly sorted carbonate sand with subordinate-rounded quartz grains and detritic glaucony (bed 1). The sediment is slightly lithified and skeletal components are typically broken and abraded. It contains a very diverse benthic foraminiferal fauna (Table 1). Miliolids (such as *Pseudotaberina malabarica*, *Peneroplis planatus* and *Austrorillina howchini*) are most abundant but strongly corroded. *Lepidosemicyclina thecideaeformis* and *Operculina* are also frequent and in a poor state of preservation. In contrast, planktonic foraminifers are rare but well-preserved. Aragonitic-preserved molluscs are also abundant. Among larger gastropod taxa, the strombid *Persististrombus daviesi* (Fig. 3A4) dominates along with *Xenophora*. Bed 1 contains high numbers of the colloniid *Bothropoma* (Fig. 3A1), the solariellid *Pagodatrochus* (Fig. 3A2), the trochid *Clanculus*, the neritid *Smaragdia* (Fig. 3A3) and the chilodontid *Perrinia* (Fig. 3A5). A diverse scaliolid and dialid assemblage with *Scaliola*, *Finella* and *Clathrofenella* is also present. Corbulids and *Glycymeris quilonensis* are the most abundant bivalves. Echinoids (Cidaroida indet., Clyperasteroida indet., Spatangoida indet.), serpulids, ostracods, bryozoans, ascidian spicules (Fig. 4O) and coralline red algae also occur, as well as well-preserved calcareous nannoplankton (Fig. 4). Besides the high abundance of *Umbilicosphaera jafarii* (Fig. 4F1, H1, I1, J, K), the nannoplankton assemblage contains common *Coronocyclus nitescens* (Fig. 4C, D, H2, I2), *Cyclicargolithus floridanus* (Fig. 4F2), *Discoaster deflandrei* (Fig. 4G) and *Reticulofenestra minuta* (Fig. 4E). *Braarudosphaera bigelowii*, *Calcidiscus leptoporus*, *Coccolithus pelagicus*, *Helicosphaera carteri*, *Reticulofenestra gelida*, *Sphenolithus belemnos* (Fig. 4L–N), *Sphenolithus moriformis* and *Tetralithoides symeonidesii* are very rare.

Bed 2 is 1.1 m thick and consists of grey to rust-coloured, poorly sorted quartz sand with clay pebbles, plant debris and lignite fragments. It shows a slight fining upward trend, from coarse- to medium-grained sand.

This sand is overlain by a 0.4-m thick, massive fossiliferous limestone (bed 3), which has a bluish-grey (fresh) to rusty (weathered) colour. In the literature, this bed is referred to as Quilon Limestone (Dey 1961; Menon 1967a, b). The well-lithified limestone bed is a poorly sorted, bioclastic *Pseudotaberina* floatstone (Fig. 5A). The matrix is a packsone (Fig. 5B, C) and

Table 1. Foraminiferal assemblage in the calcareous sand of bed 1 in Channa Kodi section.

Planktonic foraminifers

Globigerina eamesi Blow, *Globigerina leroyi* Blow & Banner, *Globigerina* cf. *officinalis* Subbotina, *Globigerina* cf. *ouachitaensis* Howe & Wallace, *Globigerina praebulloides* Blow, *Globigerina senilis* Bandy, *Globigerinella regularis* d'Orbigny, *Globigerinoides primordius* (Blow & Banner), *Globigerinoides parawoodi* Keller, *Globigerinoides subquadratus* Brönnimann, *Globigerinoides trilobus* (Reuss), *Globigerinoides* cf. *subsacculifer* Cita, Premoli Silva & Rossi, *Globigerinoides altiaperturus* Bolli, *Paragloborotalia acrostoma* (Wezel)

Larger benthic foraminifers

Pseudotaberina malabarica (Carter), *Austrotrillina howchini* (Schlumberger), *Borelis schlumbergeri* (Reichel), *Sphaerogypsina globulus* (Reuss), *Operculina complanata* (Defrance) – group, *Operculina discoidalis* (d'Orbigny) – group, *Amphistegina vulgaris* d'Orbigny, *Lepidosemicyclina thecideaeformis* (Rutten), *Nephrolepidina chavarana* Jacob & Sastri, *Nephrolepidina* sp., *Miogypsina* cf. *globulina* (Michelotti), *Miogypsina* cf. *nipponica* Matsumaru

Smaller benthic foraminifers

1. Agglutinated

Clavulina angularis d'Orbigny, *Clavulina nodosaria* d'Orbigny, *Pseudogaudryina mayeriana* (d'Orbigny), *Textularia* cf. *aegyptica* Said, *Textularia pseudogramen* Chapman & Parr, *Textularia mariae* d'Orbigny

2. Miliolid

Articulina alticostata Cushman, *Cycloforina* cf. *dorsicostata* (Venglinski), *Cycloforina contorta* (d'Orbigny), *Cycloforina reticulata* (Karrer), *Lachlanella* spp., *Lachlanella undosa* (Karrer), *Peneroplis planatus* (Fichtel & Moll), *Pseudomassilina* sp., *Pseudotriloculina consobrina* (d'Orbigny), *Pseudotriloculina inflata* (d'Orbigny), *Pseudotriloculina* cf. *microdon* (Reuss), *Pseudotriloculina* cf. *philippinensis* (Cushman), *Pseudotriloculina reversa* (d'Orbigny), *Pyrgo clypeata* (d'Orbigny), *Pyrgo lunula* (d'Orbigny), *Quinqueloculina* cf. *buchiana* d'Orbigny, *Quinqueloculina cuvieriana* d'Orbigny, *Quinqueloculina* cf. *transylvaniae* Karrer, *Quinqueloculina vulgaris* d'Orbigny, *Sigmoilopsis minuta* (Collins), *Siphonaperta agglutinans* (d'Orbigny), *Siphonaperta mediterranensis* (Bogdanowich), *Spiroloculina* cf. *attenuata* Cushman & Todd, *Triloculina affinis* d'Orbigny, *Triloculina terquemiana* (Brady), *Varidentella* cf. *pseudocostata* (Venglinsky)

3. hyaline

Acervulina mabahethi (Said), *Allassoida virgula* (Brady), *Alliatinella* sp., *Ammonia* cf. *inflata* (Seguenza), *Angulogerina* cf. *angulosa* (Williamson), *Anomalinella rostrata* (Brady), *Anomalinoides globulosus* (Chapman & Parr), *Asterigerina carinata* d'Orbigny, *Asterigerinata mamilla* (Williamson), *Bolivina* spp., *Buccella granulata* (Di Napoli), *Buchnerina milletti* (Magerel), *Cibicides mahabeti* Said, *Cibicidoides* spp., *Conorbella pulvinata* (Brady), *Discorbia globospiralis* Sellier de Civrieux, *Elphidiella dollfusi* (Cushman), *Elphidiella heteropora* (Egger), *Elphidiella minuta* (Reuss), *Elphidiella* cf. *subnodosa* (Roemer), *Elphidium angulatum* (Egger), *Elphidium* cf. *articulatum* (d'Orbigny), *Elphidium craticulatum* (Fichtel & Moll), *Elphidium striatopunctatum* (Fichtel & Moll), *Eoeponidella* sp., *Fissurina globosa* Bornemann, *Glabratella* sp., *Glandulina* sp., *Hanazawaia* cf. *boueana* (d'Orbigny), *Hanzawaia elegans* (Parker, Jones & Brady), *Hanzawaia nipponica* Asano, *Lobatula lobatula* (Walker & Jacob), *Neoconorbina terquemi* (Rzehak), *Nonion commune* (d'Orbigny), *Nonion* cf. *depressulum* (Walker & Jacob), *Nonion* cf. *elongatum* (d'Orbigny), *Nonion* cf. *germanicum* (Ehrenberg), *Nonionoides grateloupi* (d'Orbigny), *Pararotalia armata* (d'Orbigny), *Planorbulina mediterranensis* (d'Orbigny), *Planorbulinella* sp., *Porosononion* sp., *Pseudobrizalina* cf. *simpsoni* (Herron-Allen & Earland), *Pygmaeoseistron tubospina* (Matthes), *Reussella aculeata* Cushman, *Rotorbinella umbonata* Sellier de Civrieux, *Rotorbis auberi* (d'Orbigny), *Sagrinella* sp., *Trochulina dimidiata* (Parker & Jones), *Virgulopsis* sp.

contains peloids, scattered quartz and glauconite grains. The bioclasts are dominated by foraminifers (>90% of total skeletal grains; Fig. 5B, C, E). Aside from large *Pseudotaberina malabarica* (Ø 1.5 cm; Fig. 3B) and *Austrotrillina howchini*, smaller porcellaneous miliolids with triloculine and quinqueloculine chamber arrangements are mass-occurring (>80% of total foraminifers; Fig. 5). They are associated with small rotaliid foraminifers (Fig. 5B) and *Operculina*. The mollusc fauna is poorly preserved within the limestones.

Minute gastropods such as the small limpet *Calyptraea dunni* and tiny infaunal lucinid bivalves (often articulated) occur in masses; large moulds of *Persististrombus daviesi* are frequent. Serpulids (Fig. 5C), bryozoans and echinoderm fragments (asteroid plates and cidaroid spines) also contribute to the Quilon Limestone fauna. Bryozoans are represented by erect delicate branching (Fig. 5B) and erect bilaminar branching adeonoid (cf. *Adeonellopsis*) colonies as well as encrusting celleporiform taxa. Some celleporiform colonies have a central tube-like mould (Fig. 3C). The sediment is intensely bioturbated (Fig. 5D). Some *Thallassinoides* burrows are filled up with foraminiferal–mollusc rudstone. Sand pockets (mollusc–foraminiferal grainstone) with sharp erosional base are interbedded in the *Pseudotaberina* floatstone (Fig. 5D, E). The carbonate sand is dominated by miliolids and molluscs (Fig. 5D). Miogypsinids, echinoderm and bryozoan fragments are also present (Fig. 5E).

The top of the section is represented by a pedogenically altered sand unit (>1 m thick, bed 4) grading into 10-m thick laterite.

Depositional environment

The composition of the highly diverse benthic foraminiferal fauna in the carbonate sand at the base of Channa Kodi section (Table 1) is typical for a shallow coastal/inner-shelf system (Murray 2006). Seagrass vegetation is argued by the high abundance of miliolids including epiphytic taxa such as *Pseuudotaberina malabarica*, *Peneroplis planatus* and *Austrotrillina* (Brasier 1975b; Eva 1980; Bassi *et al.* 2007; James & Bone 2007; Renema 2008). Among gastropods, the high abundance of *Bothropoma*, *Pagodatrochus*,

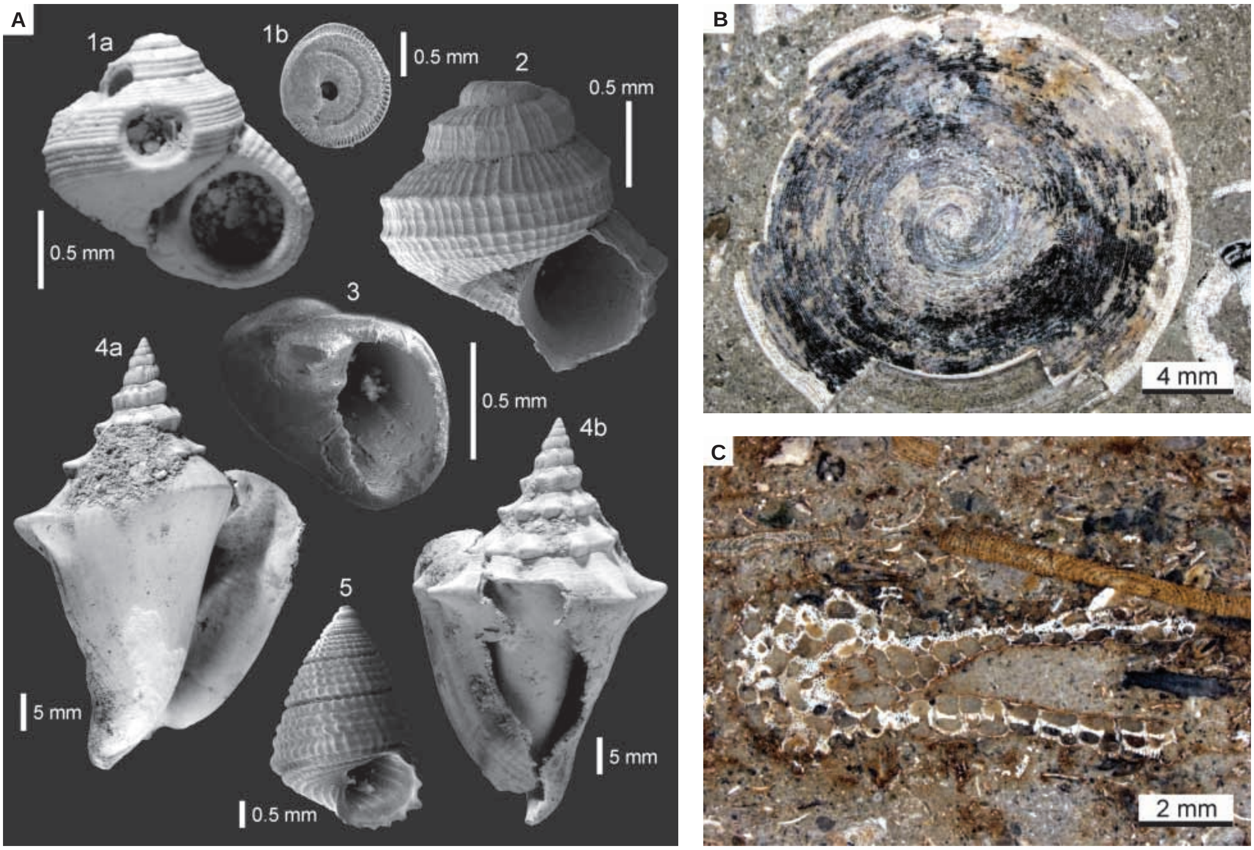

Fig. 3. Biotic evidence for seagrass. A, seagrass dwelling gastropods: 1a = *Bothropoma* sp., 1b = operculum of *Bothropoma* sp., 2 = *Pagodatrochus* sp., 3 = *Smaragdia* sp., 4a, b = *Persististrombus daviesi* Dey, 5 = *Perrinia* sp. B, *Pseudotaberina malabaric* (Carter). These large discoidal archaiasin foraminifers lived attached to seagrass blades and are the dominant faunal element in the Quilon Limestone. C, celleporiform bryozoan colony. The inner tube-like cavity indicates encrustation of an organic stem.

Smaragdia and *Perrinia* (Fig. 3A1–A3, A5) and their association with strombids (Fig. 3A4) indicate seagrass vegetation (Stoner & Waite 1991; Rueda *et al.* 2008; Zuschin *et al.* 2009). The corrosion of miliolid foraminiferal tests is interpreted by Leonard-Pingel (2005) as a result of root-etching and exposure to carbonic acids that may have been produced through decomposition of organic matter in a seagrass meadow. However, the low mud content as well as the strong abrasion and fragmentation of most skeletal components in bed 1 indicate reworking and deposition in a high-energy environment outside a seagrass meadow such as beach, tidal channel or intertidal sand flat (Parsons & Brett 1991; Beavington-Penney *et al.* 2004; Short 2005; James & Bone 2007). Therefore, such fossil epiphytic faunal assemblages often reflect concentrations of skeletons with similar hydrodynamic properties rather than biocoenosis (Davaud & Septfontaine 1995).

Heavier and denser bioclastic particles are transported as bed load over short distances or reworked in place whereas lighter and more porous particles are transported as suspension load far away from their biotope. As a consequence of this differential hydrodynamic behaviour, allochthonous microfossils often remain well-preserved (e.g. calcareous nannoplankton, planktonic foraminifers) whereas autochthonous ones may be deeply abraded (e.g. miliolids, larger foraminifera; Davaud & Septfontaine 1995). A high-energy nearshore environment is also inferred from mud pebbles and lignite clasts in the overlying quartz sand (bed 2) reflecting coastal erosion (Menon 1967a; Knight 2005).

Also, for the *Pseudotaberina malabarica* floatstone facies in bed 3 (Fig. 5), seagrass vegetation is indicated by the mass occurrence of *Pseudotaberina malabarica* (Fig. 3B), *Austrotrillina howchini* (Fig. 5B–D) and other miliolids (>90% of total skeletal grains). Additional evidence for seagrass is tube-like bioimmuration of celleporiform bryozoan colonies (Fig. 3C; Cigliano *et al.* 2006). The high micrite content of this facies (Fig. 5A–C) points to seagrass sedimentation in place because the dense canopy of a seagrass meadow baffles fine mud and detritus and the extensive rhizome system fixes the fine fraction (Brasier 1975a,b;

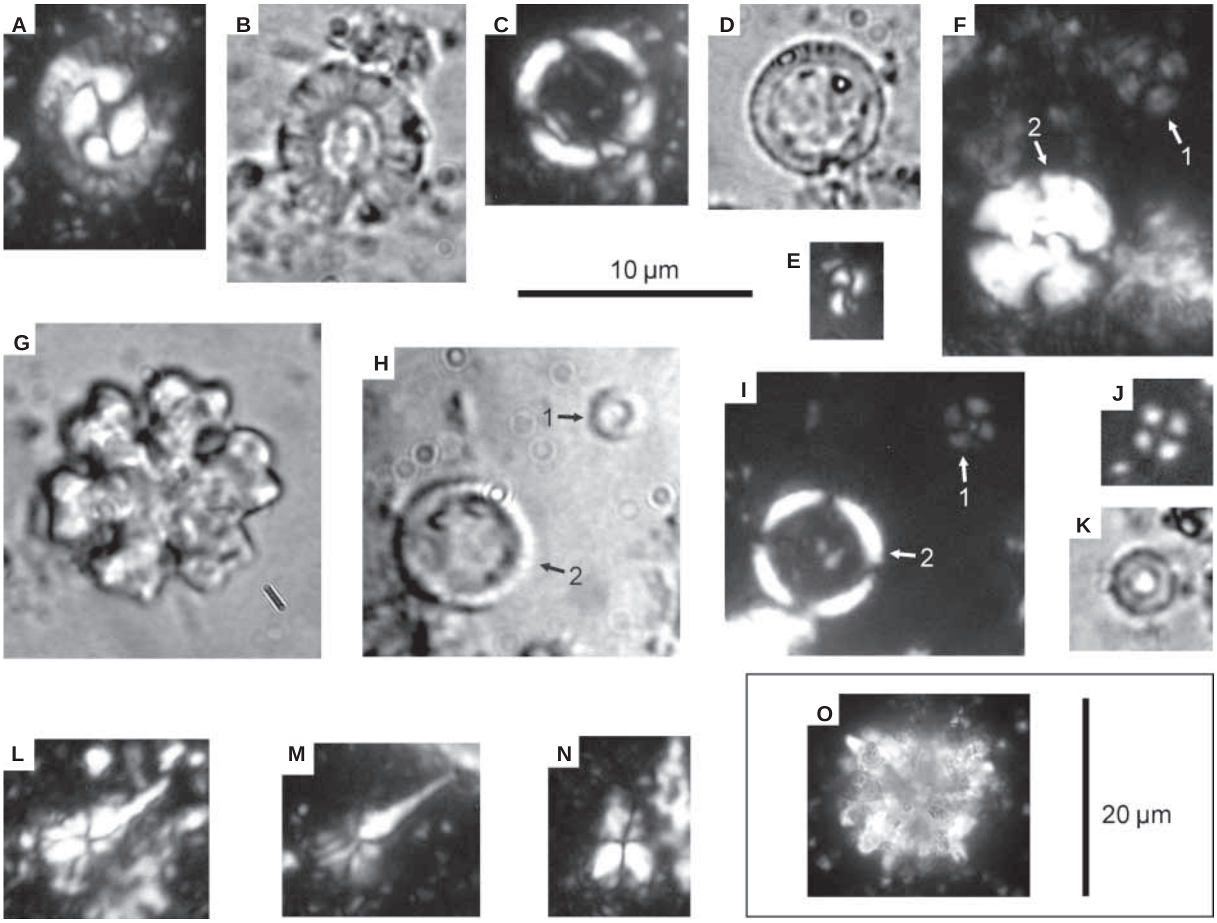

Fig. 4. Nannoplankton. A, B, *Coccolithus pelagicus* (Wallich) Schiller. C, D, H2, I2. *Coronocyclus nitescens* (Kamptner) Bramlette & Wilcoxon. E, *Reticulofenestra minuta* Roth. F1, H1, I1, J, K, *Umbilicosphaera jafarii* Mueller. F2, *Cyclicargolithus floridanus* (Roth & Hay) Bukry. G, *Discoaster deflandrei* Bramlette & Riedel. L–N, *Sphenolithus belemnos* Bramlette & Wilcoxon. O, ascidian spicule.

Petta & Gerhard 1977; Jones *et al.* 1994). Sand pockets (Fig. 5D) probably originate from storm blowouts, which caused erosion (Fig. 5E), winnowing and infilling of open, deep-excavated burrows (Wanless 1981; Wanless *et al.* 1995). A further attribute of seagrass meadows is a high organic content of the sediment. It favours the proliferation of small infaunal suspension- and deposit-feeding molluscs (Brasier 1975a; Beavington-Penney *et al.* 2004) and is displayed in the Quilon Limestone by the high abundance of small articulated lucinoids and minute gastropods.

Stratigraphy

Biostratigraphy

Pseudotaberina malabarica (Fig. 3B) is regarded as Middle Miocene marker and has been recorded from the Letter Stages Tf1 and Tf2 (Burdigalian–Serravalian; Jauri & Khare 1990; Renema 2007, 2008); Hottinger (2005) even refers to an Upper Miocene occurrence. Consistently, the mollusc fauna of Channa Kodi section shows striking affinities with the Burdigalian faunas of Kutch in NW India (Eames 1950; Sahni & Sastry 1958; Dey 1961; Verma 1977; Harzhauser *et al.* 2009).

The newly reported planktonic foraminiferal assemblage consists of *Globigerinoides altiaperturus*, *Gs. immaturus* and *Gs. primordius*, which are characteristics of the Burdigalian planktonic foraminifera zone N5/M2 (Fig. 6; Berggren *et al.* 1995). Based on the occurrence of *Sphenolithus belemnos* (Fig. 4L–N), nannoplankton zone NN3 is indicated for the Quilon Formation at Padappakkara (Fig. 6; Martini 1971).

Sequence stratigraphy

Miocene carbonates are reported from all basins of the southwestern continental margin of India (i.e. Bombay Basin, Konkan Basin, Kerala Basin) and their formation has been linked to higher sea level and a drier and warmer climate in the Middle Miocene (Campanile *et al.* 2008). The succession from tidal sand flat/beach deposits to seagrass sediments in

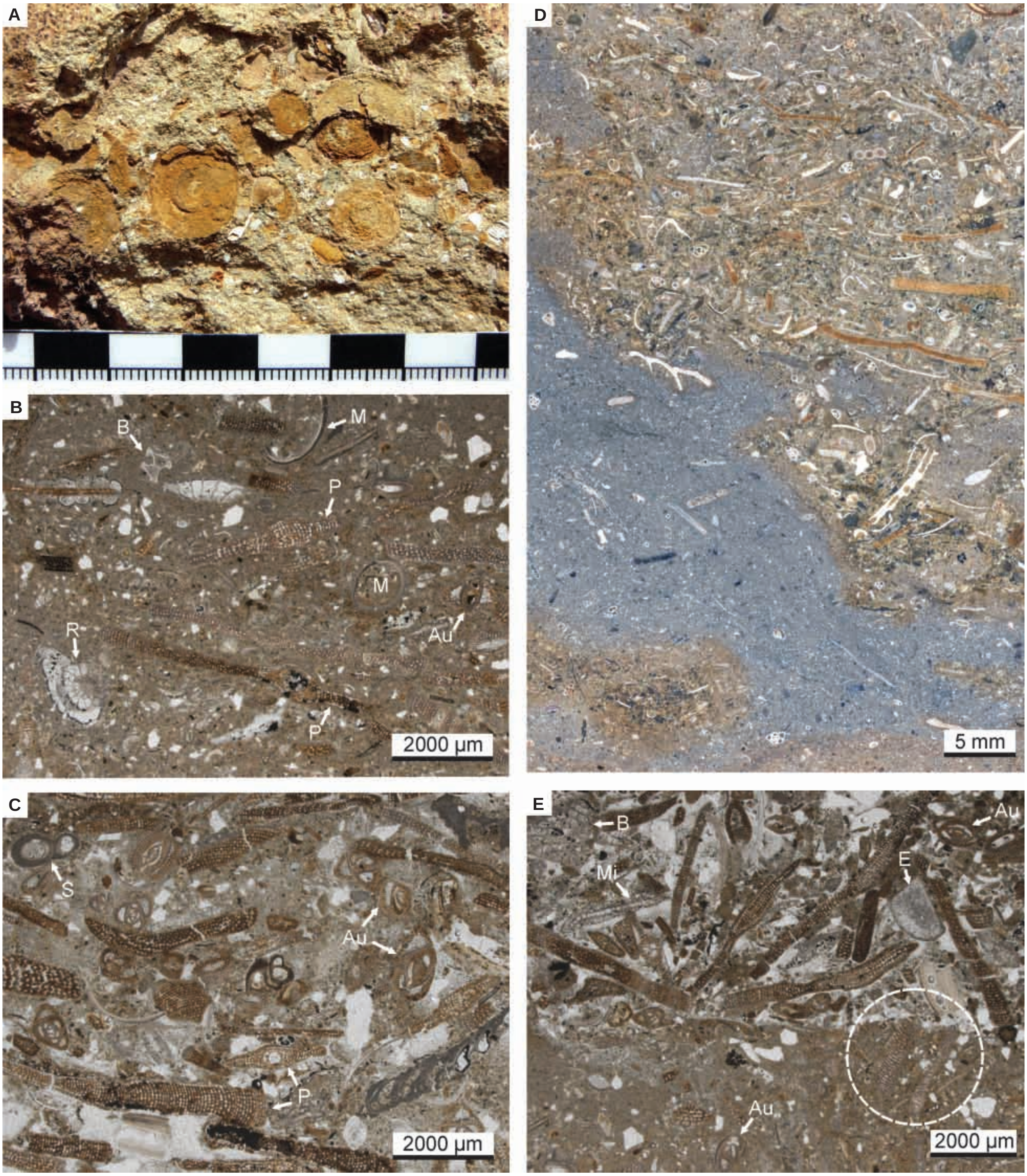

Fig. 5. Facies. A, B, the Quilon Limestone is a bioclastic *Pseudotaberina* floatstone (A) with quartz sand bearing packstone matrix (B, C); one square on the graphic scale is 1 cm. B, C, E, the fauna of the Quilon Limestone is dominated by *Pseudotaberina* (P), *Austrotrillina howchini* (Au) and molluscs (M). Small rotaliid foraminifers (R), *Miogypsina* (Mi), bryozoans (B), echinoderms (E) and serpulids (S) are associated. D, E, the occurrence of grainstone and rudstone in sandpockets is the result of storm blowouts. Later the sediment became homogenized through burrowing activity (D). Truncated *Pseudotaberina malabarica* tests at the base of sandpockets (circle in E) indicate an erosional contact.

Channa Kodi section records increasing water depth. In agreement with this interpretation, Narayanan *et al.* (2007) concluded transgressive conditions from increasing $\delta^{13}C$ values up-section in the Quilon Formation. This was the case in the upper part of NN3 during the third-order transgression that followed the Bur 3 sea level lowstand (Fig. 6). This third-order sea level rise was amplified by the higher

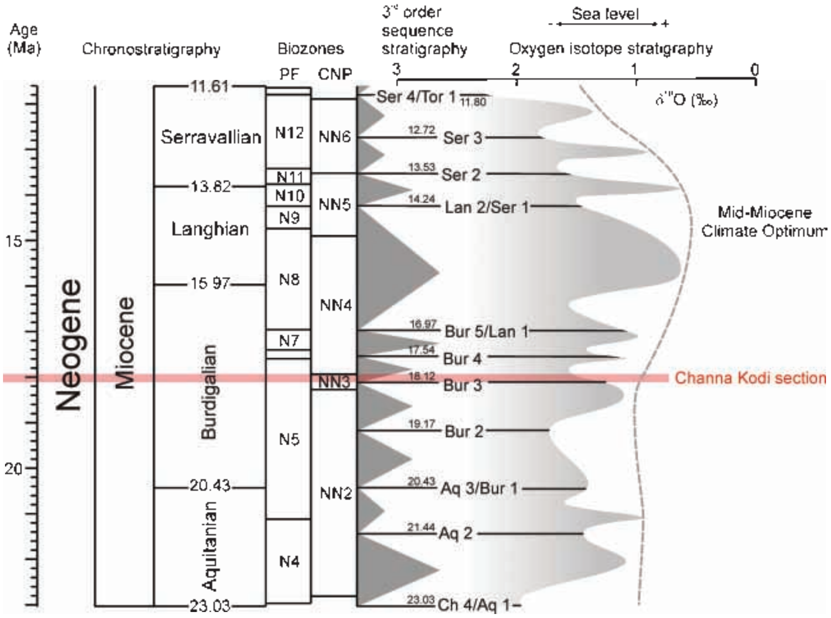

Fig. 6. Early and Middle Miocene stratigraphy after Gradstein *et al.* (2004) with third-order sequence stratigraphy of Hardenbol *et al.* (1998) and oxygen isotope stratigraphy of Abreu *et al.* (1998). These isotope records are a rough reflection of temperature and the sea level; PF: planktonic foraminiferal biozones, CNP: nannoplankton biozones.

amplitude sea level rise prior to the Middle Miocene Climate Optimum at around 15 Ma (Fig. 6).

Miocene seagrass biogeography in the Western Indo-Pacific and adjacent regions

The Western Indo-Pacific is a biogeographical region covering the tropical waters of the western and central portion of the Indian Ocean, including Africa's east coast, the Red Sea, Gulf of Aden, Persian Gulf, Arabian Sea, Bay of Bengal and Andaman Sea (Spalding *et al.* 2007). The origin of the Western Indo-Pacific was due to the collision of Africa and Eurasia and the stepwise closure of the marine connection between the Eastern and Western Tethys. This process had already started during the Late Oligocene and was completed in the Burdigalian with the development of the so-called '*Gomphotherium* Landbridge' (Adams *et al.* 1983; Rögl 1998). The disconnection prohibited migrations of shallow marine biota (e.g. molluscs, corals, echinoderms, benthic foraminifers; Harzhauser *et al.* 2007). In Channa Kodi section (Fig. 2), this is reflected by the lack of Western Tethyan elements in the highly diverse gastropod fauna (Dey 1961).

DNA divergence time estimates of seagrass species, the pantropical expansion of certain foraminifers such as *Sorites*, *Amphisorus*, *Marginopora* and *Peneroplis*, as well as the evolution of seahorses suggest that seagrasses propagated in the Indo-Pacific region during the Miocene (Brasier 1975a; Les *et al.* 2003; Teske & Beheregaray 2009). Miocene seagrasses and seagrass-associated faunas are reported from the tropical Central Indo-Pacific (Miocene – Laurent & Laurent 1926; Middle Miocene – Boudhager-Fadel & Wilson 2000; Wilson 2005; Burdigalian–Langhian – Ehrenberg *et al.* 2006) and temperate Australasian regions (*sensu* Spalding *et al.* 2007; Early to Middle Miocene – Lukasik *et al.* 2000; Collins *et al.* 2006). In the Western Indo-Pacific, the evidence of seagrasses from this time interval is, however, vague. Low-relief carbonate build-ups from the Early Miocene Batu Raja Formation (Aquitanian–Burdigalian, planktonic foraminiferal zone N5–6) in the South Sumatra Basin are interpreted as possible seagrass or algae mudbanks (Longman & Beddoes 1985; Longman *et al.* 1987). Their fauna is characterized by planktonic foraminifers, larger benthic foraminifers (*Eulepidina*), flat platy corals and branching *Porites* (Longman *et al.* 1987), which are, however, not restricted to seagrass meadows. In the Makran area (Iran), Burdigalian coral reefs were developed locally within areas of grain-supported foraminiferal limestones of a non-reefal character, which are interpreted as seagrass flats based on the foraminiferal assemblage (McCall *et al.* 1994). Although this fauna resembles the herein studied fauna (Table 1), the Makran fauna consists only of rare individuals of epiphytic soritids (*Archaias*). The reported benthic foraminifers (*Miogypsina*: dominant; miliolids, *Austrotrillina howchini*, *Borelis melo*, *Lepidocyclina*: rare) occur in a variety of shallow marine settings (including seagrass habitats; Murray 2006; Vaziri-Moghaddam *et al.* 2006).

Therefore, we interpret the fauna as reworked seagrass assemblage in which soritids were depleted due to a different hydrodynamic behaviour (Davaud & Septfontaine 1995). Thus, we conclude that the Quilon Limestone is the first evidence for a Miocene in place seagrass ecosystem in the entire Western Indo-Pacific region.

Pseudotaberina malabarica is the characteristic fossil of the Quilon Limestone (Fig. 5). But even though it has an epiphytic mode of life (Renema 2008), this species was never interpreted to thrive in a seagrass setting. *Pseudotaberina malabarica* is only reported from miliolid-rich carbonate facies in very shallow inner-shelf settings from the Indo-Pacific and West Pacific regions (Carter 1853; Cole 1957; Banner & Highton 1989; Jauri & Khare 1990; Wonders & Adams 1991; Kalantari 1992; Renema 2008). In all sites (including Channa Kodi), *Pseudotaberina malabarica* always occurs in high numbers and typically together with *Austrotrillina and miogypsinids*. Owing to these conspicuous affinities and our observations in Channa Kodi section, *Pseudotaberina malabarica* had narrow ecological constraints and therefore their mass occurrence can be used as a proxy for the identification of fossil seagrass communities. Lepidocyclinids (e.g. *Lepidosemicyclina thecideaeformis*) are also often reported in association with *Pseudotaberina malabarica* (e.g. Cole 1957; Banner & Highton 1989; Jauri & Khare 1990; Wonders & Adams 1991; Kalantari 1992; Renema 2008). Lepidocyclinids, however, inhabited low-lit and/or deep water settings, which are not favourable for seagrass (e.g. Pedley 1998; Beavington-Penney & Racey 2004). Their association with *Pseudotaberina malabarica* may display shading by seagrass (Renema *et al.* 2001). In Channa Kodi section, however, lepidocyclinids were associated with *Pseudotaberina* only in the calcareous sand of bed 1. As stated above, this sand is interpreted as reworked sediment and the *Pseudotaberina–Lepidosemicyclina* assemblage represents no biocoenosis in contrast to that of the Quilon Limestone.

Conclusions

Facies analysis and biotic content of the Burdigalian Quilon Limestone at its type locality in onshore Kerala Basin (SW India) indicate that the sediment was deposited in a seagrass meadow. Calcareous nannoplankton and planktonic foraminifers, here described first from the Quilon Formation, indicate that seagrass vegetation was initiated during nannoplankton biozone NN3 through a marine ingression into coastal brackish lagoons and swamps probably caused by the third-order sea level rise after the Bur 3 sea level lowstand (Hardenbol *et al.* 1998) and amplified by the higher ranking sea level rise at the onset of the Middle Miocene global warming. Biostratigraphical data and the composition of the gastropod fauna show that the sedimentary succession formed after the total breakdown of faunal relationships between Eastern and Western Tethys and soon after the installation of the *Gomphotherium* Landbridge. This makes the Quilon Limestone the earliest documented Western Indo-Pacific seagrass bed and fills a time gap in the evolution of seagrass environments. *Pseudotaberina malabarica* is considered a proxy for the recognition of Miocene seagrass environments in the Indo-Pacific region.

Acknowledgements. – We thank two anonymous reviewers for their constructive comments. Funding through the FWF (Fonds zur Förderung der wissenschaftlichen Forschung) via grant P-18189-N10 is gratefully acknowledged.

References

Abreu, V.S., Hardenbol, J., Haddad, G.A., Baum, G.R., Droxler, A.W. & Vail, P.R. 1998: Oxygen isotope synthesis: A Cretaceous ice-house?. *In* Graciansky, P.-C., Hardenbol, J., Jacquin, T. & Vail, P.R. (eds.): *Mesozoic and Cenozoic Sequence Stratigraphy of European Basins, SEPM Special Publication 60*, 75–80. SEPM Society for Sedimentary Geology, Tulsa.

Adams, C.G., Gentry, A.W. & Whybrow, P.J. 1983: Dating the terminal Tethyan event. *Utrecht Micropaleontology Bulletin 30*, 273–298.

Banner, F.T. & Highton, J. 1989: On *Pseudotaberina malabarica* (Carter) (Foraminiferida). *Journal of Micropalaeontology 8*, 113–129.

Bassi, D., Hottinger, L. & Nebelsick, J.H. 2007: Larger foraminifera from the Upper Oligocene of the Venetian area, north-eastern Italy. *Palaeontology 50*, 845–868.

Beavington-Penney, S.J. & Racey, A. 2004: Ecology of extant nummulitids and other larger benthic foraminifera: applications in palaeoenvironmental analysis. *Earth-Science Reviews 67*, 219–265.

Beavington-Penney, S.J., Wright, V.P. & Woelkerling, W.J. 2004: Recognising macrophyte-vegetated environments in the rock record: a new criterion using 'hooked' forms of crustose coralline red algae. *Sedimentary Geology 166*, 1–9.

Berggren, W.A., Kent, D.V., Swisher, C.C. & Aubry, M.-P. 1995: A revised Cenozoic geochronology and chronostratigraphy. *In* Berggren, W.A., Kent, D.V., Aubry, M.-P. & Hardenbol, J. (eds.): *Geochronology, Time Scales and Global Stratigraphic Correlations: A Unified Temporal Framework for a Historical Geology*, 129–212. SEPM Special Publication 54, SEPM, Tulsa.

Boudhager-Fadel, M.K. & Wilson, M. 2000: A revision of some larger foraminifera of the Miocene of southeast Kalimantan. *Micropaleontology 46*, 153–166.

Brasier, M.D. 1975a: An outline history of seagrass communities. *Palaeontology 18*, 681–702.

Brasier, M.D. 1975b: The ecology and distribution of recent foraminifera from the reefs and shoals around Barbuda, West Indies. *Journal of Foraminiferal Research 5*, 193–210.

Campanile, D., Nambiar, C.G., Bishop, P., Widdowson, M. & Brown, R. 2008: Sedimentation record in the Konkan–Kerala Basin: implications for the evolution of the Western Ghats and the Western Indian passive margin. *Basin Research 20*, 3–22.

Carter, H.J. 1853: Description of *Orbitolites malabarica* (H. J. C.), illustrative of the spiral and not concentric arrangement of chamers in d'Orbigny's order Cyclostegues. *Annals and Magazine of Natural History Series 2/11*, 425–427.

Cigliano, M., Cocito, S. & Gambi, C. 2006: Epibiosis of *Calpensia nobilis* (Esper) (Bryozoa: Cheilostomida) on *Posidonia oceanica* (L.) Delile rhizomes: effects on borer colonization and morphochronological features of the plant. *Aquatic Botany 86*, 30–36.

Cole, W.S. 1957: Larger foraminifera from Saipan Island. *United States Geological Survey Professional Paper 280-I*, 321–360.

Collins, L.B., Read, J.F., Hogarth, J.W. & Coffey, B.P. 2006: Facies, outcrop gamma ray and C–O isotopic signature of exposed Miocene subtropical continental shelf carbonates, North West Cape, Western Australia. *Sedimentary Geology 185*, 1–19.

Davaud, E. & Septfontaine, M. 1995: Post-mortem onshore transportation of epiphytic foraminifera: recent example from the Tunesian coastline. *Journal of Sedimentary Research A65*, 136–142.

Den Hartog, C. 1970: Origin, evolution and geographical distribution of seagrasses. *Verhandelingen-Koninklijke Nederlandse Akademie van Wetenschappen Afdeling Natuurkunde 59*, 12–38.

Dey, A.K. 1961: The Miocene mollusca from Quilon, Kerala (India). *Memoirs of the Geological Survey of India, Palaeontologia Indica, New Series 36*, 1–117.

Dorenbusch, M., Grol, M.G.G., Nagelkerken, G. & van der Velde, G. 2006: Seagrass beds and mangroves as potential nurseries for the threatened Indo-Pacific humphead wrasse, *Cheilinus undulatus* and Caribbean rainbow parrotfish, *Scarus guacamia*. *Biological Conservation 129*, 277–282.

Eames, F.E. 1950: On the ages of certain upper tertiary beds of Peninsular India and Ceylon. *Geological Magazine 87*, 233–252.

Ehrenberg, S.N., Eberli, G.P. & Baechle, G. 2006: Porosity–permeability relationships in Miocene carbonate platforms and slopes seaward of the Great Barrier Reef, Australia (ODP Leg 194, Marion Plateau). *Sedimentology 53*, 1289–1318.

Eva, A.N. 1980: Pre-Miocene seagrass communities in the Caribbean. *Palaeontology 23*, 231–236.

Gradstein, F.M., Ogg, J.G. & Smith, A.G. 2004: *A Geologic Time Scale 2004*, 589 pp. Cambridge University Press, Cambridge.

Hardenbol, J., Thierry, J., Farley, M.B., Jacquin, T., Graciansky, P.-C. & Vail, P.R. 1998: Mesozoic and Cenozoic sequence chronostratigraphic framework of European Basins. *In* Graciansky, C.-P., Hardenbol, J., Jacquin, T. & Vail, P.R. (eds.): *Mesozoic and Cenozoic Sequence Stratigraphy of European Basin, SEPM Special Publication 60*, 13–603. SEPM Society for Sedimentary Geology, Tulsa.

Harzhauser, M., Kroh, A., Mandic, O., Piller, W.E., Göhlich, U., Reuter, M. & Berning, B. 2007: Biogeographic responses to geodynamics: a key study all around the Oligo-Miocene Tethyan Seaway. *Zoologischer Anzeiger 246*, 241–256.

Harzhauser, M., Reuter, M., Piller, W.E., Berning, B., Kroh, A. & Mandic, O. 2009: Oligocene and Early Miocene gastropods from Kutch (NW-India) document an early biogeographic switch from Western Tethys to Indo-Pacific. *Paläontologische Zeitschrift 83*, 333–372.

Haunold, T.G., Baal, C. & Piller, W.E. 1997: Benthic foraminiferal associations in the northern Bay of Safaga, Red Sea, Egypt. *Marine Micropaleontology 29*, 185–210.

Hemminga, M.A. & Duarte, C.M. 2000: *Seagrass Ecology*, 298 pp. Cambridge University Press, Cambridge.

Hoeksema, B.W. 2007: Delineation of the Indo-Malayan centre of maximum marine biodiversity: the coral triangle. *In* Renema, W. (ed.): *Biogeography, Time and Place: Distributions, Barriers and Islands*, 117–178. Springer, Dordrecht.

Hottinger, L. 2005: Geometrical constraints in foraminiferal architecture: consequences of change from planspiral to annular growth. *Studia Geologica Polonica 124*, 99–115.

Ivany, L.C., Portell, R.W. & Jones, D.S. 1990: Animal-plant relationships and paleobiogeography of an Eocene seagrass community from Florida. *Palaios 5*, 244–258.

Jacob, K. & Sastri, V.V. 1951: The occurrence of *Austrotrillina* in the Quilon limestone, South India. *Science and Culture 16*, 326.

James, N.P. & Bone, Y. 2007: A Late Pliocene–Early Pleistocene, inner-shelf, subtropical, seagrass-dominated carbonate: Roe Calcarenite, Great Australian Bight, Western Australia. *Palaios 22*, 343–359.

Jauri, A.K. & Khare, N. 1990: Some observations on the Miocene foraminifera from Kachchh, Western India. *Geoscience Journal 11*, 117–122.

Jones, C.G., Lawton, J.H. & Shachak, M. 1994: Organisms as ecosystem engineers. *Oikos 69*, 373–386.

Kalantari, A. 1992: Lithostratigraphy and microfacies of Zagros orogenic area S.W. Iran. *National Iranian Oil Company Exploration and Production Geological Laboratories Publication 12*, 1–421.

Khosla, S.C. & Nagori, M.L. 1989: Ostracoda from the Quilon beds (Lower Miocene) of Kerala. *Memoires of the Geological Society of India 14*, 1–57.

Knight, J. 2005: Processes of soft-sediment clast formation in the intertidal zone. *Sedimentary Geology 181*, 207–214.

Laurent, L. & Laurent, J. 1926: Etude sur un plante fossile des dépôt du tertiaire marine du sud de Célébes, *Cymodocea micheloti* (Wat.) nob. *Jaarboek voor het Mijnwezen van Nederlands Indie 54*, 167–190.

Leonard-Pingel, J.S. 2005: *Molluscan taphonomy as a proxy for recognizing fossil seagrass beds*. Unpublished MSc Thesis, 140 pp. Louisana State University, Baton Rouge.

Les, D.H., Crawford, D.J., Kimball, R.T., Moody, M.L. & Landolt, E. 2003: Biogeography of discontinuously distributed hydrophytes: a molecular appraisal of intercontinental disjunctions. *International Journal of Plant Sciences 165*, 917–932.

Longman, M.W. & Beddoes, L.R. 1985: Oil-productive Miocene algal and seagrass carbonate mudbanks, South Sumatra, Indonesia. *AAPG Bulletin 69*, 280.

Longman, M.W., Maxwell, R.J., Mawson, A.D.M. & Beddoes, L.R. 1987: Characteristics of a Miocene intrabank channel in Batu Raja Limestone, Ramba Field, south Sumatra, Indonesia. *AAPG Bulletin 71*, 1261–1273.

Lukasik, J.J., James, N.P., McGowran, B. & Bone, Y. 2000: An epeiric ramp: low-energy, cool-water carbonate facies in a Tertiary inland sea, Murray Basin, South Australia. *Sedimentology 47*, 851–881.

Martini, E. 1971: Standard Tertiary and Quaternary calcareous nannoplankton zonation. *In* Farinacci, A. (ed.): *Proceedings 2nd Planktonic Conference Roma*, 739–785. Technoscienza 2, Roma.

McCall, J., Rosen, B. & Darell, J. 1994: Carbonate deposition in accretionary prism settings: Early Miocene coral limestones and corals of the Makran Mountain Range in Southern Iran. *Facies 31*, 141–178.

Mehrotra, D.K. 1982: On the occurrence of fish remains from the Quilon beds of Kerala coast. *Journal of the Geological Society of India 23*, 408–410.

Menon, K.K. 1967a: The lithology and sequence of the Quilon Beds. *Proceedings of the Indian Academy of Sciences 65*, 20–25.

Menon, K.K. 1967b: Origin of diagenetic pyrite in the Quilon Limestone, Kerala, India. *Nature 213*, 1219–1220.

Moisette, P., Koskeridou, E., Cornée, J.J., Guillocheau, F. & Lécuyer, C. 2007: Spectacular preservation of seagrasses and seagrass-associated communities from the Pliocene of Rhodes. *Palaios 22*, 200–211.

Murray, J. 2006: *Ecology and Applications of Benthic Foraminifera*, 426 pp. Cambridge University Press, Cambridge.

Narayanan, V., Anirudhan, S. & Grottoli, A.G. 2007: Oxygen and carbon isotope analysis of the Miocene limestone of Kerala and its implications to palaeoclimate and its depositional setting. *Current Science 93*, 1155–1158.

Orth, R.J., Carruthers, T.J.B., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck, K.L., Hughes, R., Kendrick, G.A., Kenworthy, W.J., Olyarnik, S., Short, F.T., Waycott, M. & Williams, S.L. 2006: A global crisis for seagrass ecosystems. *BioScience 56*, 987–996.

Padmalal, D. & Seralathan, P. 1991: Record of fossil echinoid, *Lovenia forbesi*, from the subsurface Quilon beds (Lower Miocene), Kerala. *Journal of the Zoological Society of Kerala 1*, 82–85.

Parsons, K.M. & Brett, C.E. 1991: Taphonomic processes and biases in modern marine environments: an actualistic perspective on fossil assemblage preservation. *In* Donovan, S.K. (ed.): *The Processes of Fossilization*, 22–65. Columbia University Press, New York.

Pedley, M. 1998: A review of sediment distribution and processes in Oligo-Miocene ramps of southern Italy and Malta

(Mediterranean divide). *In* Wright, W.P. & Burchette, T.P. (eds.): *Carbonate Ramps*, 163–179. Geological Society, London, Special Publications 149.

Petta, T.J. & Gerhard, L.C. 1977: Marine grass banks – a possible explanation for carbonate lenses, Tepee Zone, Pierre Shale (Cretaceous), Colorado. *Journal of Sedimentary Petrology 47*, 1018–1026.

Raha, P.K. & Sinha-Roy, S. 1982: Glauconite in the Quilon Limestone (Early Miocene) of coastal Kerala Sedimentary Basin. *Current Science 51*, 608–609.

Rao, M.R. 1995: Palynostratigraphic zonation and correlation of the Eocene–Early Miocene sequence in Alleppy district, Kerala, India. *Review of Palaeobotany and Palynology 86*, 325–348.

Rao, K.P. & Ramanujam, C.G.K. 1975: A palynological approach to the study of Quilon Beds of Kerala State in South India. *Current Science 44*, 730–732.

Renema, W. 2007: Fauna development of larger benthic foraminifera in the Cenozoic of Southeast Asia. *In* Renema, W. (ed.): *Biogeography, Time and Place: Distributions, Barriers and Islands*, 179–215. Springer, Dordrecht.

Renema, W. 2008: Internal architecture of Miocene *Pseudotaberina* and its relation to Caribbean archaiasins. *Palaeontology 51*, 71–79.

Renema, W., Hoeksma, B.W. & van Hinte, J.E. 2001: Larger benthic foraminifera and their distribution patterns on the Spermonde shelf, South Sulawesi. *Zoologische Verhandelingen Leiden 334*, 115–149.

Rögl, F. 1998: Paleogeographic considerations for Mediterranean and Paratethys Seaways (Oligocene to Miocene). *Annalen des Naturhistorischen Museums Wien 99A*, 279–310.

Rueda, J., Salas, C., Urra, J. & Marina, P. 2008: Herbivory on *Zostera marina* by the gastropod *Smaragdia viridis*. *Aquatic Botany 90*, 253–260.

Sahni, A. & Mitra, H.C. 1980: Lower Miocene (Aquitanian–Burdigalian) palaeobiogeography of the Indian subcontinent. *Geologische Rundschau 69*, 824–848.

Sahni, M.R. & Sastry, M.V.A. 1958: Lower Miocene (Gaj) fauna from Travancore-Cochin, South India. *Journal of the Palaeontological Society of India 3*, 219–223.

Shankar, U., Thakur, N.K. & Redid, S.I. 2004: Estimation of geothermal gradients and heat flow from Bottom Simulating Reflector along the Kerala–Konkan basin of Western Continental Margin of India. *Current Science 87*, 250–253.

Short, A.D. 2005: Carbonate sandy beaches. *In* Schwartz, M.L. (ed.): *Encyclopedia of Coastal Science*, 218–220. Springer, Dordrecht.

Spalding, M.D., Fox, H.D., Allen, G.R., Davidson, N., fernanda, Z.A., finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A. & Robertson, J. 2007: Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *BioScience 57*, 573–583.

Stoner, A.W. & Waite, J.M. 1991: Trophic biology of *Strombus gigas* in nursery habitats: diets and food sources in seagrass meadows. *Journal of Molluscan Studies 57*, 451–460.

Teske, P.R. & Beheregaray, L.B. 2009: Evolution of seahorses' upright posture was linked to Oligocene expansion of seagrass habitats. *Biology Letters 5*, 521–523.

Unsworth, R.K.F., Salinas, P., Garrard, S., Jompa, J., Smith, D.J. & Bell, J.J. 2008: High connectivity of Indo-Pacific seagrass fish assemblages with mangrove and coral reef habitats. *Marine Ecology Progress Series 353*, 213–224.

Vaidyanadhan, R. & Ramakrishnan, M. 2008: *Geology of India*, 994 pp. Geological Society of India, Bangalore.

Vaziri-Moghaddam, H., Kimiagari, M. & Taheri, A. 2006: Depositional environment and sequence stratigraphy of the Oligo-Miocene Asmari Formation in SW Iran. *Facies 52*, 41–51.

Verma, K.K. 1977: Cancroid crabs from the Quilon beds (Lower Miocene) of Kerala, India. *Journal of the Palaeontological Society of India 20*, 305–313.

Wanless, H.R. 1981: Fining-upwards sedimentary sequences generated in seagrass beds. *Journal of Sedimentary Petrology 51*, 445–454.

Wanless, H.R., Cottrelol, D.J., Tagett, M.G., Tedesco, L.P. & Warzeski, E.R. 1995: Origin and growth of carbonate banks in south Florida. *In* Monty, C.L.V., Bosence, D.W.J., Bridges, P.H. & Pratt, B.R. (eds.): *Carbonate Mud-Mounds, their Origin and Evolution*, 439–473. International Association of Sedimentologists Special Publications 23, Blackwell Science, Oxford.

Wilson, M.E.J. 2005: Development of equatorial delta-front patch reefs during the Neogene, Borneo. *Journal of Sedimentary Research 75*, 114–133.

Wonders, A.A.H. & Adams, C.G. 1991: The biostratigraphical and evolutionary significance of *Alveolinella praequoyii* sp. nov. from Papua New Guinea. *Bulletin of the British Museum (Natural History), Geology 47*, 169–175.

Zuschin, M., Janssen, R. & Baal, Ch. 2009: Gastropods and their habitats from the northern Red Sea (Egypt: Safaga) part 1: Patellogastropoda, Vetigastropoda and Cycloneritimorpha. *Annalen des Naturhistorischen Museums Wien 111A*, 74–158.